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## Gait choice in desert-living black-backed jackals

F. Goldenberg<sup>1,2</sup>, M. Glanzl<sup>1,2</sup>, J. R. Henschel<sup>2</sup>, S. M. Funk<sup>3</sup> & E. Millei<sup>1</sup><sup>1</sup> Department of Behavioural Biology, University of Vienna, Vienna, Austria<sup>2</sup> Gobabeb Training and Research Centre, Gobabeb, Namibia<sup>3</sup> Durrell Wildlife Conservation Trust, Jersey, Channel Islands, UK

### Correspondence

Florian Goldenberg, Department of Behavioural Biology, University of Vienna, Althanstr. 14, A-1090 Vienna, Austria.

Email: florian.goldenberg@univie.ac.at

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### ABSTRACT



Gait selection is a strategy used by quadrupeds to meet the demands of locomotion under variable environmental conditions. The movement of black-backed jackals *Canis mesomelas* within a desert area was investigated. The usage and distribution of gaits in three distinct desert environments in the Namib Desert, Namibia, were analysed. The areas were chosen based on topographical differences: a bare, a featureless sand plain in an interdune valley, a large sand dune and a narrow dune valley with clumped plant growth. Fresh jackal tracks were recorded by GPS once a week for 1 year. Gait types, gait segment lengths and the rate of switches between gaits were analysed. Trot was the most frequently used gait in all areas, followed by walk and the two types of gallop. Jackals used faster gaits, with the lowest number of gait switches in the interdune plain. Movements on the sand dune were characterized by shorter gait segment lengths and frequent gait changes. In the dune valley, movements were slower and the rate of gait changes was intermediate between the other two areas. The strongest influence on gait choice and on gait changes was found to be the terrain topography, mainly the grade. Gait and track choice can be seen as a dynamic adaptation to a demanding environment like the Namib Desert.

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### Introduction



Black-backed jackals *Canis mesomelas* are very adaptable carnivores. They are abundant in savannah, scrub and desert terrain, but are absent in dense foliage. On numerous occasions, they follow human refuse into villages and suburbs, or live on farmland, getting into conflict with livestock farmers. Their distribution ranges in southern Africa (subspecies *Canis mesomelas mesomelas*) up to the Zambezi river and in eastern Africa (subspecies *Canis mesomelas schmidtii*) north and east of the Olduvai rift (IUCN Canid Specialist Group, 2004). Prey items range from insects and small rodents to small or weak antelope, often also carrion or fruits (Avery & Avery, 1987). The jackals' hunting strategy depends mostly on the type of prey and the number of hunters. For instance, insects and rodents are usually hunted by solitary jackals that catch them by pouncing, whereas antelope are hunted in pursuit by pairs or small groups of jackals (McKenzie, 1997).

Pairs and, if present, their offspring usually inhabit overlapping home ranges and defend them as territories (Moehtman, 1979). The average home-range size for black-backed jackals in South Africa was found to be 18 km<sup>2</sup> (Rowe-Rowe, 1982). Home ranges of young animals are larger, but overlap with adult's home ranges (Ferguson, Nel & de Wet, 1983). The size and shape of the home ranges depends mainly on the amount of energy (food) that is needed and therefore on body size, activity and food distribution (McNab, 1963). This was shown for golden jackals by MacDonald (1979), and for black-backed jackals by Ferguson *et al.* (1983). In some areas, however, it was found that food abundance, rather than food distribution, affects home-range size (Hiscocks & Perrin, 1988). Additionally, factors such as population density, competition, sex and age can also influence home-range structure, such as described in the resource dispersion hypothesis (MacDonald, 1983).

