

The ecology and behaviour of a protected area Sri Lankan leopard (*Panthera pardus kotiya*) population

ANDREW M. KITTLE^{1,*}, ANJALI C. WATSON¹ & T. SAMINDA P. FERNANDO^{1,2,†}

¹*The Wilderness & Wildlife Conservation Trust, 130 Reid Avenue, Colombo 4, Sri Lanka*

²*Department of Zoology, University of Colombo, Colombo, Sri Lanka*

Abstract: Data on the population density, spatial organization, diet and behaviour of a protected, arid zone Sri Lankan leopard (*Panthera pardus kotiya*) population are presented, and discussed in the context of the influence of dominant intra-guild competition. Spatially explicit density estimates were based on direct observations and remote camera images of individually identified leopards. Home range estimates were supplemented with spoor data. Average total population density was 21.7/100 km² and resident adult density 12.1/100 km². Adult male home ranges averaged 22.5 km² (N = 3), overlapped with neighbouring male ranges and with ranges of ≥ 4 adult females. Female “core areas” averaged 1.6 km² (N = 4) and exhibited no overlap. Diet was comprised mainly of spotted deer (*Axis axis*), consumed in proportion to availability. Sambar (*Rusa unicolor*) contributed minimally to overall diet but was preferred. Observed leopards were mostly solitary (84.2%, N = 247) but significantly less so than in populations with dominant intra-guild predators. They were observed more frequently during crepuscular periods and nocturnally, when they were also more active, than diurnally. Tree caching of kills was uncommon (13.7%, N = 51). Overall, whereas social organization appears unaffected by the absence of dominant intra-guild competition, results suggest subtle behavioural adaptations, such as decreased secrecy and preference for larger prey. This study provides valuable information on a poorly understood, endangered leopard population and provides fresh insights into the role of intra-guild competition on carnivore community structure; particularly that carnivore population density appears determined by prey availability, not competition with dominant inter-specifics.

Key words: Behaviour, diet, intra-guild competition, population density, Sri Lankan leopard, spatial organization, sociality.

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Introduction

Leopards are the most geographically and climatologically widespread large felid and remain extant in pockets of forested habitat throughout the Indian sub-continent (Henschel *et al.* 2008). The Sri Lankan leopard (*Panthera pardus kotiya*) is an endangered sub-species (Deraniyagala 1956;

Kittle & Watson 2008; Meijaard 2004; Miththapala *et al.* 1996; Uphyrkina *et al.* 2001), distributed throughout the island with the exception of portions of the densely populated southwestern wet zone (Watson & Kittle 2004). Their Sri Lankan range encompasses a variety of habitats including montane, sub-montane, tropical rain, monsoonal dry evergreen and arid zone scrub forests (Kittle *et*

*Corresponding Author; e-mail: akittle@uoguelph.ca; akittle@wwct.org

†Present address: Department of Zoology, Open University of Sri Lanka, Nawala, Nugegola 10250

al. 2012; Phillips 1980; Watson & Kittle 2004). Despite a wide distribution within the island, this endangered sub-species is under increasing threat from habitat destruction, forest fragmentation, trapping and hunting (Brooks *et al.* 2002; Erdelen 1988; Kittle *et al.* 2014; Santiapillai *et al.* 1982). Of the natural vegetation areas extant in Sri Lanka when declared a Global Biodiversity Hotspot with India's Western Ghats in 1999 (Myers *et al.* 2000), only 10–20% in the dry zone and <5% of the wet and montane zones remain intact (Sloan *et al.* 2014). Estimates using Global Forest Watch data show the loss of 5 441.25 hectares/year of forest with >30% canopy cover from 2001–12. The cumulative loss (65, 295 hectares) over this period represents ~1% of the island's total area.

The Sri Lankan leopard represents the only leopard population known to have evolved as the top predatory carnivore in its ecosystem (Guggisberg 1975; Miththapala *et al.* 1996; Turner 1997), having been isolated from dominant intra-guild competitors at least since Sri Lanka split off from the Indian sub-continent ~5,000–10,000 ybp (Deraniyagala 1992; Yokoyama *et al.* 2000). Evidence indicates that the Sri Lankan lion (*Panthera leo sinhaleyus* Deraniyagala 1939) became extinct in the region before the arrival of culturally modern humans ca. 37,000 ybp and more recent tiger fossil evidence was C¹⁴ dated to ~16,500 ybp (Manamendra-Arachchi *et al.* 2005). Given its position as the apex predator in the system, the Sri Lankan leopard has the potential to greatly affect the composition and structure of that system (Ripple *et al.* 2014). In order to determine the leopards' role in this island ecosystem an increased understanding of its ecology and behaviour is vital. As such, the objective of this study was to provide new and updated information from a relatively unknown region regarding the space use, population structure, diet and behaviour of a protected area leopard population historically free of dominant intra-guild competition.

Dominant intra-guild competitors can impose ecological and behavioural constraints on subordinate intra-guild species (Broekhuis *et al.* 2013; Creel & Creel 1996; Durant 1998; Vanak *et al.* 2013). We hypothesize here that the absence of dominant competitors can result in the release of sub-ordinates from such constraints, the result of which can be manifest in space use patterns, sociality and prey selection. When released from suppression by dominant competitors, carnivores have been shown to reduce habitat selection,

allowing them to maintain larger ranges (St-Pierre *et al.* 2006). Alternately however, they sometimes maintain smaller ranges because avoidance of intra-guild competitors is unnecessary and resources are therefore more accessible (Kamler *et al.* 2013). Typically, carnivore range size is inversely correlated with habitat quality (Marker & Dickman 2005; Kittle *et al.* 2015) so in the absence of dominant competitors leopards should be able to more easily select for high quality areas. Therefore, due to the long term absence of intra-guild competition we would expect their home ranges to be smaller and resulting population density higher here than other areas with comparable available prey biomass and dominant intra-guild competitors. However, if leopard habitat selection is restricted by dominant intra-guild competitors, their absence should result in relaxed constraints and larger ranges. If leopards have adopted particular behavioural strategies, including a solitary, nocturnal activity pattern and the caching of kills in trees, in order to avoid the intra-guild competitors with which they have co-evolved (Stander *et al.* 1997), then leopards in Sri Lanka should be more openly gregarious, more diurnal and cache kills in trees less frequently than populations with or recently released from intra-guild competition. Finally, if leopards circumvent competition by including a range of smaller prey in their diets (Bailey 1993) leopards here might be expected to rely less on smaller prey, instead maximizing profitability by focusing hunting efforts on the capture of larger prey items (Stephens & Krebs 1986).

