



## Social organization of a solitary carnivore, the leopard, inferred from behavioural interactions at marking sites

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Intraspecific interactions shape animal social networks and regulate population dynamics. Species with solitary life histories rely on communication cues for population regulation, especially olfaction for many terrestrial mammals. Increasing evidence shows complex social structures among presumably solitary species and although social factors may play a key role in spatial organization, we lack insights into how species with solitary life histories structure and maintain sociospatial systems. Herein, we applied a social network approach to decode leopard, *Panthera pardus*, behaviour and interactions at marking sites that we monitored with camera traps. We found that leopard social units within our study area consisted of up to five individuals and that same-sex and opposite-sex interactions were equally likely to occur. Individuals behaved and responded differently depending on the type of interaction, serving both territorial and reproductive purposes. Temporal segregation allowed intersexual co-occurrence, while same-sex co-occurrence may be facilitated through familiarity with stable neighbours. Central individuals interacted within and outside their social unit and appeared fundamental to group stability. The removal of these individuals, such as through legal harvest or pre-emptively as an attempt to minimize depredation, may weaken social cohesion and ultimately affect population demography. Our findings on intraspecific co-occurrence in a solitary carnivore depict a complex social structure that can be important for population stability and might occur in other solitary species.

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Intraspecific interactions shape animal social networks and regulate population dynamics (Clutton-Brock, 2016; Shizuka & Johnson, 2020). In terrestrial mammals, diverse selective pressures have contributed to the evolution of social behaviour such that the net benefits of close association with conspecifics exceed the costs of it (Macdonald, 1983; Silk, 2007). While intraspecific behavioural interactions have been researched extensively for social mammals, the sociospatial organization of mammals with solitary life history strategies has received less attention (Clutton-Brock, 2016). Territoriality, prey availability and kinship are thought to determine the sociobiology of solitary mammals (Diefenbach et al., 2006; Elbroch et al., 2016; Ferreras et al., 1997; Hamilton, 1964; Macdonald, 1983). For example, female

behavioural decisions are primarily dependent on availability of prey and refuge areas for young, while male behaviour is mainly dependent on the distribution of breeding females (Clutton-Brock, 2016; Sandell, 1989).

Solitary species rely on indirect cues to maintain social systems, especially olfaction for many terrestrial mammals (Johnson, 1973). The functional role of scent-marking behaviour is generally similar among mammals and mainly serves reproductive and territorial purposes (Ralls, 1971). The manifestation of specific behaviours and strategies may, however, vary considerably among species and can be influenced by the presence of land tenure systems (Allen, Wittmer et al., 2016). Among the Felidae, scraping, urine spraying and faecal marking are the behaviours most frequently exhibited to manifest olfactory cues and these are often deposited along territory borders, in territorial core areas and/or at communal marking sites (Harmsen et al., 2010; Melzheimer et al., 2020; Rafiq et al., 2020; Smith et al., 1989; Vogt et al., 2014).

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Most felid species are considered solitary because of their specialized hunting strategy (Kleiman & Eisenberg, 1973; Sunquist & Sunquist, 2002), with only lions, *Panthera leo*, (Schaller, 1972), cheetahs, *Acinonyx jubatus* (Caro & Collins, 1987) and domestic cats, *Felis catus*, showing forms of sociality (Bradshaw, 2016). However, being solitary does not preclude a complex social structure, which in felids is characterized by female philopatry and varying degrees of intra- and intersexual range overlap (Sunquist & Sunquist, 2002). Moreover, recent evidence from pumas, *Puma concolor*, and jaguars, *Panthera onca*, has challenged the conventional view that most large felids are exclusively solitary (Elbroch et al., 2017; Jędrzejewski et al., 2022) and there is increasing evidence of direct interactions and structured social networks among other presumably solitary species (Dalerum, 2005; Graw et al., 2019; Lühns & Kappeler, 2013; Quaglietta et al., 2014; Stenhouse et al., 2005).

Leopards, *Panthera pardus*, have the largest distributional range of any wild felid, with remarkable adaptability in diet and habitat requirements (Balme et al., 2020; Jacobson et al., 2016; Stein et al., 2020). They have a polygynous mating system where male territories overlap with several females (Bailey, 2005) and display intrasexual territoriality with the proportion of home range overlap varying among populations (Bailey, 2005; Marker & Dickman, 2005; Rouse et al., 2021). In high-density systems, territoriality appears to be relaxed, indicative of risk aversion to avoid injury or death following territorial disputes (le Roex et al., 2022b). Leopards are solitary, but display subtle behavioural adaptations such as decreased secrecy in the absence of dominant predators (Kittle et al., 2017; Stander et al., 1997). They only associate as mating pairs, or as mothers with offspring until cubs reach 13–22 months of age (Estes, 1991; Fattebert et al., 2015). Male leopards maintain territories through a boundary scent-marking strategy, while female scent-marking strategies are less understood (Bothma & Coertze, 2004; Rafiq et al., 2020). Male leopards exhibit a strong defensive response to strangers, but appear to be more tolerant towards residential neighbours, which may be attributed to a 'dear-enemy effect' (Christensen & Radford, 2018; Rafiq et al., 2020). Female leopards form matrilineal kin clusters, where related females display higher range overlap with each other than with unrelated females (Fattebert et al., 2016). According to the resident fitness hypothesis and as seen in other polygynous mammals, female leopards tolerate the costs of increased resource competition due to the benefits they gain from inclusive fitness through reduced kin competition (Fattebert et al., 2015, 2016).

