

# Hunting behaviour in West African forest leopards

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## Abstract

The leopard (*Panthera pardus*) is a major predator of mammals within the rainforest ecosystem of West Africa. Most of the available information on leopard hunting behaviour comes from studies conducted in open savannah habitats, while little is known about forest leopards. Our radio-tracking data and scat analysis show that forest leopards differ in various ways from the savannah populations. Forest leopards are diurnal and crepuscular hunters who follow the activity pattern of their prey species. They exhibit seasonal differences in activity patterns, and they develop highly individualized prey preferences. These findings challenge the widespread notion of leopards as opportunistic nocturnal predators.

*Key words:* predation, carnivore, taï forest, selective hunting, monkey alarm calls

## Résumé

La panthère *Panthera pardus* est un prédateur majeur de mammifères dans l'écosystème de la forêt pluviale en Afrique Occidentale. La plupart des renseignements sur le comportement de chasse des panthères est tirée d'études menées dans des habitats ouverts de la savane, tandis que peu est connu sur les panthères forestières. Les données que nous avons rassemblées par radio-émetteurs et les analyses des crottes montrent plusieurs différences entre les panthères forestières et des populations de savane. Les panthères forestières sont des chasseurs diurnes et crépusculaires qui suivent le schéma d'activité de leur proie. Ils déploient des différences saisonnières et développent des préférences de proie fortement individualisées. Nos conclusions défont l'image répandue des panthères comme prédateurs opportunistes nocturnes.

## Introduction

It is widely believed that leopards are opportunistic and nocturnal predators that hunt their prey in proportion to abundance (Bailey, 1993; Johnson *et al.*, 1993; Stuart & Stuart, 1993; Bothma & LeRiche, 1994; Bodendorfer, 1994). However, most of the available evidence comes from savannah habitats while little is known about forest leopard behaviour. Information from Ituri forest, DR Congo (Hart, Katembo & Punga, 1996) and Taï forest, Ivory Coast (Jenny, 1996), suggests that hunting behaviour of forest leopards may differ considerably from that of savannah individuals. In a previous study, we have documented a large prey spectrum in a population of forest leopards in the Taï forest (Zuberbühler & Jenny, 2002). Here, we present data from radio-tracking and scat analyses to describe the hunting behaviour and individual prey preferences of forest leopards. Our data show that forest leopards (a) are diurnally and crepuscularly active, (b) exhibit seasonal differences in activity, and (c) may develop individual preferences for particular prey species.

## Methods

Data were collected by the first author in about 100 km<sup>2</sup> of undisturbed primary rain forest of Taï National Park, Ivory Coast (5°50'N, 7°20'W; Jenny, 1996). Three adult leopards were captured and equipped with radio-transmitters (Jenny, 1996). Two of them were monitored from tree platforms during day and night-time intervals ('Cosmos', adult male, 56 kg, 5 February 1993 to 8 May 1994; day: 82 h, night: 23 h; 'Adele', adult female, 34 kg, 16 August 1993 to 30 June 1994; day: 244 h, night: 92 h; night: 18:00–06:00 GMT, corresponding to the onset of sunset and sunrise). From the platforms it was possible to score the individuals' activity as either 'moving' or 'resting', depending on the stability of the received signal. Readings were taken every 15 min (location accuracy ±0.01 km<sup>2</sup>).