Jackals have been observed to move large distances within their home ranges, especially during foraging (Kaunda, 2001). Additionally, they have to avoid larger predators like lions or hyena in most habitats and, possibly, human persecution. The presence of superior predators has been shown to influence movement and activity budgets (Switalski, 2003). The daily activity pattern shows two peaks: one around sunrise and one in the evening (Ferguson, Galpin & de Wet, 1988). It has also been shown that the activity is higher during summer, because of the scarcity of food. The paths taken within the home range can be highly consistent to a degree where imprinted 'highways' in the soil are created (Hiscocks & Perrin, 1988). On the other hand, in a highly unpredictable environment, fractal movement of jackals has been found (Atkinson *et al.*, 2002), fractal movement being defined here as any animal movement that does not follow a predictable spatial pattern. To differentiate it from Brownian random movement (which is not fractal), the pattern must be scale invariant (Mandelbrot, 1982). The scale can be spatial or temporal, the latter meaning no systematic change in the pattern over extended time periods. During the inactive periods of the day, jackals mostly stay at resting places within vegetation cover, if available (Kaunda, 2001).

In most terrestrial animals, locomotion is adapted to specific needs via different gaits (Hildebrand, 1976). Canids have four main gaits – walk, trot, canter and gallop. The gaits are an adaptation to different moving speeds. Trot is more economical than walk at a moderate speed and, likewise, gallop is more economical than trot at faster speeds (Narua & Waldron, 1995). Therefore, they are deliberately chosen during movement, depending on the situation. For various speed ranges, optimal gaits exist, which require the smallest possible energy expenditure (Hoyt & Taylor, 1981). Within each gait, the step and stride lengths increase with speed (Jayes & Alexander, 1978). A second method to increase speed, usually combined with increase of stride length, is to increase the stride frequency. The observed variation in home-range size, habitat utilization and space utilization indicates that black-backed jackals have a great flexibility in movement and energy utilization.

Movement patterns have been investigated extensively in canids, but research has almost exclusively focused on domestic dogs for veterinary aims (Off & Matis, 1997). These studies have all been conducted under laboratory conditions. Therefore, the results and conclusions are biased by these laboratory conditions, such as a homogeneous substrate (almost non-existent in the wild), animals running in perfectly straight lines or the missing possible influence of the weather. Under such conditions, the gait choice is purely influenced by movement speed. Although movement studies in the wild would avoid artefacts introduced by laboratory conditions, only very little is known about wild canids (Hildebrand, 1976, 1977; Switalski, 2003). Considering the jackals' great ecological flexibility and capability to utilize extreme environments like the Namib Desert in Namibia, the movement and energy utilization is expected to be specifically adapted to environmental conditions.

Here, we compare the movement of black-backed jackals within different desert habitats. A population of jackals lives in the Kuiseb River Valley on the northern edge of the Namib Sand Sea. Food, with the exception of a few insect species, mainly occurs in clumps around vegetation, like !Nara or riverbed vegetation (Glanz et al., submitted). Very often, food patches are separated by large distances of barren areas. Therefore, activity and movement has to be synchronized with the availability of water and food. We compared movements within three habitat types. We utilized study areas distinguished by their terrain structure and their ecology, with the first being a vegetationless flat plain, the second a ragged sand dune and the third a sandy valley with multiple clumped patches of vegetation. Gait choice, the length of tracks and the frequency of switches between gaits are measured in relation to the surrounding terrain in order to elucidate use of energy in relation to terrain and potential availability of resources.

## Materials and methods



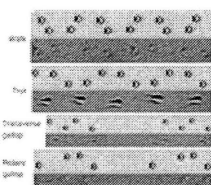
Research was conducted in the Namib-Naukluft Park, Republic of Namibia, at the edge of the Kuiseb river valley near the Gobabeb Training and Research Centre (23°33'40"S, 15°02'14"E, 410 m m.s.l.). The average annual rainfall is 10 mm, daily temperatures range from 0 to 30 °C in winter and from 10 to 45 °C in summer. The Kuiseb is an ephemeral river flowing only several days per year during the annual rainy season. This, however, suffices to maintain a permanent aquifer below the riverbed and dense vegetation along the river (a linear oasis). Further water influx is by fog, occurring on average 60 days year<sup>-1</sup>. Apart from man-made wells, no perennial water sites exist. North of the river valley lie the gravel plains of the central Namib; south of the Kuiseb is the Namib Sand Sea. Along the river valley, several small, simple villages of the indigenous tribe of the Nama people are established.