The spatial dynamics of leopard populations suggest a structured social organization, where familiarity may be maintained through olfactory communication at communal marking sites. These sites can be diverse and include trees, shrubs, grass clumps and sand (Bothma & Coertze, 2004; Rafiq et al., 2020). Estes (1991) described large trees with inclined trunks and large branches as preferred scent-marking posts by leopards. Prominent landscape features may aid landmark-based navigation and could help delineate territory boundaries (Fagan et al., 2013). Consequently, large trees may be revisited more frequently than other marking sites, and some used by multiple conspecifics as well as by other species (Verschuere et al., 2021).

Considerable research effort has focused on investigating leopard ranging patterns and scent-marking strategies (Bothma & Coertze, 2004; Fattebert et al., 2016; Marker & Dickman, 2005; Rafiq et al., 2020; Rodríguez-Recio et al., 2022; Rouse et al., 2021). Despite recent evidence suggesting that social factors structure leopard spatial organization (le Roex et al., 2022a; 2022b), we lack insights into how their sociospatial systems are organized and maintained. Social network analysis is a common technique to investigate social and ecological interactions among conspecifics and could bring insights into the sociobiology of leopards also

(Croft et al., 2008). Social networks and, more broadly, the study of intraspecific interactions increase our understanding of how local processes drive population level properties and ultimately guide species management (Farine & Whitehead, 2015). Herein, we applied a social network approach and analysed leopard behaviour and interactions noninvasively at intraspecific communication sites (marking trees). Our objectives were to determine (1) the mechanisms of information transfer, (2) the direction of information flow and (3) the level of temporal segregation to facilitate shared use of space.

## METHODS

### Study Area

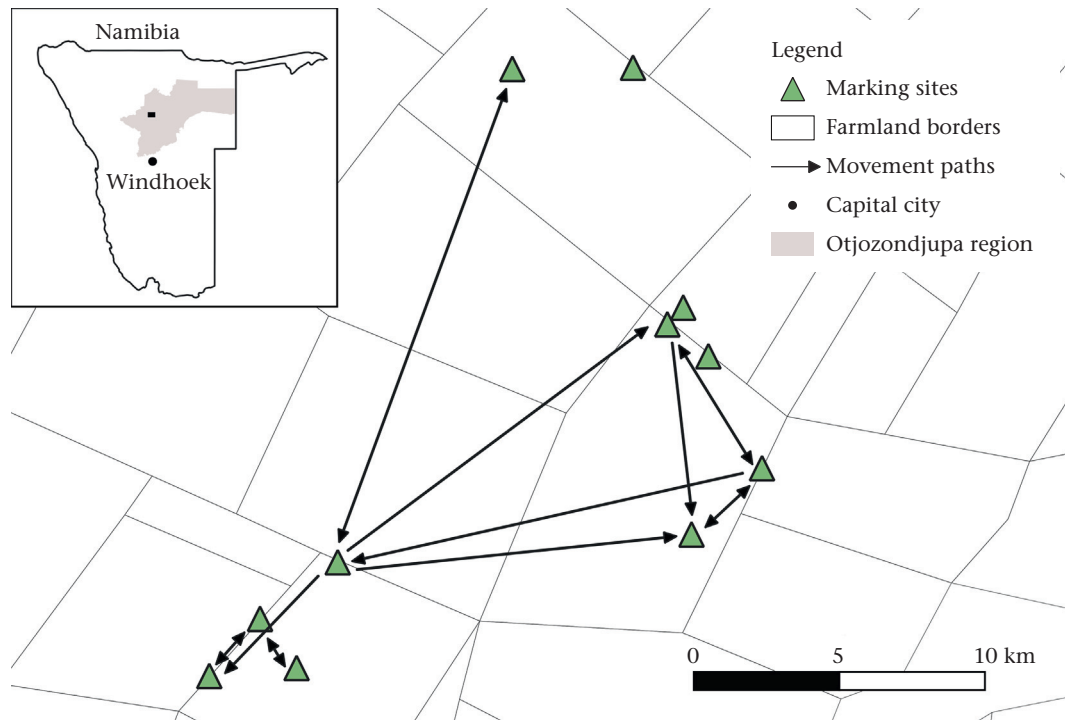
The study was conducted on freehold farmland covering 269 km<sup>2</sup> (minimum convex polygon) in north-central Namibia (20°28'56"S, 17°2'24"E; Fig. 1). The area is semiarid with an annual mean rainfall of 450 mm concentrated between November and April, the wet season (Mendelsohn et al., 2002). The area is characterized by thorn bush and tree and woodland savannah vegetation, where bush encroachment is prevalent (Barnard, 1998). Primary land use practices are livestock (cattle and small stock) farming and wildlife ranching, including fenced game farms, ecotourism and trophy hunting (Marker-Kraus et al., 1996). The latter only occurs in the broader landscape, that is, outside the minimum convex polygon-delineated area, and direct persecution associated with livestock losses is also present in the broader region. The leopard is a top predator in this system as lions and spotted hyaenas, *Crocuta crocuta*, were extirpated in the 1980s (Stein et al., 2010). Other sympatric large carnivores are the brown hyaena, *Parahyaena brunnea*, and cheetah.