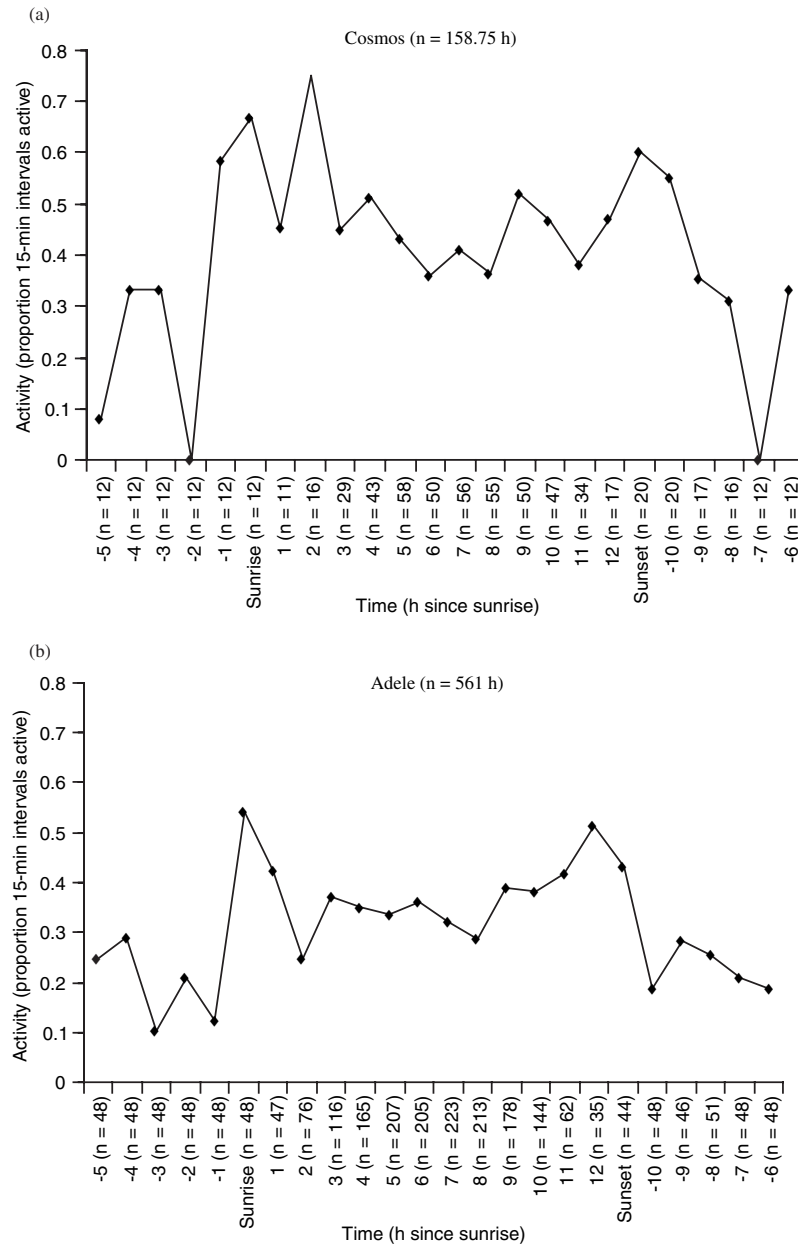
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Both individuals were also followed through the forest at 30–150 m (Cosmos, day: 72 h, night: 20 h; Adele, day: 411 h, night: 44 h). Additionally, a third individual was followed for a short time ('Cora'; adult female; 32 kg, 14 June 1994 to 28 August 1994; day: 10 h, night: 0 h). During a proportion of these follows it was also possible to score activity as either 'moving' or 'resting' (Adele n = 225 h; Cosmos n = 53.75 h). In addition, it was possible to make some qualitative observations concerning the

individuals' hunting behaviour, notably (a) hiding, usually in dense thickets, (b) approaching monkey groups, and (c) making kills.

Faecal samples were collected from Adele while following her and by tracking her spoor from an infrared-triggered photo-trap set-up along a trail frequently used by her. This allowed us to compare Adele's individual prey spectrum with that of the wider local leopard population



**Fig 1** Relative activity patterns of two radio-collared leopards plotted as a function of onset of sunrise and sunset (data from platform monitoring and direct follows combined). (a) Cosmos (n = 158.75 h); (b) Adele (n = 561 h).

as determined by scat surveys (Hoppe-Dominik, 1984; Zuberbühler & Jenny, 2002).

## Results and discussion

### Activity patterns

Platform monitoring indicated that both individuals were more active during the day (46.5%) than at night (28.9%), in sharp contrast to savannah individuals (Hamilton, 1976; Bailey, 1993). Relative peaks at dawn and dusk corresponded closely with sunrise and sunset (Fig. 1). Direct follows of leopards at night are extremely difficult to conduct in dense rainforest habitat. In total, we managed to obtain ranging data for  $n = 179$  h combined over the 16-month study period (platform data and focal follows). These data revealed that at night activity patterns typically showed only one of two patterns: (a) complete inactivity ( $>10$  h) or (b) travelling over large distances, suggesting that although our data set is small, it accurately represents the nocturnal activity patterns. Daytime activity showed a more evenly distributed pattern, but inactive periods were always short ( $<5$  h). This activity pattern is comparable with that of Asian forest leopards (Karanth & Sunquist, 1995).

For Adele, the lowest monthly activity rates were observed during the rainy period, perhaps because heavy rainfall increased her hunting success. Percent activity per month was significantly negatively correlated with rainfall (Spearman-rank correlation,  $n = 11$ ,  $r_s = -0.718$ ,  $z = -2.271$ ,  $P < 0.03$ ).

*Ad libitum* observations during direct follows revealed two interesting aspects of hunting behaviour: (a) during periods of inactivity the three individuals often hide in dense thickets and (b) after making a kill, they remained at the same place for two to three consecutive days.

Similar to savannah individuals there was a distinct sex-difference in ranging behaviour (Rabinowitz, 1989). Cosmos was moving in 40.4% of all monitored intervals ( $n = 53.75$  h), while Adele only moved during 20.1% of time ( $n = 225$  h). Adele tended to remain within a relatively small core area of about one hectare (14.2% of intervals;  $n = 561$  h; platform and focal data combined).