Three distinctively different desert areas, each covering c. 2 km<sup>2</sup>, were compared. The selected areas were (1) an interdune plain; (2) a sand dune (Station dune) (3) an innerdune valley (!Nara valley). They were defined by the following characteristics:

- (1) The interdune plain was a flat (height differences <2 m) expanse, located between two large sand dunes. It was covered with hard, size-sorted sand that occasionally crystallizes into larger rocks or hard surfaces. Vegetation only occurred along the edges in very small patches of scrub.
- (2) The sand dune (Station dune) was part of a large, linear dune, oriented in a north-south direction and rising up to 60 m above the surrounding plains. It had a ragged structure with several crests and peaks as well as flats and bowls, separated by steep inclinations. It consisted mainly of fine sand, which was packed hard on the windward areas and very loose and soft on the crests and leeward areas. Vegetation consisted of small shrubs and sharp-leaved grass limited to the edges and flat areas.
- (3) The innerdune valley (!Nara valley) was a narrow, flat valley within a large dune structure covered in moderately packed dune sand. It was filled with many individual hummocks up to 5 m in height, and flat, sandy areas in between. The hummocks were created by !Nara plants *Acanthosycius horridus*, which grow in very dense patches and collect sand between their stems. Other types of vegetation could be found in irregular patches between the hummocks.

All three areas were investigated with equal effort for tracks of black-backed jackals *C. mesomelas* at least twice a month for a full year from May 2004 until May 2005. Only tracks left within the last 12–24 h were followed and recorded by hand-held GPS (Garmin III+ and Garmin eTrex, precision ±5 m). The freshness of the tracks was ascertained by making vehicle tracks (car or quadbike) around the investigated area on the previous day. This measure was unnecessary on the dune, because the pure sand substrate was not stable for more than a day. Track recording was set to 10 m intervals and waypoints (marked and saved coordinates) were taken at all points of interest, such as gait switches, changes in terrain structure or defecation spots. The gaits of the jackals, as well as terrain grade were noted. Every change in gait (gait switch), sand or terrain was marked as a waypoint. Terrain grade was categorized as being level at an inclination below 5°, moderate at an inclination between 5° and 20° and steep at an inclination above 20°.

We analysed movement parameters by simulating the four possible gaits (walk, trot, transverse gallop and rotary gallop) on a computer using a commercial software package (Animal movement CD-ROM, Alexander, 1997) and take the created tracks as a reference for determining gaits from tracks in the field (Fig. 1). The simulation allows to adjust for body length, stride length and the time sequence for each leg. The animal is then moved in a straight line while creating the appropriate track. The recorded GPS tracks were transferred to a PC and processed by the software 'Touratech QuoVadis 3' (Touratech AG, Niedereschach, Germany) to calculate the lengths of tracks and gait segments, the directions and position of the tracks within the areas. From these data the following parameters were derived: track length was defined as the total length of one recorded track, irrespective of gait or terrain. Gait segment length was the length of a single part (segment) within one track without a gait change. Along each single track, the number of switches from one gait to another was counted. We calculated a relative index of switches per 100 m by dividing the number of gait switches by the length of the whole track and multiplying with 100. For statistical analysis, SPSS 13.0 (SPSS Inc., Chicago, IL, USA) was used to conduct non-parametric and multivariate tests. Where we used data sets for more than two samples, Bonferroni's correction was applied.