### Data Collection

Between June 2010 and August 2011, we continuously monitored 11 marking trees with camera traps as part of a long-term camera trapping survey (see Fabiano et al., 2020). Camera traps were deployed initially to monitor cheetah activity (Fabiano et al., 2020), yet leopard activity at these sites was common and unaffected by cheetah activity (Verschuere et al., 2021). We used infrared Bushnell Trophy Cam (Bushnell Corporation, Overland Park, KS, U.S.A.) cameras and deployed two cameras per site, facing each other at a slight angle, mounted ca. 75 cm above the ground and approximately 5 m apart. Cameras were programmed to take pictures with a 30 s delay between triggers and produced a burst of three photos per trigger taken within 1 s. Cameras were visited every week to check for functionality and change the memory card and/or batteries. Mean spacing of camera trap sites was 14.9 km ( $\pm$  8.3 km).

### Individual Identification

We identified individual leopards manually, based on unique rosette patterns. Manual identifications were verified using a computer-assisted identification algorithm (Verschuere et al., 2023). Sex was determined based on physical appearance, such as large body size, head size, the presence of a dewlap or external genitalia (male) or accompanying dependents (female) (Balme et al., 2012; Henschel & Ray, 2003). We acknowledge difficulties in distinguishing females from subadult males (Balme et al., 2012), but errors may have been reduced because of the continuous effort and repeated visits of individuals. When we were unsure about the sex of an individual, it was classified as unknown sex.



**Figure 1.** Study area map with monitored scent-marking sites and movement paths of leopards inferred from uniquely identified individuals based on camera trap data.

### *Behavioural States and Activity Budgets*

To understand the biological mechanisms of information transfer, we classified observed behaviours into behavioural states with distinct ecological functions and developed an ethogram for leopards at marking trees (Stanton et al., 2015). We recorded different behaviours during individual visits using the scan sampling method on each 30 s consecutive photograph (Lehner, 1992). Scan sampling is a widely used method to quantify behavioural observations whereby all behaviours displayed by all individuals are recorded during pre-established sampling periods with fixed intervals (Altmann, 1974).

We determined the sequence of behavioural states that solitary leopards displayed at marking sites and generated a kinematic diagram. This diagram shows the flow of the behaviours and is based on the transition frequency, which is the percentage of times a given behaviour followed another (Brockmann, 1994). A Pearson chi-square test of independence was used to detect whether the observed sequence of behaviours differed from a hypothetical random frequency distribution.

We estimated activity budgets of solitary leopards (i.e. not females accompanied by cubs or mating pairs) by calculating the proportional occurrence of each behavioural state as the number of records for each state divided by the total number of records (Altmann, 1974). We used a Pearson chi-square test to compare activity budgets between males and females, and between individuals that were recently preceded by another individual and individuals that were not preceded (see definition ‘interaction’ below).

We acknowledge the likelihood that certain displayed behaviours may have been undetected during the 30 s intervals between photographs. However this interval is below the 5 min recommended to yield reliable information when applying this method (de Oliveira et al., 2018). Additionally, it is unlikely that behaviours were missed altogether during the study, although we recognize that the kinematic diagram and activity budgets may be skewed

towards state behaviours such as resting or moving, while event behaviours such as marking and inspecting may be underrepresented.

### *Temporal Segregation*

To determine the degree of temporal segregation by leopards at marking sites, if any, we generated activity patterns for males and females using the package *camtrapR* (Niedballa et al., 2016). We also determined the coefficient of overlap (Dhat1 for small sample sizes, Ridout & Linkie, 2009) between the sexes and we compared activity patterns using the Watson–Wheeler test in the package *circular* (Agostinelli & Lund, 2017).

To further understand the behavioural response towards conspecifics, we calculated the time (days) between consecutive female–female (FF), female–male (FM), male–female (MF) and male–male (MM) co-capture events (Allen, Yovovich et al., 2016; Harmsen et al., 2009). We excluded consecutive visits of the same individual, individuals of unknown sex and two individuals simultaneously. We used a one-way ANOVA with the log-transformed time interval as response variable explained by the combination of sexes during co-capture events.

### *Social Network Analysis*

We used social network theory to investigate connections among individuals (e.g. interactions), which represent channels for the transmission of information among individuals (Blonder et al., 2012). Individuals are depicted as nodes and interactions as edges in the social network graph. Distance between nodes depicts the strength of the interactions and the arrow represents the direction of information flow.

Interactions occurred when two different individuals were photographed at the same marking tree location within 26 days of each other. This value was the mean intervisit interval between

leopard visits in our study system and is below the individual revisit time of 29.55 days reported for a leopard population in Botswana (Rafiq et al., 2020).