Materials and methods

Study Area

Ruhuna (Yala) National Park (RNP) is located within Sri Lanka's southeastern arid zone (Fig. 1) and part of the 1,518 km² Yala Group of National Reserves. The study area (N 6°16'24", E81°23'31") is a 103 km² section within RNP's southernmost Block I. Dissecting the study area were 116 km of unpaved roads, approximately 50% of which were frequented by tourist jeeps. During the study period, February 2001–May 2002, > 20, 000 vehicles/year entered Block I, with a monthly peak > 2500 in August and December (Panwar & Wickramasinghe 1997). This persistent vehicular presence has ensured the RNP's fauna is well habituated to human presence.

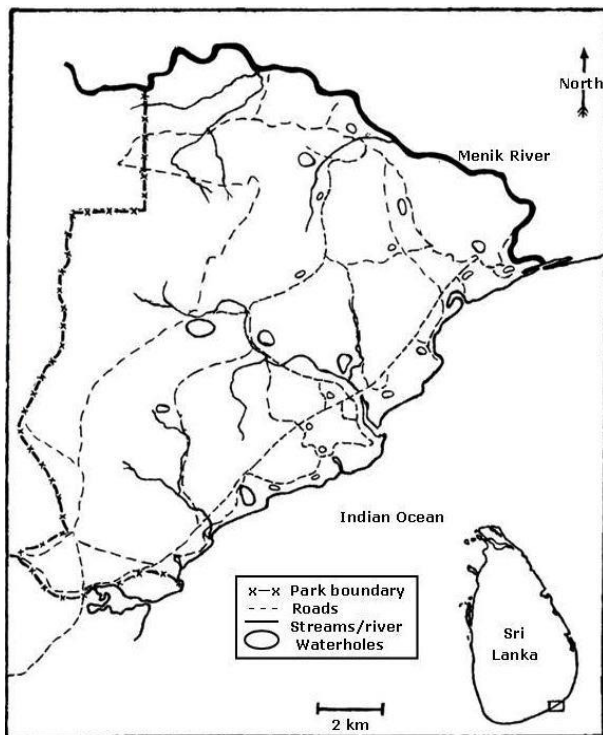


Fig. 1. Map of Ruhuna (Yala) National Park, Block I, and its location within Sri Lanka.

Block I is mostly composed of woody scrub < 5 m in canopy height interspersed with taller monsoon forest (Mueller-Dombois 1972; Santiapillai *et al.* 1981). Tall, climax forest with thin under-story characterizes the northern riparian zone whereas dense, often thorny scrub is the dominant forest type throughout the remainder of this coastal Block. *Manilkara hexandra* and *Drypetes sepiera* are the two most abundant canopy species. Open plains (< 0.5 km²) characterized by various grass and sedge species occur around both seasonal and permanent waterholes (Chambers *et al.* 1983).

RNP was once the site of an extensive civilization (Rohana/Ruhuna Kingdom 2 BC–1000 AD) that used hydraulic management practices to collect and maintain rain water (Jayawardhena 1993). As a result, dozens of artificial reservoirs, some maintained by park authorities, form perennial and annual water holes within the study area and serve to increase the water available for wildlife in a naturally arid habitat. Numerous ruins and caves are found within rocky outcrops that rise up to 250 m. These outcrops are quartzofeldspathic gneiss erosion remnants and are dominant features in otherwise flat terrain (Mueller-Dombois 1972). Rock waterholes within

these inselbergs are important sources of freshwater during the dry season. The Menik River forms the northern boundary of Block I and several seasonal streams flow through.

Temperature at sea level averages 25–28 °C with a maximum of 37 °C (Mueller-Dombois 1972). Annual rainfall is < 1000 mm spread unevenly throughout the year. The dry season (< 50 mm/month) predominates lasting from mid-May to mid-October. The wet season (100–200 mm/month), from mid-October to end-January results from convectional rains and the northeast monsoon. An intermediate season characterized by occasional inter-monsoonal rains spans February to mid-May.

Observations, range use and behavioural data

During the 237 days of the study observations were conducted between 05:00 and midnight which included heightened activity periods (Hayward & Slotow 2009) as well as perceived times of peak leopard visibility (Bailey 1993; Chambers *et al.* 1984; de Silva & Jayaratne 1994). Sightings were opportunistic except at pre-determined kill sites or when leopards had been specifically tracked. The entire study area was surveyed every 96 hours except during the dry season peak (September to mid-October) when the park was closed. This restricted access to the western boundaries for this period.

Time, GPS location, habitat, number of leopards, age/sex (Bailey 1993; Jenny 1996) and activity were recorded at each sighting. Due to familiarity with vehicles, leopards were typically observed from close range (10–50 m). All sightings were recorded on still film and/or video with night observations conducted using 10 × 40 infrared binoculars and a hand-held spotlight with infrared filter. Individual leopards were identified from facial and body spot pattern markings (Fig. 2; Henschel & Ray 2003; Kelly 2001; Miththapala *et al.* 1989).