**Figure 1** Illustration of four different gait types simulated (top) and observed (bottom) for black-backed jackals *Canis mesomelas*: (a) walk – pawprints are grouped pairwise and alternate direction; (b) trot – equidistant pawprints almost in line; (c) transverse gallop – pawprints are grouped into quadruplets and alternate individually; (d) rotary gallop – pawprints are grouped into quadruplets and alternate pairwise. [Normal View]

## Results

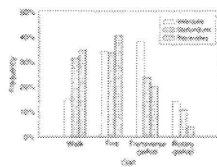


A total of 221 tracks were recorded in the three different study areas (plain:  $n=35$ , dune:  $n=66$ , valley:  $n=120$ ). The resulting track densities over the entire time period are 17.5 tracks km<sup>-2</sup> in the plain, 33 tracks km<sup>-2</sup> on the dune and 60 tracks km<sup>-2</sup> in the valley. The mean track length did not differ significantly between the three studied areas (Table 1; Kruskal–Wallis,  $\chi^2=2.54$ ,  $P>0.05$ ). The length of the tracks varied from 5 m up to 3006 m, with the widest range in the valley. Track length was randomly distributed in the interdune, had a slight bias towards shorter tracks on the dune and was strongly shifted to relatively shorter tracks in the valley. This is supported by the mode of the length, with 360 m for the plain, 78 m on the dune and 54 m in the valley.

**Table 1** Mean, mode, minimum and maximum track length for the three research areas

|              | <i>n</i> | Mean length (m) | Standard deviation (m) | Mode (m) | Minimum length (m) | Maximum length (m) |
|--------------|----------|-----------------|------------------------|----------|--------------------|--------------------|
| Interdune    | 35       | 492             | 267                    | 360      | 91                 | 1131               |
| Station dune | 66       | 452             | 315                    | 78       | 41                 | 1244               |
| !Nara valley | 120      | 596             | 494                    | 54       | 5                  | 3006               |

Within all three areas, 31.1% of all track segments were walk, 37.3% trot, 22.8% transverse gallop, 7.3% rotary gallop and the remainder (1.5%) was unidentifiable. The difference in the gaits used between the three areas was highly significant (Kruskal–Wallis test,  $\chi^2=35.41$ ,  $P<0.001$ ) (Fig. 2). Trot and gallop are predominant in the plain, and walk and trot in the other two areas. *Post hoc* tests of the pairwise differences between two areas remained significant after Bonferroni's correction (Mann–Whitney *U*-test, Bonferroni's corrected,  $Z=-5.77$ ,  $P<0.01$  for the plain and the valley,  $Z=-3.22$ ,  $P<0.01$  for the dune and the valley and  $Z=-3.5$ ,  $P<0.01$  for the dune and plain). In the plain, a bias towards faster gaits (mainly transverse gallop and rotary gallop) was found, while the valley showed a bias towards slower gaits (walk and trot). Gaits at the dune were similar to the intermediate across all study sites (Fig. 2).



**Figure 2** Frequency of gait types observed in three study sites characterized by different habitat types;  $n$  (plain)=35,  $n$  (dune)=66,  $n$  (valley)=120. [Normal View]

When comparing the segment lengths between the individual gaits, the longest segments could be found in trot in all three areas (Table 2a), followed by rotary gallop or, in the case of !Nara valley, walk, with no more than half that of trot. The gaits other than trot are almost equal for the dune and !Nara valley, while the plain shows a strong bias towards the gallops, especially rotary gallop. When pooling the data from the three sites (Table 2b), trot still stands out over the other three gaits. Segment lengths, irrespective of gait type, are the shortest at the dune (Table 2c), followed by the valley and the interdune. When comparing segment lengths between gait types and taking the areas into account, a highly significant difference between the three areas is highlighted (MANOVA, Wilks'  $\lambda=0.936$ , d.f.=4,  $P<0.001$ ).