The direction of the interaction was determined by the direction of information transfer, that is, from the preceding individual to the following individual. When two individuals were captured simultaneously, both were considered as preceding and following visitor. We calculated network measures of centralization, which indicate the extent to which the network is dominated by one or a few nodes (i.e. individual(s)). We calculated node degree, which shows the number of interacting individuals per individual, and betweenness centrality, which lists the main connector in the network. Additionally, we calculated an assortativity coefficient, which quantifies the extent to which connected nodes share similar properties, in this case, whether nodes of the opposite sex tend to connect more with each other than nodes of the same sex. We used one-way ANOVA models with the number of incoming and outgoing edges as response variables to determine whether males or females were more or less likely to precede or to follow a visit in an interaction. Subgroups within which many interactions occurred and between which few interactions occurred were detected based on a hierarchical agglomeration algorithm (Clauset et al., 2004).

Social network analysis and statistical tests were performed in R v.4.0.4 (R Core Team, 2021). A significance threshold of 0.05 was considered. We used the R packages CMRnet (Silk et al., 2021) and igraph (Csardi & Nepusz, 2006).

#### Ethical Note

The research was authorized by the Namibian National Commission on Research Science & Technology under Section 21 of the Research Science and Technology Act No. 23 of 2004 and adhered to the requirements of the guidelines for Ethical Treatment of Animals in Applied Animal Behaviour and Welfare Research standards of the International Society for Applied Ethology. No formal ethical review was conducted as camera trapping is minimally invasive and no concerns for animal welfare arose.

## RESULTS

Our study captured 124 independent leopard visits over 6017 camera trapping nights. Leopards were identified for 82% of visits ( $N = 102$ ), resulting in 29 individuals (15 females, 10 males, four unknown sex). Females accounted for most visits (55%), followed by males (29%) and individuals of unknown sex (16%). Two females were accompanied by cubs and accounted for 18% of visits. The number of individuals visiting the same marking site ranged from one to seven (mean =  $3.7 \pm 2.1$  SD). Individual leopards were captured at one to four marking sites (mean =  $1.4 \pm 0.7$  SD). We identified 80 visits that were associated in a dyadic interaction, that is, within the 26-day threshold of a visit by another individual, of which six were simultaneous visits by a male and a female, 11 where a male followed another male, 12 where a female followed another female, 16 where a male followed another female, 15 where a female followed another male and 20 that included an individual of unknown sex.

#### Behavioural States and Activity Budgets

A total of five behavioural states ('Inspecting', 'Marking', 'Moving', 'Resting', 'Social') encompassing 14 behaviours were exhibited by leopards visiting scent-marking sites (Appendix Table A1). The behavioural state exhibited most often by solitary individuals was 'Moving' (44%), followed by 'Resting' (24%), 'Inspecting' (19%) and 'Marking' (8%). There was a significant difference in the frequency

of different behaviours observed between males and females (chi-square test:  $\chi^2_3 = 20.04$ ,  $P < 0.001$ ), and in whether the visit was preceded by a different individual or not (chi-square test:  $\chi^2_3 = 31.56$ ,  $P < 0.001$ ). Males were observed to display marking and inspecting behaviours more often than females, particularly when preceded by another male (Fig. 2).

We observed one behavioural state in 41% of leopard visits, a sequence of two behavioural states in 36% of visits, a sequence of three behavioural states in 15% of visits and a sequence of four behavioural states in 8% of visits. When a sequence of behavioural states was observed during the same visit, behavioural states did not follow one another randomly (chi-square test:  $\chi^2_9 = 176.53$ ,  $P < 0.001$ ). The initial behavioural state was most likely to be followed by 'Moving', then 'Resting', 'Inspecting' and 'Marking' (Fig. 3). Individuals appeared to move more after 'Marking', after 'Resting' and after 'Inspecting', than vice versa. Individuals rested more after 'Marking' and after 'Inspecting', than vice versa. Individuals rarely marked after 'Inspecting' or vice versa.

#### Temporal Segregation

Activity of leopards was mostly nocturnal and crepuscular (Fig. 4), with 62% of visits occurring at night (1900–0600 hours), 19% during twilight (0600–0700 and 1800–1900 hours) and 19% during the day (0700–1800 hours). Activity patterns between males and females overlapped by 63% and were different (Watson–Wheeler test:  $W_2 = 14.07$ ,  $P < 0.001$ ). Female leopards showed a peak in activity during early mornings and were more active during the day, while male leopards were more active throughout the night.

The time between consecutive visits of different individuals was not influenced by the sex of the preceding or following visitors, although males tended to return slightly quicker following a visit by a female or a male (ANOVA:  $F_{3,50} = 0.29$ ,  $P = 0.835$ ; Fig. 5).