Two infrared camera traps (Trailmaster TM1550 Active, Goodson & Associates Inc., Lenexa, KS) were used to supplement direct observations, set from 18.30–06.30 on pre-determined animal trails with high leopard spoor activity (Karanth & Nichols 2002). Leopards were categorized as residents or transients according to a combination of age, territorial marking behaviour, cub-rearing and frequency of observations (Mizutani & Jewell 1998). Available photographic records of known age individuals

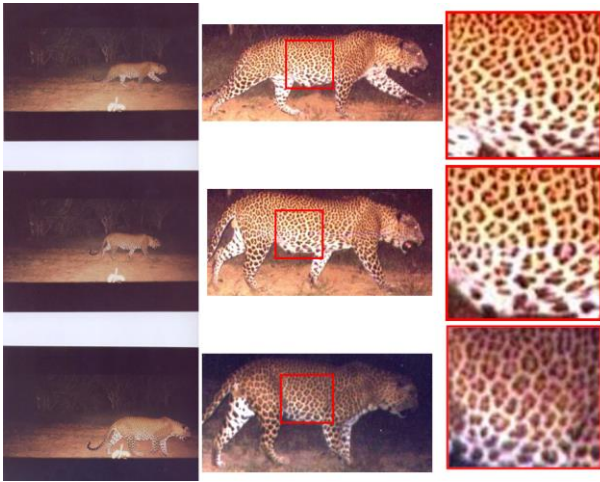


Fig. 2. Individual identification of leopards using spot pattern markings. Left panel shows three adult male leopards photo-captured at the same location in Ruhuna (Yala) National Park between February and May 2002. Middle panel shows close up of each individual with red square highlighting a portion of the right flank. Right panel shows zoomed in image of this highlighted portion with distinct spot patterns clearly visible. The top two images show the same adult male whereas the bottom image is of a different adult male. Although the flanks of the animals are shown here, leopards have distinct spot mark configurations all over the body and face which can be used for distinguishing individuals.

were cross-referenced to ensure accurate age estimates (Balme *et al.* 2012).

Pugmark analysis was used to complement observations where possible, with individual pugmarks, as well as stride and step lengths, measured and a width: length ratio determined for each pug (Henschel & Ray 2003). Complete left and right sets of pugmarks were traced on a 35 × 30 cm framed glass sheet using a fine-tipped non-permanent marker and then re-traced on paper for permanency. Only clearly visible pugmarks deposited in fine sand, < 5 mm deep over hard, flat ground were traced in order to avoid errors resulting from differential substrates (Smallwood & Fitzhugh 1993; Stander *et al.* 1997). All were traced by the same researcher (AMK) to reduce observer error (Nath 2000). It is acknowledged that differential substrates can impact observer detection of spoor, but most roads and road edges and all “game” trails were composed of fine sand which substantially reduced observer bias. Although male and female leopards could be identified by their spoor, we were unable to

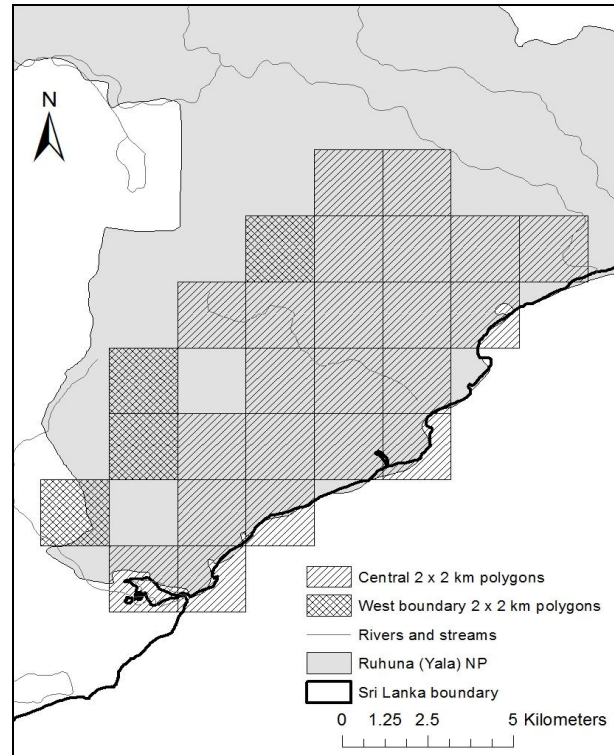


Fig. 3. Polygons (2 × 2 km) used in the spatially explicit capture-recapture (secr 2.91) framework to estimate leopard density in Ruhuna (Yala) National Park.

identify adult females individually.

However, the tracks of the 5 adult resident males in the study area were distinct due to gross morphological differences (Fig. S1, Supplementary Material; Smallwood & Fitzhugh 1993; Van Dyke *et al.* 1986). Although pugmark analysis has been largely discredited when applied to counting carnivores (Karanth *et al.* 2011), the successful field identification of these distinctive pugmarks was verified from video and camera trap images and data were subsequently used only to complement direct sightings for adult male home range estimation (Balme *et al.* 2012). Female “core areas” were based entirely on direct sightings and sighting locations of dependent cubs (Bailey 1993) since individuals could not be distinguished from spoor. These core areas are assumed to be smaller than true home ranges and were calculated for all females with ≥ 15 recorded locations. We defined male home ranges and female core areas using minimum convex polygons (MCP) of all recorded locations (Convex Hull extension for Arc View 3.2, ESRI systems).

Population density estimation

Spatially explicit capture recapture models (package “secr 2.9” in R) were used to estimate the density of leopards within the study area. Since the study was undertaken as repeated searches, the study area was first divided into a 2×2 km grid (Fig. 3) and each grid square ($N = 26$) treated as a polygon detector in the SECR framework (Efford 2011). In this setup the spatial coordinates of each corner of each grid square were used to define polygons, with the spatial coordinates of each sighting therefore falling within a given polygon. Each of the 16 months of the study was considered an individual occasion and the number of individual leopards detected within each grid square on each occasion was determined.

The number of days per month that the study area was searched varied (mean = 14.7, range = 8–25). This variation was accommodated using adjustments for varying effort within the SECR framework so that each day searched/month was represented by a search effort of 0.1 so that 10 days/month = 1.0, 25 days/month = 2.5 (Efford *et al.* 2013). The extent of the study area that was searched per month also varied. Specifically, the western boundary portion (Fig. 3) was not searched during the initial 7 months of the study (Feb. through Aug. 2001). Then during September and half of October (the 8th and 9th months of the study) only these boundary sections were accessible due to closure of the central part of the park. For the rest of the study, all parts of the study area were accessed. This variation was reflected by reducing the search effort value to 0 for the relevant grid squares that comprised the western boundary area for the months (occasions) when they were not searched and similarly reducing the search effort value to 0 for the central grid squares for the months (occasions) when they were not accessible. This flexibility of the SECR framework allows for unbiased density estimates from a variety of study designs (Russell *et al.* 2012; Thompson *et al.* 2012).