**Table 2 (a)** Mean length of individual track segments according to gait type and study area

|                    | Interdune |                 |                        | Stationdune |                 |                        | !Nara valley |                 |                        |
|--------------------|-----------|-----------------|------------------------|-------------|-----------------|------------------------|--------------|-----------------|------------------------|
|                    | $n$       | Mean length (m) | Standard deviation (m) | $n$         | Mean length (m) | Standard deviation (m) | $n$          | Mean length (m) | Standard deviation (m) |
| Walk               | 14        | 76              | 106                    | 144         | 47              | 55                     | 217          | 41              | 47                     |
| Trot               | 32        | 322             | 274                    | 155         | 104             | 177                    | 252          | 229             | 319                    |
| Transversal gallop | 36        | 103             | 130                    | 109         | 33              | 37                     | 124          | 36              | 45                     |
| Cyclic gallop      | 13        | 164             | 204                    | 49          | 50              | 73                     | 24           | 31              | 50                     |

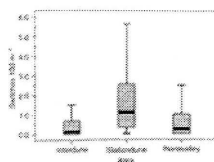
**Table 2 (b)** Mean length and extreme values of individual track segments according to gait type pooled from all study areas

|                    | $n$ | Mean length (m) | Standard deviation (m) | Minimum length (m) | Maximum length (m) |
|--------------------|-----|-----------------|------------------------|--------------------|--------------------|
| Walk               | 375 | 45              | 53                     | 1                  | 300                |
| Trot               | 439 | 191             | 282                    | 3                  | 1720               |
| Transversal gallop | 269 | 44              | 65                     | 1                  | 492                |
| Cyclic gallop      | 86  | 62              | 107                    | 2                  | 739                |

**Table 2 (c)** Mean length and extreme values of individual track segments for the study areas

|              | $n$ | Mean length (m) | Standard error (m) | Minimum length (m) | Maximum length (m) |
|--------------|-----|-----------------|--------------------|--------------------|--------------------|
| Interdune    | 95  | 181             | 221                | 4                  | 828                |
| Station dune | 461 | 63              | 115                | 1                  | 982                |
| !Nara valley | 622 | 115             | 226                | 2                  | 1720               |

The three areas differed significantly concerning gait switches (Kruskal–Wallis test,  $\chi^2=21.86$ ,  $P<0.001$ ) (Fig. 3). The lowest switching rate was found in the interdune with less than once per track, followed closely by the valley, and the highest rate was recorded at the dune (almost two per track). In a *post hoc* test (Tamhane  $T^2$ ), the differences between the interdune and the dune ( $T^2=1.027$ ,  $P<0.001$ ) as well as between the valley and the dune are significant ( $T^2=0.853$ ,  $P<0.01$ ), whereas no significant difference was found between the interdune and the valley ( $T^2=0.174$ ,  $P>0.05$ ).



**Figure 3** Gait switch index (gait switches per 100 m) within the study sites. Interdune: median=0.12, first quartile=0.0, last quartile=0.75, min=0.0, max=3.88,  $n=35$ . Station dune: median=1.13, first quartile=0.32, last quartile=2.58, min=0.0, max=6.41,  $n=66$ . !Nara valley: median=0.24, first quartile=0.0, last quartile=1.04, min=0.0, max=4.86,  $n=120$ . [Normal View]

## Discussion



We investigated the movement of a carnivore in a desert environment on the gait level. Implications on energetic budgets and environmental adaptation are possible with higher

precision compared with using pure positional data. A strong influence of the topographic qualities of an area on gait choice was found, which in turn are assumed to affect energy optimizations of the jackals.

There is a strongly different utilization of the three desert areas observed. The high variety and the greater abundance of short tracks in the valley may indicate higher activity within that area. In contrast, the low number of tracks and the far lower variability in the interdune suggest low jackal activity and mainly transitory movements. Based on the importance of !Nara plants as a food source (Muelier, 2000; Glanzl *et al.*, submitted), the valley can be expected to be a foraging area. The dense vegetation of the !Nara hummocks is also habitat to various insects and small rodents, which in turn are the preferred food of the jackals, increasing the likelihood of them foraging in this area. The other two areas seem to be used for transit and, to some degree, hunting. The distinction between the interdune and the dune is based on the higher terrain complexity of the dune as compared with the flat and featureless plain.