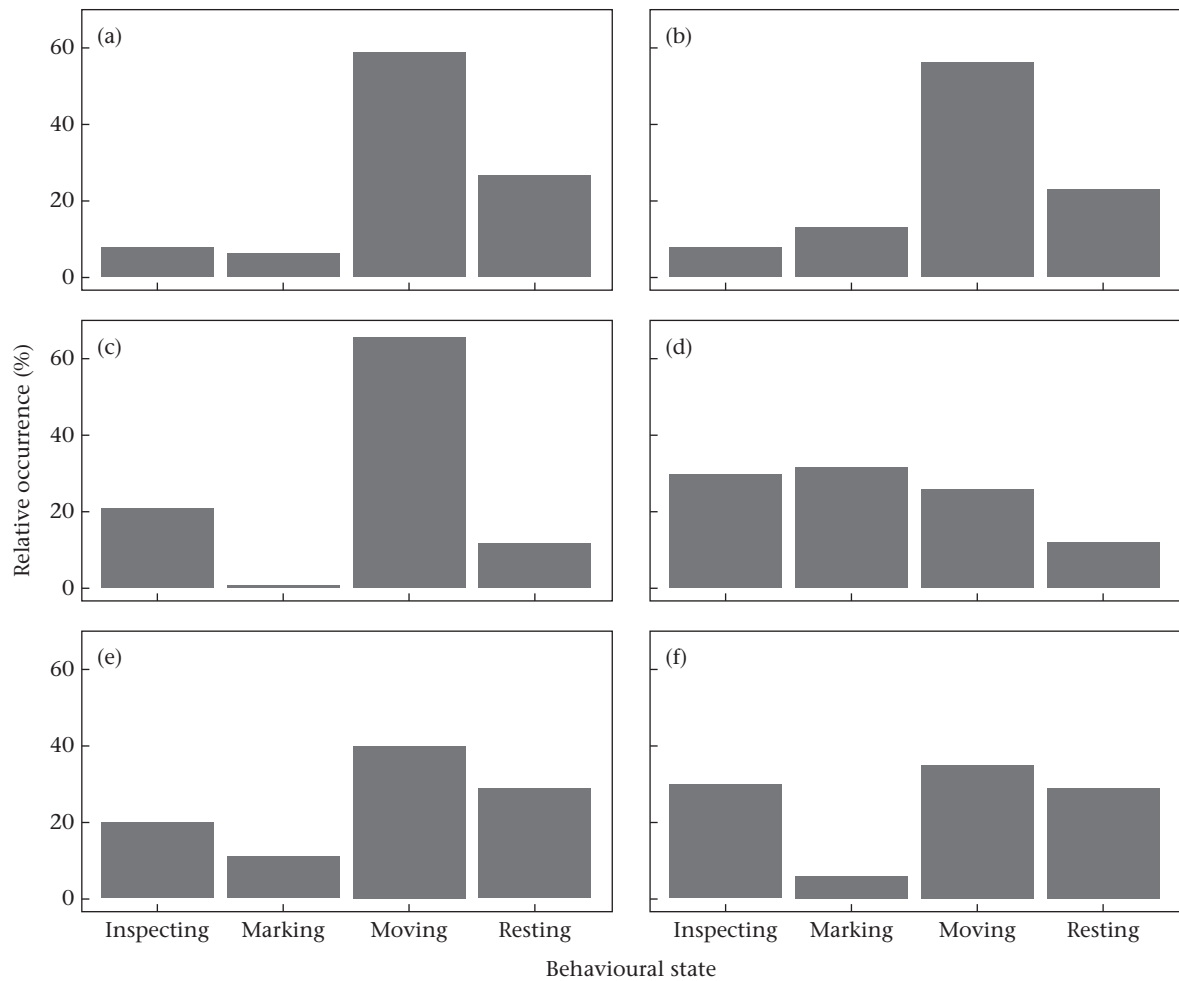
#### Social Network Analysis

Our network consisted of six subgroups, within which interactions between individuals were more common than with other individuals (Fig. 6). Each subgroup included both males and females (mean =  $3 \pm 1.3$  SD) individuals. Interactions were observed in 4% of all possible dyads of individuals, which reflects a decentralized network. Male M3 followed by a female (F2) and a male (M1) had the highest node degrees and node betweenness centralities (Appendix Table A2). The assortativity coefficient was  $-0.14$ , indicating a tendency of nodes to connect with nodes of the opposite sex, but this was not significant ( $t$  test:  $t_{26} = -0.74$ ,  $P = 0.46$ ). Male and female leopards were equally likely to precede (ANOVA:  $F_{1,23} = 0.04$ ,  $P = 0.849$ ) or to follow (ANOVA:  $F_{1,23} = 1.70$ ,  $P = 0.205$ ) visits in an interaction.