Estimating a population density over a 16 month period violates the assumptions of a closed population, even for relatively long-lived species (Karanth & Nichols 2002). In order to fulfill these assumptions, the full study duration was divided into 4×4 month sessions. For each of these sessions, closed population SECR analysis using maximum likelihood was undertaken resulting in 4 population density estimates across the study (Borchers and Efford 2008). This had the twin

benefits of meeting closed population assumptions and describing a range of density estimates which should reduce potential bias resulting from a single estimate. A biological rationale for 4 month sessions is that leopard gestation is 90–106 days (Hunter *et al.* 2013) and then cubs only emerge from den sites at ~ 6–8 weeks (Le Roux & Skinner 1989).

A separate detection history was determined for each session and analysis undertaken using the half-normal detection function and a buffer = 8000 m as this was the buffer distance at which log-likelihood estimation stabilized. There is little consistency in the literature regarding whether estimated population densities are calculated for all individuals regardless of age or status (e.g. Harihar *et al.* 2009) or for only resident adult individuals (e.g. Chase Grey *et al.* 2013). Both calculations were undertaken here with all individuals included in the total estimate and only adults included in the resident estimation since sub-adults may be transients and cubs are dependent and often difficult to observe (Karanth 1995).

Prey abundance and diet

Prey abundance was determined using a road strip census (Hirst 1969) with a modified fixed visibility profile (Norton-Griffiths 1978). The study site was divided into three sectors according to habitat type. The southeast sector (21.1% of the study area) is a coastal strip interspersed with open plains; the southwest sector (46.5%) is forested interior, bordered on its western boundary by settlement areas; and the northeast sector (32.4%), bordered to the north by the Menik River, is sloping and well-drained, characterized by numerous small to medium tanks that hold water through most of the year. Road transects (15.6–18.4 km) were delineated for each sector and a visibility index determined for medium to large leopard prey species in the dry, wet and intermediate seasons (Bailey 1993). The visibility distance was used to determine strip width per season which was multiplied by transect length to establish the total seasonal area of each transect (Norton-Griffiths 1978). Open areas where visibility exceeded that of the road strip were measured on a 1:50 000 topographical map and added to the total transect area. Thirty transects were conducted, 10/sector, between 16:00–19:00 hrs at 5–10 km h⁻¹ (Hirst 1969). To incorporate seasonal fluctuations in prey abundance three

Table 1. Weight of leopard prey (kg) in Ruhuna (Yala) National Park.

Species	Male	Female	Young
Buffalo (<i>Bubalus bubalis</i>)	350 ^a	220 ^a	100 ^a
Sambar (<i>Rusa unicolor unicolor</i>)	215 ^b	163 ^b	45.5 ^c
Wild boar (<i>Sus scrofa</i>)	110 ^a	55 ^a	20 ^a
Axis deer (<i>Axis axis</i>)	75.5 ^a	49.5 ^a	22.7 ^c

^aPhillips 1980; ^bSantiapillai *et al.* 1981; ^cSchaller 1967

transects in each sector were conducted in each of the dry and intermediate seasons and four in the wet season. Age and sex class of all observed individuals were recorded. Average seasonal abundance counts were divided by the associated seasonal transect areas to determine seasonal densities (individuals km⁻²). These were then amalgamated to determine a yearly average prey density. Each transect represented a different sized sector of the study area, so the relative contribution of each transect to the total study area prey data was weighted by the proportional size of the sector that it described.

The total biomass (kg km⁻²) of potential leopard prey in the study area was determined by multiplying the number of individuals in each age/sex class comprising the sector densities by their respective kg weights (Table 1) and weighting each sector's contribution to the total as before. Age and sex classes considered potential leopard prey were determined from analysis of kills and consultations with RNP staff. Due to low detectability, the abundance of small potential prey species such as grey langurs (*Semnopithecus priam*), Sri Lanka spotted chevrotain (*Moschiola meminna*), black-naped hare (*Lepus nigricolis*) and porcupine (*Hystrix indica*) were not determined, and the smaller age classes of larger prey (e.g. wild boar piglets and axis deer fawns) may be under-represented. As a result the total available biomass is expected to be higher than indicated. As this potential bias arising from variation in detectability can be accommodated using distance sampling techniques (Buckland *et al.* 2001, 2007), it is recommended that future estimates utilize this more robust methodology.

Carcasses were located opportunistically, often from odour and/or predator behavioural cues. Kills were differentiated from scavenged carcasses by identifying puncture wounds on the throat and nape of neck and from signs of struggle (Bailey

1993; Kruuk & Turner 1967; Sunquist & Sunquist 2002). Prey species, age and sex were determined by visual inspection. Kills were monitored to track leopard feeding activity, scavenging by other species and the possible moving of carcasses. Leopard scat samples were collected both opportunistically and during regular trail monitoring, air dried and stored in zip-loc bags. To differentiate between leopard and fishing cat (*Prionailurus viverrinus*) scat only samples with bolus width > 2.5 were retained (Henchel & Ray 2003). To prepare samples for microscopic analysis each was washed and sieved to eliminate unwanted particles. Bones, quills, nails, hoofs and vegetation were manually separated, identified and the remaining hairs mixed and oven dried at 60° C for 24 hours. Dried samples were then placed in a shallow dish, a point grid placed over and 50 hairs randomly sampled (Ciucci *et al.* 2004). Microscopic analysis followed Amerasinghe *et al.* 1990.

Statistical analysis was carried out using SPSS version 12.0 software (SPSS Inc., Chicago, USA) and R (version 2.15.1). Means are presented with the standard deviation (\pm). The Kolmogorov-Smirnov and Shapiro-Wilk tests were used to determine normality of variables and non-parametric tests when the assumption of normality was violated. Homogeneity of variance was determined using Levene's test (Zar 2010). All tests were two-tailed unless otherwise stated and data log-transformed where warranted.

Results

Data was obtained from 6719 minutes of direct observation over 247 sightings (mean length = 27.2 min., range 0.5–363), 19 camera trap photographs from 40 trap nights, and 24 visitor photographs and video occasionally used to confirm identifications. Mean daily observer travel distance was 96.7 km day⁻¹ during which 1,100 sets of pugmarks were recorded and 450 tracings made.