During daytime follows, a monkey group came within 50 m of the hiding leopard in 60 of 97 hiding bouts (7.4% of time;  $n = 130$  h). In contrast, when the observer sat at one of ten randomly chosen observation points throughout the study area, monkeys came within 50 m only four of

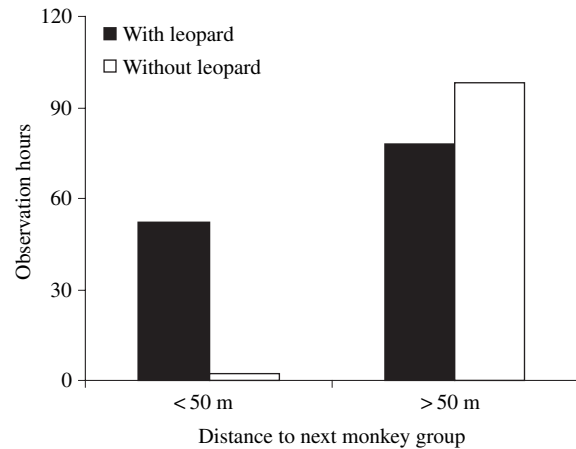


Fig 2 Number of observation hours the observer was sitting close ( $<50$  m) or far ( $>50$  m) from the nearest monkey group after (a) having followed Adele (black bars) or (b) having walked to one of ten randomly selected points throughout the study area.

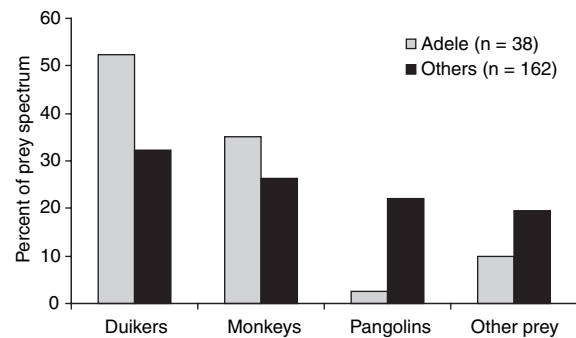


Fig 3 Prey spectrum of focal animal Adele compared with the average prey spectrum of other leopards in the study area. Duikers and monkeys all weigh several kilograms and are amongst the biggest mammalian prey available in the forest.

ten times (1.9% of time;  $n = 99$  h; Fig. 2), a statistically significant difference ( $z = -3.092$ ;  $P < 0.01$ ; Binomial test; two-tailed), suggesting that leopards selectively chose hiding spots close to monkey groups (Zuberbühler, Jenny & Bshary, 1999).

### Prey spectrum

Adele was not an opportunistic hunter but developed individual prey preferences. First, Adele avoided chimpanzee parties: in six of fifteen cases of drumming and/or screaming of a chimpanzee party 100–250 m away, she

started moving in the opposite direction or changed direction when already moving. Approach was never recorded. However, leopards may scavenge on already dead chimpanzees: In two cases, a female or a subadult male leopard dragged a dead juvenile chimpanzee (10–20 kg) for 50–80 m before devouring it. Second, Adele consumed duikers and monkeys significantly more often than other leopards ( $\chi^2 = 41.49$ , d.f. = 8,  $P < 0.01$ ; Fig. 3). A successful attack on a primate was observed once during Adele's 91 observed hiding bouts when she killed a sooty mangabey, *Cercocebus atys*. Third, Adele rarely consumed pangolins, although pangolin remains were common in other leopard faeces (Hoppe-Dominik, 1984; Zuberbühler & Jenny, 2002). Thirty-eight fresh faeces could be assigned to Adele with reasonable confidence. Only one sample (2.6%;  $n = 38$ ) contained pangolin scales (population average: 26.7%;  $n = 150$ ; Fig. 3). Moreover, leopard faeces containing pangolin remains varied both regionally and temporarily. In the south-east part of the study area, 40.0% of faeces ( $n = 50$ ) contained pangolin remains, whereas in the north-west this was only true for 15.2% of faeces ( $n = 138$ ). In addition, in the north-west a sudden and dramatic change in faeces containing pangolin remains coincided with the suspected death of a resident leopard: Before March 1993, 32.7% ( $n = 55$ ) of faeces contained pangolin remains. Afterwards, the rate dropped to 3.6% ( $n = 83$ ). No comparable change was observed in the south-east (before March: 36.7%;  $n = 30$ ; after March: 45.0%;  $n = 20$ ). There were no obvious habitat differences across the study area that could have explained uneven distribution of prey animals.

In sum, our data suggest that forest leopards may differ from savannah individuals in important ways. First, they are predominantly diurnally and crepuscularly active. Second, one focal animal did not consume some potential prey species, such as chimpanzees and pangolins, but often others, such as duikers and monkeys. One possible interpretation of this finding is that forest leopards develop individual prey preferences. The population density of leopards is high in the Taï forest with substantial range overlap particularly between the sexes (Jenny, 1996), suggesting that individuals experience strong competition

forcing them to use different resources within the shared range.

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