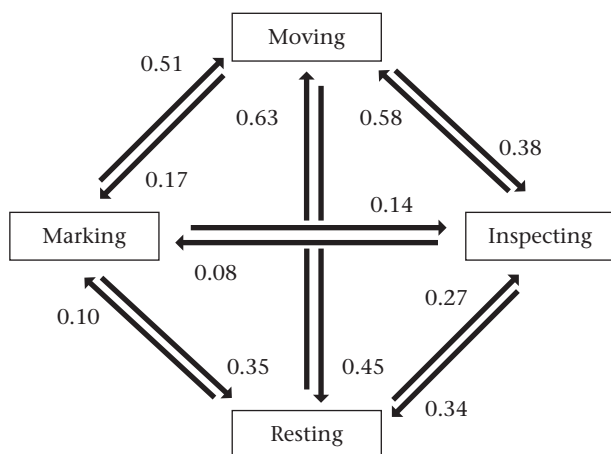
## DISCUSSION

Olfactory communication is critical for population regulation and social organization, in particular of solitary species (Johnson, 1973; Ralls, 1971). Our findings bolster growing evidence that solitary species support structured social networks, in which social units are formed and maintained through regular intraspecific and behavioural interactions (Dalerum, 2005; Elbroch et al., 2017; Graw et al., 2019; Lühns & Kappeler, 2013; Quaglietta et al., 2014; Stenhouse et al., 2005). Social units, also referred to as spatial groups (Macdonald, 1983), of solitary species represent dispersed social systems, where home range overlap of members of the same unit is variable and greatly relaxed unlike gregarious species (Müller & Thalmann, 2000). Members of the same social unit are





**Figure 2.** Activity budgets of solitary leopards at marking sites in relation to conspecifics. (a) Female preceded by another female; (b) male preceded by a female; (c) female preceded by a male; (d) male preceded by another male; (e) female with no interaction; (f) male with no interaction.

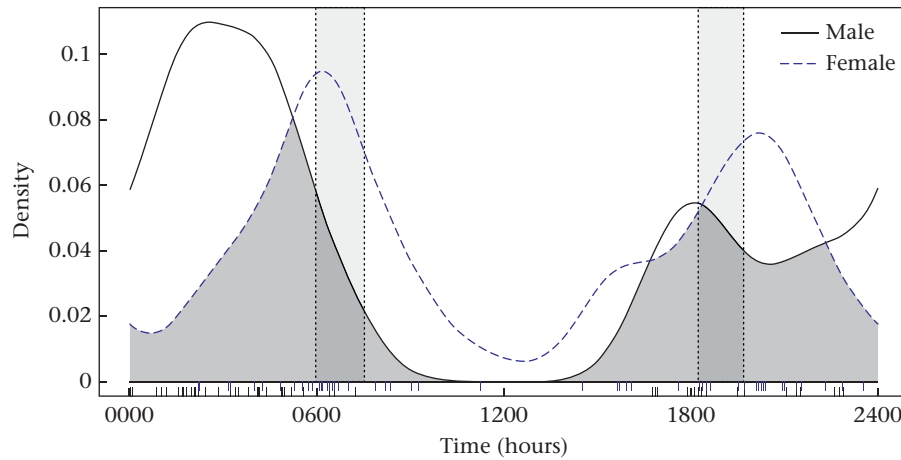


**Figure 3.** Kinematic diagram showing the sequence of behaviours displayed by solitary leopards at marking sites. Values indicate the transitional frequency, which is the proportion of times one behaviour followed another behaviour during the same visit.

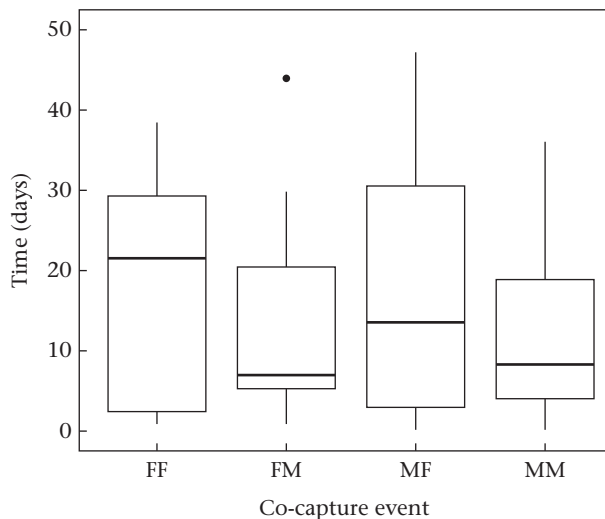
generally more tolerant towards each other (Wiens & Zitzmann, 2003), which for leopards may be attributed to a dear-enemy effect in males (Rafiq et al., 2020) and to natal philopatry in females (Fattebert et al., 2015, 2016).

Our results reveal the underlying structure of leopard sociality and complement previous research elucidating the sociobiology of solitary species. Social units have also been identified in solitary species such as the slow loris, *Nycticebus coucang*, and white-footed sportive lemur, *Lepilemur leucopus* (Dröscher & Kappeler, 2014; Wiens & Zitzmann, 2003), whereas other presumably solitary species aggregate during feeding events (Elbroch et al., 2017; Twining & Mills, 2021), are only solitary when foraging (Dorning & Harris, 2017; Graw et al., 2019; Owens & Owens, 1978), or display significant flexibility in their sociality (Rostain et al., 2004; Stenhouse et al., 2005).

Carnivore societies can be diverse and are largely determined by the distribution of resources (Macdonald, 1983). We documented leopards to be exclusively solitary outside a reproductive context, concordant with earlier research showing that leopards did not aggregate, but staggered activities in different parts of shared ranges (Bailey, 2005; Stander et al., 1997). Conditions for group formation in felids relate to prey aggregation and concentrated access to females as seen in lions, cheetahs and recently also in jaguars (Caro, 1994; Jędrzejewski et al., 2022; Mosser & Packer, 2009). Dense habitat and intraguild competition may restrict leopard sociality (Stander et al., 1997), yet in high-density systems, leopards appear to prioritize access to mating partners over monopolizing home ranges (le Roex et al., 2022b). This relaxed territoriality suggests relatively frequent social interactions and



**Figure 4.** Leopard activity patterns at marking trees for males and females. The vertical dotted lines denote the earliest and latest sunrise and sunset times throughout the year. The dark grey area below the curves indicates the overlap in activity patterns.