Population and home range attributes

A total of 53 leopards of all age/sex classes and social categories were observed within the study area from 277 sightings during the study period, of which 19 (5 male, 14 female) were determined to be adult residents (Table 2).

Table 2. Age, sex and status breakdown of all leopards observed during study period (February 2001–May 2002).

Sex	Age	Status	Number
Male	Adult	Resident	5
		Transient/unknown	3
	Sub-adult	Resident	10
	Cub	Resident	2
	Unknown	Unknown	1
Female	Adult	Resident	14
		Transient/unknown	3
	Sub-adult	Resident	4
	Cub	Resident	0
	Unknown	Unknown	3
Unknown	Cub	Resident	8
Total	All	Individuals	53
Total	Adult	Resident	19

The average estimated total population density from spatially explicit capture-recapture analysis ranged from 17.0 to 26.6/100 km² across the four sessions with the average estimated adult resident density ranging from 10.0 to 14.7/100 km² (Table 3). The mean home range size of resident males with ranges entirely within the study area was 22.5 ± 1.7 km² (N = 3, range = 20.5–25.8 km²) (Fig. 4). These ranges showed considerable overlap including a central 0.8 km² was used by three resident males (Fig. 4). Adult female core areas averaged 1.58 ± 0.33 km² (N = 4, range = 0.99–2.35 km²) (Fig. 4) and were exclusive of other adult females. Adult male resident home ranges overlapped territories of ≥ 4 adult female residents.

Sociality, activity patterns and behaviour

Sightings were predominantly of solitary leopards (84.2%), with most group sightings consisting of females and their young (41.0%), cubs (20.5%) or courting pairs (23.1%). Leopards in Sri Lanka (N = 707; de Silva & Jayaratne 1994; Muckenhirn & Eisenberg 1973; Santiapillai *et al.* 1982; present study) were observed to be alone less frequently than in studies with dominant intra-guild competitors (N = 440; Bailey 1993; Hamilton 1981; Schaller 1972; chi square test, $\chi^2 = 29.21$, $df = 1$, $P \leq 0.0001$).

Male leopards were sighted more frequently than females (chi square test, $\chi^2 = 13.27$, $d.f. = 1$; $P \leq 0.0001$). The probability of seeing a leopard during crepuscular periods (5:00–7:00 and 17:00–19:00) was 0.21 h⁻¹, at night (19:00–24:00) 0.20 h⁻¹ and in the daytime (7:00–17:00) 0.04 h⁻¹ (Fig. 5).

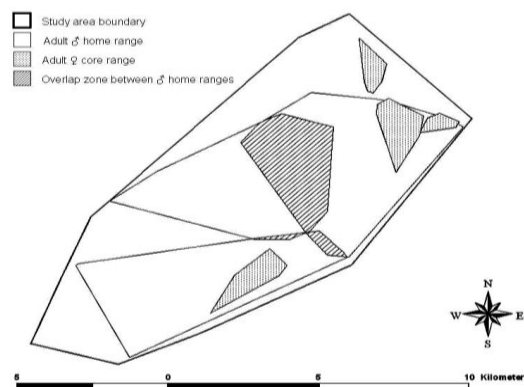


Fig. 4. Home ranges of 3 adult male leopards and their areas of overlap, as well as the core areas of 4 adult female leopards. Male home ranges are the minimum convex polygon (MCP) of all sightings and verified spoor locations (mean number of locations = 70, range: 51–96). Female core ranges are the MCP of all sighting locations of individually identified females and their dependent cubs (if applicable) (mean number of sightings = 20.8, range = 18–28). Leopards for with insufficient data to estimate home range or core area sizes (see Materials and methods) were not included.

The timing of observations influenced whether leopards were active or inactive (chi square test, $\chi^2 = 15.58$, $df = 2$, $P < 0.001$). The probability that leopards were active during sightings was 0.70 (N = 247), including 0.67 during crepuscular periods (N = 126), 0.55 during diurnal sightings (N = 40) and 0.83 during nocturnal sightings (N = 81). Activity levels were significantly higher during nocturnal sightings than either crepuscular (chi square test, $\chi^2 = 9.04$, $df = 1$, $P < 0.01$) or diurnal (chi square test, $\chi^2 = 13.37$, $df = 1$, $P < 0.001$) sightings.

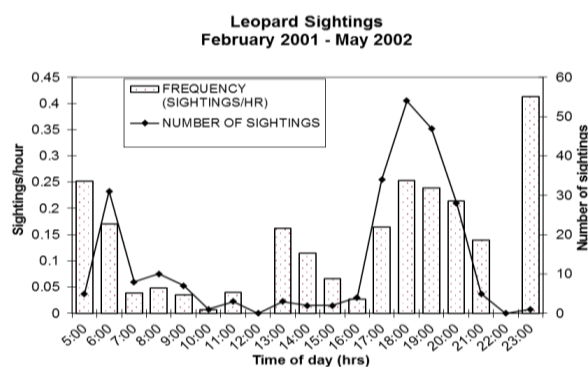


Fig. 5. Number and frequency of leopard sightings (N = 247) across all hours of observation in the Ruhuna (Yala) National Park study area between February 2001 and May 2002.

Table 3. Estimated leopard density across 4–4-month sessions in the 103.7 km² study area in Ruhuna (Yala) National Park.

Session	Months	Polygons searched		Individuals		Detections		Occupied polygons		Density (/100km ²)		95% Confidence Interval	
		Total	Adult	Total	Adult	Total	Adult	Total	Adult	Total	Adult		
1	Feb.–May 2001	88	25	15	95	49	32	28	24.7	12.3	16.6–36.8	7.3–20.9	
2	Jun.–Sep. 2001	70	32	19	77	45	32	25	26.6	14.7	18.2–38.8	8.9–24.3	
3	Oct. 2001–Jan. 2002	104	24	14	65	37	30	22	18.6	10.0	12.2–28.3	5.7–17.4	
4	Feb.–May 2002	104	28	20	77	40	27	19	17.0	11.4	11.4–25.4	6.6–19.9	
Average	Feb. 2001–May 2002	91.5	27.3	17.0	78.5	42.8	30.3	23.5	21.7	12.1	14.6–32.3	7.1–20.6	

Prey abundance and predation

Axis deer were most abundant and comprised the largest proportion of available biomass (Table 3). There was considerable temporal variation in prey abundance with axis deer dry season density significantly lower than in the wet season (t-test, $t = -5.11$, $df = 2$, $P < 0.05$; Table 4). Spatial variation was also conspicuous with significantly fewer axis deer in the southeast sector than the southwest sector in the dry season (t-test, $t = -3.88$, $df = 4$, $P < 0.05$) or the northeast sector in the wet season (t-test, $t = -2.85$, $df = 6$, $P < 0.05$). The southwest consistently had the fewest buffalo (ANOVA $F_{2,6} = 20.504$, $P < 0.01$).