Trot is the most frequently encountered gait, except in the plain. In all three areas, this gait makes up at least one-third of all tracks. The usage of the other three gaits is correlated with the habitat types of the three study sites. The slower gaits are the majority in the valley and the dune. In the plain the two variants of gallop are utilized in more than 50% of the tracks. Two related factors are most likely to influence such gait choice here: first, the type of activity the jackal follows, and second the terrain structure. The two most important activity types related to the track patterns within the research areas are assumed to be foraging and transiting. The former requires the jackal to be very flexible in movement, to react fast and to cover an area extensively while searching for suitable food. This requires a rather slow but steady pace that can be kept for some time. Thereby, the time spent within a given area is maximized while energy expenditure is minimized (Atkinson *et al.*, 2002). According to Hildebrand (1976) and Alexander (2003), trot is the most energy-efficient gait at an intermediate speed. As speed is not an issue while foraging, especially because no chasing is needed here, the slower gaits are preferred. Walk allows for an even slower speed and higher flexibility, at a less favourable cost of transport (Cavagna, Hegelund & Taylor, 1977; Reilly, McElroy & Biknevicius, 2007).

When transiting, the main issues are how to optimize between a high speed of movement and a low energy consumption relative to the covered distance, and a mostly preselected direction. The transport cost of the two types of gallop for dog-sized animals is lower than that of other gaits at higher speeds, covering a larger distance in a shorter time (Reilly *et al.*, 2007). Gallop offers very high movement speeds at the cost of manoeuvrability, which can usually be reduced in transit. Depending on temporal constraints, a mix of trot and gallop would be ideal. These expected patterns for foraging and transits can be observed in the valley and the plain, respectively. The dune, however, which is also a transitory area, does not fit that pattern. This area has a vastly more complex terrain, with steep, alternating inclinations and soft sand, both of which are sparse to non-existent in the other two areas. In other words, the terrain structure is assumed to be the stronger influence on gait choice on the dune, independent of activity. Speed and energetic efficiency is still aimed to be maximized. The gallops, especially the faster rotary gallop, are difficult to maintain on a loose and steep terrain. Additionally, if the terrain structure is unstable or unpredictable, a high movement speed can be dangerous. A specifically terrain-adapted mix of gaits is therefore observed, where the cheapest gait is not necessarily the preferred one.

The shortest mean segments were found on the dune. The dune is the most differentiated terrain, with only short passages within one type of terrain and sand. Accordingly, segments on the flat interdune are on average three times as long. The valley is intermediate, where the reduction compared with the interdune is based on the foraging behaviour, and the increase compared with the dune is based on the simpler terrain. In relation to the total track lengths, these differences are even more pronounced, highlighting the influence of the area.

Within one gait type, the jackals stay for the longest distances in trot. The total amount of energy needed for locomotion is influenced by the structure of the terrain and the vertical component of the locomotion (like walking up- or downhill). Energy conservation in trotting is greatest at intermediate speeds while faster gaits are more efficient at higher speeds (Cavagna *et al.*, 1977). Therefore, trot is the ideal multi-purpose gait, and the mentioned result is not surprising. Less expected is the fact that walk and transverse gallop share the shortest segments. Even though it can be argued that the animals stay in gallop for a shorter time period due to terrain constraints, the far higher speed would yield longer segments. This is exemplified in the longer rotary gallop phases than the transverse gallop ones. However, even these are very short compared with trot, indicating a significantly higher preference towards staying in trot.

Gaits are very often changed on the dune, almost every 50 m. The other two areas show a far lower switching rate. Similar to the higher fraction of slower gaits on the dune, the unstable, complex terrain necessitates a more frequent shift between gaits to adapt properly to the substrate. This is not the case with the simpler terrain structures of the interdune and the valley.

Further clarification on the relationships between movement and habitat could be gained from large-scale movement patterns, using telemetry.