**Figure 5.** Time (days) between consecutive female–female (FF), female–male (FM), male–female (MF) and male–male (MM) co-capture events at camera traps. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circle is an outlier.

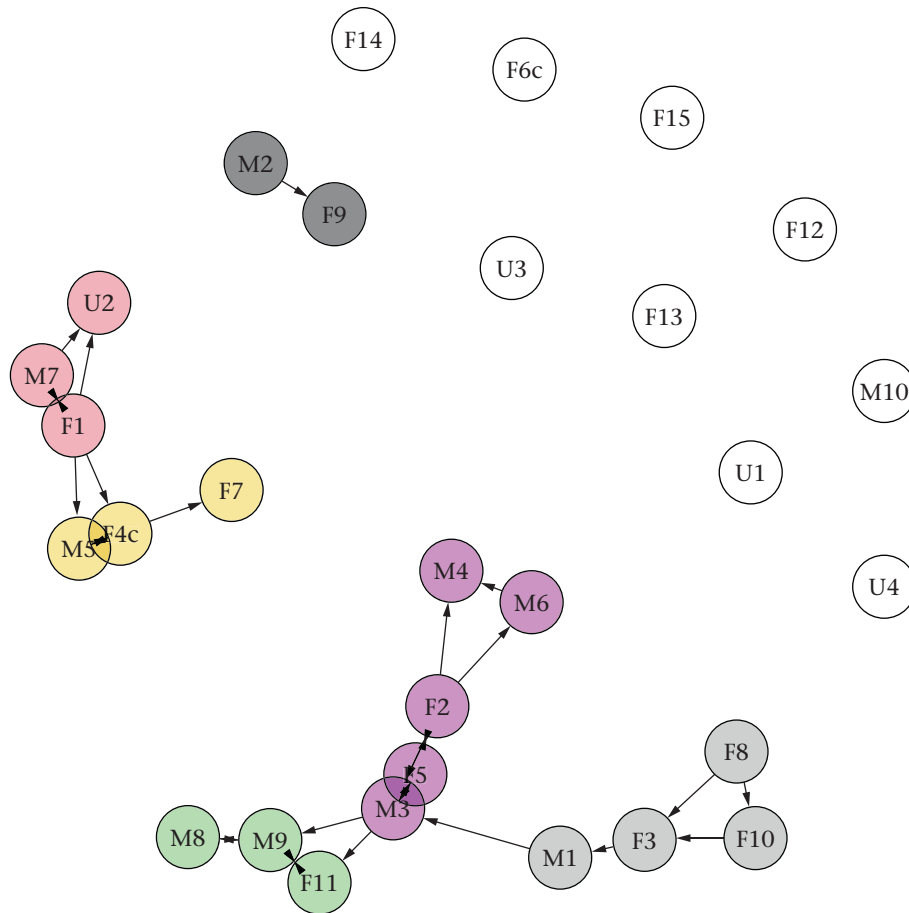
high conspecific tolerance among leopards which warrants further investigation.

Social units within our leopard population consisted of up to five leopards and included individuals from different age and sex classes. Kinship structure could not be determined as we lack genetic measures of relatedness. We also lack detailed trait-based information, but individuals with a high node degree and betweenness centrality were likely to be residents and displayed interactions outside their social unit. These individuals are key for group stability and improve cohesion among social units (Lusseau & Newman, 2004; Wey et al., 2008). Male M3, for example, was a large adult with a permanent established territory. Territories of adult male leopards overlap with the home ranges of multiple females and males actively demarcate territory boundaries (Fattebert et al., 2016; Rafiq et al., 2020). The removal of central individuals may disrupt social structure, with anthropogenic pressures being a major threat towards social stability (Belton et al., 2018; Bond et al., 2021; Parsons et al., 2009; Shannon et al., 2013). Central individuals are naturally replaced following territorial disputes (Polis, 1981), yet displacement through lethal management may have adverse

effects on social structure and consequently demography of large felids (Davidson et al., 2011; Maletzke et al., 2014; Packer et al., 2011; Peebles et al., 2013; Spong et al., 2000; Teichman et al., 2016). Species management therefore requires careful consideration of social structure as population declines may be masked by source–sink dynamics and mesopredator release (Packer et al., 2009; Robinson et al., 2008).