Of the 221 scat samples collected, identifiable material was detected in 214, of which 185 could

be compared to the available prey from abundance transects (Fig. 6). Axis deer and water buffalo occurred in scat at expected ratios given their availability (exact binomial test, $P > 0.1$) whereas wild boar was marginally selected against (exact binomial test, $P < 0.1$) and sambar deer strongly selected for (exact binomial test, $P < .0001$). Other species detected in scat were black-naped hare (9.8% of scats), porcupine (2.3%), grey langur (0.9%), toque macaque (*Macaca sinica sinica*, 0.5%), unidentified snake (0.5%) and peafowl (*Pavo cristatus*, 0.5%).

Leopards were observed feeding on 64 carcasses representing a wide range of species, of which 51 were identified as kills (Fig. 7). Of these, star tortoise (*Geochelone elegans*), land monitor (*Varanus cepedianus*) and Indian pangolin (*Manis crassicaudata*) were not detected from scat analysis. One sub-adult elephant (*Elaphus maximus*) was scavenged after it drowned in a water hole and the carcass pulled out by National Park staff. Of kills, 61.5% of axis deer carcasses identified ($N = 26$) were adult, whereas all buffalo carcasses were of sub-adults or calves (Fig. 8). Of the 4 sambar kills detected, 3 were of adult males whereas a single adult wild boar kill was detected (Fig. 8).

Of all kills, 13.7% were secured in trees. Wild boars were detected scavenging from 38.8% of 49 monitored carcasses. Other scavengers included ruddy mongoose (*Herpestes smithii*; 36.8%), Large-billed Crow (*Corvus macrorhynchos*; 22.5%), land monitor (8.2%), mugger crocodile (*Crocodylus palustris*; 6.1%), sloth bear (*Melursus ursinus*; 4.1%) and Hawk Eagle (*Spizeatus cirrhatus*; 2%). A small but widespread population of jackals (*Canis aureus*) inhabits the study area, but these were never observed to directly scavenge from a leopard kill.

Table 4. Estimated prey densities and biomass of main large-size leopard prey species within the study area.

Species	Density (individuals km ⁻²)		Biomass (kg km ⁻²)	
	Total	Available	Total	Available
Axis deer (<i>Axis axis</i>) ^a	121.0	121.0	6111.9	6111.9
Water buffalo (<i>Bubalus bubalis</i>) ^b	31.9	4.9	6641.0	502.0
Wild boar (<i>Sus scrofa</i>) ^c	8.0	7.0	431.4	316.5
Sambar (<i>Rusa unicolor</i>) ^a	0.8	0.8	133.0	133.0
Total biomass			13317.3	7063.4

^aall age and sex classes are potential leopard prey; ^bonly non-adults are potential leopard prey; ^cfemales and young are potential leopard prey

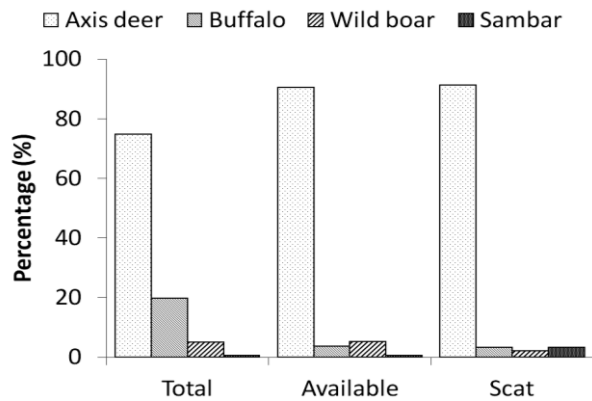


Fig. 6. The proportion of the four most common large prey species in the study area (Total), available to leopards (Available) and detected in leopard scat (Scat) in Ruhuna (Yala) National Park study area between February 2001 and May 2002.

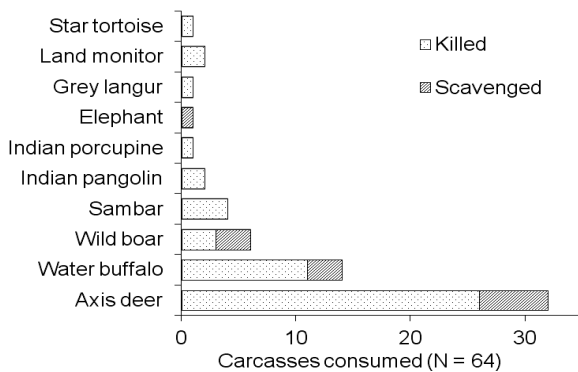


Fig. 7. Identification by species of all carcasses consumed by leopards during the course of the study. The number killed and scavenged are indicated for each species.

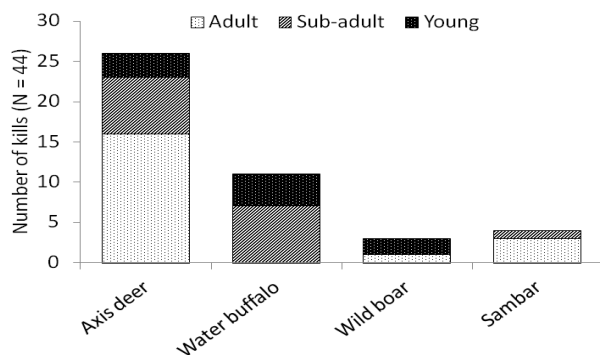


Fig. 8. The age classes of all axis deer, water buffalo, wild boar and sambar killed during the course of the study. Adult animals were fully grown and of reproductive age; sub-adults were $\frac{1}{2}$ to $\frac{3}{4}$ size with partially formed antlers, horns or tusks; and young were $< \frac{1}{2}$ size with minimal or no antlers, horns or tusks.