This study represents the first quantification of terrain-adapted movement in wild canids. Similar results have already been shown for domestic animals like dogs (Carrier, Gregerson & Silverton, 1998) and horses (Hoyt & Taylor, 1981), and for humans (Minetti, Ardigo & Saibene, 1994). In contrast, very little has been published on wild mammals (Hildebrand & Hurley, 1985, on elephant, cheetah, pronghorn and rabbit, Switalski, 2003, on competitor-adapted movement in coyote). As expected, trot seems to be the preferred form of transport in jackals. The selected gait is influenced by the type of activity performed and the terrain structure. Changes between gaits occur quite often and are instantaneous. Furthermore, jackals are conservative concerning the route taken, sticking to certain paths that have been proven to be reliable. In the more stable areas, this behaviour helps save energy because the likelihood of unexpected obstacles is reduced. However, this can no longer be assumed for a shifting sand dune, as the terrain is only stable for as little as an hour. Our study shows that jackals can adapt their movement to a variety of terrains and activities by gait choice, thereby optimizing the cost of transport.

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#### References



- Alexander, R.M. (1997) *Animals in Action*, CD-ROM, United Soft Media.
- Alexander, R.M. (2003). *Principles of animal locomotion*. Princeton and Oxford: Princeton University Press.
- Atkinson, R.P.D., Rhodes, C.J., MacDonald, D.W. & Anderson, R.M. (2002). Scale-free dynamics in the movement patterns of jackals. *Oikos* **98**, 134–140.
- Avery, G. & Avery, D.M. (1987). Prey of coastal black-backed jackal *Canis mesomelas* (Mammalia: Canidae) in the Skeleton Coast Park, Namibia. *J. Zool. (Lond.)* **213**, 81–94.
- Carrier, D.R., Gregersen, C.S. & Silverton, N.A. (1998). Dynamic gearing in running dogs. *J. Exp. Biol.* **201**, 3185–3195.
- Cavagna, G.A., Hegelund, N.C. & Taylor, C.R. (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimising energy expenditure. *Am. J. Physiol.* **233**, 243–261.
- Ferguson, J.W.H., Galpin, J.S. & de Wet, M.J. (1988). Factors affecting the activity patterns of black-backed jackals *Canis mesomelas*. *J. Zool. (Lond.)* **214**, 55–69.
- Ferguson, J.W.H., Nel, J.A.J. & de Wet, M.J. (1983). Social organisation and movement patterns of black-backed jackals *Canis mesomelas* in South Africa. *J. Zool. (Lond.)* **199**, 487–502.
- Glanzl, M., Goldenberg, F., Funk, S.M., Henschel, J.H. & Millesi, E. Food composition of black-backed jackals (*Canis mesomelas*) in the Namib Desert. *J. of Mammalian Biology*, in press.
- Hildebrand, M. (1976). Analysis of tetrapod gaits: general considerations and symmetrical gaits. In *Neural control of locomotion, advances in behavioural biology*, Vol. **18**: 203–236. Herman, R.M. et al. (Eds). New York: Plenum Press.
- Hildebrand, M. (1977). Analysis of asymmetrical gaits. *J. Mammal.* **58**, 131–156.
- Hildebrand, M. & Hurley, J.P. (1985). Energy of the oscillation legs of a fast-moving cheetah, pronghorn, jackrabbit and elephant. *J. Morphol.* **184**, 23–31.
- Hiscocks, K. & Perrin, M.R. (1988). Home range and movement of black-backed jackals at Cape Cross Seal reserve, Namibia. *S. Afr. J. Wildl. Res.* **18**, 97–100.
- Hoyt, D.F. & Taylor, C.R. (1981). Gait and the energetics of locomotion in horses. *Nature* **292**, 239–240.
- IUCN Canid Specialist Group (2004). *Canids: foxes, wolves, jackals and dogs – 2004 status survey and conservation action plan*. Sillero-Zubiri, C., Hoffmann, M. & Macdonald, D.W. (Eds). Cambridge: IUCN Publication Services.
- Jayes, A.S. & Alexander, R.McN. (1978). Mechanics of locomotion of dogs (*Canis familiaris*) and sheep (*Ovis aries*). *J. Zool. (Lond.)* **185**, 289–308.

Kaunda, S.K.K. (2001). Spatial utilization by black-backed jackals in southeastern Botswana. *Afr. Zool.* **36**, 143–152.

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