The exchange of information occurred at communal marking sites through various behavioural mechanisms that were similar to those described in other solitary felids (Allen, Wittmer et al., 2016). Individuals behaved and responded differently depending on sex, serving mainly territorial and reproductive purposes (Johnson, 1973; Ralls, 1971). Asserting dominance and claiming territories may be prioritized by male leopards as demonstrated by the increase in frequency of marking behaviours we documented during male interactions. These results tie into recent evidence from Botswana where male leopards were more likely to advertise and inspect areas where they were more likely to encounter same-sex strangers (Rafiq et al., 2020). Male individuals of various felid species frequently visit marking sites for territorial marking and information gathering (Cornhill & Kerley, 2020; Smith et al., 1989; Vogt et al., 2014; Wooldridge et al., 2019), while in some species, such as the puma, advertisement for mates may overshadow the importance of deterring competitors and claiming territories (Allen, Yovovich et al., 2016). We would expect the latter to occur in high-density leopard systems with relaxed territoriality (le Roex et al., 2022b). In our system, male leopards were less responsive towards females in terms of behavioural display at marking sites yet returned quickly following female visits. Female advertisement was generally low, but frequent use of marking sites and increased frequency of inspecting behaviour during male interactions suggest that female leopards use marking sites to assess potential mates as also observed in pumas (Allen et al., 2014). This may relate to observations of extralimital mating excursions by female leopards to undermine female monopoly (le Roex et al., 2022b). There was little indication of same-sex territoriality between females, which supports the resident fitness hypothesis in matrilineal kin clusters (Fattebert et al., 2015, 2016).

Intersexual range overlap allowed for frequent sharing of marking sites, while same-sex interactions may have occurred along territory boundaries or between resident and transient individuals. Shared use of space was facilitated through temporal segregation between the sexes, which could protect females with cubs from infanticidal males (Balme & Hunter, 2013; Odden & Wegge, 2005; Steyaert et al., 2013). Temporal segregation



**Figure 6.** Social network of leopards inferred from uniquely identified individuals based on camera trap data. Nodes depict individuals, edges represent interactions and subgroups are coloured. F = female, M = male, U = unknown sex, F#c = female with accompanying cubs.

between male and female leopards has also been attributed to differences in predation pressures (Havmøller et al., 2020), but this hypothesis is unlikely in our study system where no other dominant predators are present.

Solitary species, such as the leopard, employ adaptive and varied mechanisms to structure and maintain sociospatial systems. Our findings reflect such mechanisms and show novel insights into patterns of intraspecific co-occurrence in a solitary carnivore. Further research is needed to explore more fine-scale behavioural responses to olfactory cues as well as to investigate behavioural plasticity among individuals. This requires adjustments to study design and ideally an experimental framework, which will enable additional insights into the social lives of solitary species.

#### Author Contributions

Conceptualization: S.V., E.F. and B.C.; Data collection: E.F. and L.M.; Data analysis: S.V., E.N. and E.F.; Writing – Original draft: S.V.; Writing – Review & editing: all authors; Project administration & Funding acquisition: L.M. All authors approved publication.

#### Data Availability

The data that support the findings of this study are available in the open repository Zenodo: <https://doi.org/10.5281/zenodo.7337572>.

#### Declaration of Interest

The authors have no competing interests to declare.

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## Appendix

**Table A1**  
Leopard ethogram at marking sites

Behavioural state and ecological function	Behaviour	Definition
Marking	Defecating	Discharging faeces on the ground or tree stem
	Rubbing	Rubbing any part or entire length of body against tree stem
	Scratching	Gripping tree stem or branches with front claws
	Urine spraying	While standing with tail raised vertically, spraying urine backwards against tree stem or on the ground
Moving	Away	Moving away from tree
	Climbing	Ascending or descending tree
	Towards	Moving towards tree
Inspecting	Investigating	Showing attention to specific stimulus by sniffing or pawing at it
Resting	Climbed	Resting on tree branch
	Sitting	Resting in upright position, with the hindlegs flexed and resting on the ground, while front legs are extended and straight
	Standing	Upright position and immobile, with all four paws on the ground and legs extended
Social	Lying down	Resting while body is on the ground in a horizontal position, including on its side, back, belly
	Reproduction	Sniffing the genital part or tail of other
	Kin	Mother interacts with cub in playful manner

**Table A2**  
Summary of network characteristics

ID	Sites captured	Subgroup	Node degree	Betweenness centrality
F1	2	A	5	3
F2	2	B	6	21
F3	2	C	3	18
F4c	2	D	4	3
F5	1	B	4	0
F6c	1	–	0	0
F7	1	D	1	0
F8	1	C	2	0
F9	1	E	1	0
F10	1	C	2	0
F11	2	F	3	0
F12	1	–	0	0
F13	1	–	0	0
F14	1	–	0	0
F15	1	–	0	0
M1	1	C	2	24
M2	1	E	1	0
M3	4	B	7	34
M4	1	B	2	0
M5	1	D	3	0
M6	3	B	2	0
M7	1	A	3	0
M8	1	F	2	0
M9	1	F	5	9
M10	2	–	0	0
U1	1	–	0	0
U2	1	A	2	0
U3	1	–	0	0
U4	1	–	0	0
Mean ( $\pm$ SD)	1.38 ( $\pm$ 0.73)	3.33 ( $\pm$ 1.3) IDs/subgroup	2.07 ( $\pm$ 1.98)	3.86 ( $\pm$ 8.79)

F = female, M = male, U = unknown sex, F#c = female with accompanying cubs.