Discussion

The resident population density of leopards in RNP is among the highest recorded either regionally (see Kalle *et al.* 2011 and Thapa *et al.* 2014 for summary of South Asian surveys) or internationally (see Chase Grey *et al.* 2013 for summary of African densities). Many published estimates are not clear about the inclusion of cubs and/or sub-adults (e.g. Borah *et al.* 2013; Harihar *et al.* 2009) so the relative abundance of RNP leopards might be higher still. The estimated SECR densities indicate an average across sampled sessions of 30.4 leopards, including 16.9 resident adults residing within the 140 km² of RNP Block I. All of the studies with estimated leopard densities higher than RNP come from systems with multiple large predators and abundant available prey (Bailey 1993; Harihar *et al.* 2009; Kalle *et al.* 2011; Maputla *et al.* 2013). Together with the results from this study, it suggests that prey availability, not competition with dominant inter-specifics, underlies variation in leopard density (Carbone & Gittleman 2002; Markar & Dickman 2005).

The leopard densities estimated during the first two sessions were notably higher than during the latter two sessions (Table 3) when the western boundary of the park was regularly searched (Fig. 3). This supports previous research suggesting variation in leopard density within RNP with a higher density in the central and coastal sectors (de Silva & Jayaratne 1994). These areas are less prone to human poaching pressure than the western boundary and contain the open plains upon which prey congregate to feed (de Silva & Jayaratne 1994). Targeted prey abundance surveys in the western boundary region would help to further clarify the factors underlying this potential variation.

The land tenure system of RNP's leopards is of the structure described for most other populations and is consistent with expectations for solitary felids in that male home ranges were larger than those of females, a number of which they overlapped (Bailey 1993; Mizutani & Jewell 1998; Odden & Wegge 2005; Rabinowitz 1989; but see Marker & Dickman 2005).

Females select ranges of a size sufficient to provide adequate prey for themselves and their cubs and contain micro-habitats suitable for cub rearing whereas male ranges are probably not determined directly by prey availability, but instead by an effort to maximize access to females

(Kitchener 1991; Sandell 1989). This results in the same observed pattern for males and females whereby their home range size is inversely related to available prey biomass. In the absence of female leopards, the home range size of a male in Addo Elephant National Park in South Africa was well predicted from available prey biomass (Hayward *et al.* 2009). In RNP the average core area of a female home range is small (1.58 km²), suggesting a high available prey biomass, which is in fact observed (Table 3). The mean resident male home range in RNP was small relative to those determined in other studies (Table 5), but notably where prey biomass was greater male home range size was correspondingly smaller (Karanth & Sunquist 2000). The very small size and close proximity of resident female core ranges in RNP also suggests small home ranges. This clearly aligns with the observed strong inverse correlation between available prey biomass and leopard home range size (Hayward *et al.* 2009; Marker & Dickman 2005).

There was no observed overlap of resident female core areas and little evidence of home-range overlap during the study period. When combined with the observed overlap in male ranges, this indicates Macdonald *et al.*'s (2010) OE social group arrangement. Females with overlapping home ranges, especially those that are related, have been observed (Bailey 1993; Stander *et al.* 1997) however some felid populations do inhabit exclusive home ranges (Mizutani & Jewell 1998; Rabinowitz & Nottingham Jr. 1986). Sandell (1989) argues that solitary female carnivores should exhibit non-overlapping home ranges when food resources are stable and evenly distributed, spatially and temporally. There was substantial spatial and temporal variation in available prey in

this study, however the prey base during the leanest period and in all sectors was still substantial (Table 4), which may reduce the impact of this variation, and possibly allow for exclusive ranges. More thorough documentation of full female home ranges is needed to clarify this possibility. Home-range overlap between resident males was conspicuous and is common across leopard populations (Bailey 1993; Grassman 1999; Marker & Dickman 2005; Norton & Henley 1987; Stander *et al.* 1997). Resident males in RNP appear to have exclusive core areas that are considerably smaller than their home ranges and might be the equivalent of the 8–10 km² exclusive “prime areas” described by Muckenhirn & Eisenberg (1973).

Sighting results support previous observations that male leopards are more visible than females, possibly explaining the over-representation of males in population estimates based solely on visual observations of unidentified individuals (Bailey 1993; Eisenberg & Lockhart 1972; Muckenhirn & Eisenberg 1973). In RNP it was sub-adult males that were most conspicuous. This has been identified as the primary reason for some male-biased sex ratios previously documented (Eisenberg & Lockhart 1972). The resident sex ratio (1M: 2.8F) in RNP indicates a prevalence of females, consistent with documented leopard social structure (Bailey 1993; Hamilton 1981; Mizutani & Jewell 1998).

In RNP 86.4% of scat samples (N = 214) contained hair from medium to large mammal prey (axis deer, water buffalo, wild boar and sambar) consistent with previous observations here (Amerasinghe *et al.* 1990; Amerasinghe & Ekanayake 1992). Leopards tend to prefer prey between 10–40 kg with the strongest preference

Table 5. Estimated prey densities of main leopard prey species within the southeast, southwest and northeast sectors of the study area in the dry, wet and intermediate (inter) seasons. Dry season transects were conducted in June, July and August; wet season transects in November, December, January and February; and intermediate season transects in March, April and May. Densities include all age/sex classes.

Species	Density (individuals km ⁻²)								
	Southeast			Southwest			Northeast		
	Dry	Wet	Inter	Dry	Wet	Inter	Dry	Wet	Inter
Axis deer (<i>Axis axis</i>) ^a	41.4	98.8	81.4	72.9	165.2	123.6	83.4	201	171.9
Water buffalo (<i>Bubalus bubalis</i>) ^b	34.7	41.3	49.3	15.3	13.5	19.3	39.1	54.2	51.8
Wild boar (<i>Sus scrofa</i>) ^c	5.3	11.8	11.3	0.0	17.0	4.4	4.7	11.0	9.6
Sambar (<i>Rusa unicolor unicolor</i>) ^a	0.3	3.7	1.4	0.0	1.4	0.0	0.5	0.6	0.4

^aall age and sex classes are potential leopard prey; ^bonly non-adults are potential leopard prey; ^cfemales and young are potential leopard prey

for animals 23–25 kg (Hayward *et al.* 2006). Young axis deer fit this size (Table 1) but overall axis deer are taken in proportion to their availability in RNP. Conversely sambar, the largest deer available here, seem to be selected by leopards. Seidensticker (1976) found leopards selecting for smaller age/sex classes of sambar in Royal Chitwan National Park, Nepal, however in RNP 75% (N = 4) of sambar carcasses detected were of adult males (215 kg, Santiapillai *et al.* 1981). Despite potential bias in carcass detection toward larger age/sex classes and a small sample size, this indicates that leopards at least include the largest sambar age/sex class in their diet here. This suggested preference for larger prey may be expected given the absence of intra-guild competition as leopards might expand the breadth of their prey range to incorporate more profitable species (Karanth & Sunquist 1995). Furthermore, apart from their size sambar fit the profile of preferred leopard prey in that they occur in small herds, typically in dense habitat (Hayward *et al.* 2006). Conversely, adult buffalo, including females (220 kg, Phillips 1980) which are of similar size to adult male sambar, were not detected in carcasses, although two adult buffalo killed in poacher's wire snare traps were scavenged. The gregarious nature of buffalo and their preference for open habitat (Hayward *et al.* 2006) combined with effective anti-predation behavioural strategies (Hoogesteijn & Hoogesteijn 2008) might underlie this difference, constraining leopards to exploit only calves, the most vulnerable age class. Wild boars were represented in the diet disproportionately less than their availability. This may be due to wild boar being an aggressive species with the potential to injure or kill potential predators (Jedrzejewski *et al.* 1992), and thus, typically killed only by larger felids (Hayward *et al.* 2012; Hayward *et al.* 2014). In Sri Lanka, an individual male wild boar can displace a full grown male leopard (A. Kittle & A. Watson, personal observation). Wild boars have been selected against by wolves in some areas of their European range (Okarma 1997) but seem to be selected for in the Mediterranean region (Davis *et al.* 2012). This differential regional selection pattern might result from morphological differences (the Mediterranean wild boars are smaller) or from differences in alternate prey availability (Davis *et al.* 2012). The under representation of wild boar in leopards' diet has also been seen in the central hill country of Sri Lanka where alternate prey is less available (Kittle *et al.* 2014).

The lack of dominant intra-guild competitors in Sri Lanka may be why leopards here are less frequently seen alone. While groups > 2 are rare across all studies, Sri Lankan leopards are more often seen in pairs, either as courting adults or females with cubs. Although leopards in RNP are highly habituated, it is unlikely that this alone underlies these observations as compared studies also come from protected areas with high tourist visitation (*i.e.* Kruger National Park and Serengeti National Park). Female leopards spend considerable time with cubs in the presence or absence of dominant intra-guild competition (Stander *et al.* 1997); however they may be more circumspect in their movements when potentially dangerous intra-guild competitors are present given that cubs are particularly vulnerable (Bertram 1978; Schaller 1972). Despite the significant difference in observed sociality between Sri Lankan leopards and those where dominant predators exist, 80.6% of leopard observations in Sri Lanka were of solitary animals (de Silva & Jayaratne 1994; Muckenhirn & Eisenberg 1973; Santiapillai *et al.* 1982; this study).

The mostly crepuscular and nocturnal activity of leopards in RNP is also consistent with widely observed leopard behaviour (Bailey 1993; Bothma & Le Riche 1984; Grassman 1999; Ramesh *et al.* 2012, but see Ngoprasert *et al.* 2007), although leopards observed diurnally were still active 55 % of the time. Bias arising from observers failing to see inactive animals is expected to have inflated the proportion of active observations however this bias should be equal across time periods making relative comparisons valid. Where leopard activity is observed to be predominantly diurnal, it is typically attributed to an adaptation to the diurnal behaviour patterns of prey (Ilany 1981; Jenny & Zuberbühler 2005; Norton & Henley 1987) although Ngoprasert *et al.* (2007) suggest behavioural adaptations to human traffic underlie observed periods of activity.

Tree caching of kills is most typical in open habitats with high interaction rates with other carnivores and where the preferred method of securing resources, dragging them into dense thickets, alerts too many scavengers (Stander *et al.* 1997). Bailey (1993) found 84% (N = 55) of leopard kills stashed in trees in predator-abundant Kruger National Park. In Zimbabwe's Matapos National Park, where hyenas and jackals are absent, 2.6% (N = 38) of kills were treed (Smith 1977) and in the Kalahari, where lion and hyena densities are low, Bothma & Le Riche (1984) found 17% (N = 24) of

carcasses in trees. Asian leopards appear to tree cache less often regardless of potential competitors (Eisenberg & Lockhart 1972; Karanth & Sunquist 2000; Sunquist & Sunquist 2002) possibly because dense vegetation is more available for discreetly securing kills (Stander *et al.* 1997). So whether the low levels of tree caching observed in this study represent the absence of intra-guild competition or the availability of secure caching locations on the ground is unknown.

In summary this research provides some much needed baseline ecological data regarding an endangered leopard sub-species that has been free of dominant intra-guild competitors for thousands of years. Leopards in RNP appear to have the same general population and spatial structure as most other populations irrespective of the absence of dominant intra-guild competitors (Bailey 1993; Grassman 1999; Jenny 1996; Mizutani & Jewell 1998; Odden & Wegge 2005; Rabinowitz 1989; Simcharoen *et al.* 2008; but see Marker & Dickman 2005; Norton & Lawson 1985) but there is some evidence to suggest possible behavioural adaptations to this absence. These include a higher frequency of observations of groups > 1 and an indication of selection for larger prey, although small prey items are still well represented in leopard diet here. The relatively small home range sizes and high population density observed would be predicted in the absence of dominant competitors, but can also be attributed to the abundance of available prey in RNP.

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