Behavioral Ecology, 2026, 37, arag092
https://doi.org/10.1093/beheco/arag092
Published: 28 July 2026
Original article

Maternal status of female leopards drives spatio-temporal interactions between the sexes

Taisiia V. Marchenkova [1,2,3*], Alexander N. Reebin[4], Anna A. Yachmennikova[2], Dina S. Matiukhina[1], Ekaterina Y. Blidchenko[1], Darya A. Maksimova[1], Viktor B. Storozhuk[1], Alexey S. Titov[1], Claudio Sillero-Zubiri[3], and Mohammad S. Farhadinia[5]

[1]Federal State Budgetary Institution Joint Directorate of Kedrovaya Pad' State Biosphere Nature Reserve and Land of the Leopard National Park, Ministry of Natural Resources and Environment of the Russian Federation, 2 Dalzavodskaya street, 690001, Vladivostok, Primorsky Krai, Russia

[2]Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, 33 Leninsky Prospect, 119071, Moscow, Russia

[3]Wildlife Conservation Research Unit, Department of Biology, University of Oxford, Life and Mind Buildingm South Parks Road, OX13EL, Oxford, United Kingdom

[4]ANO 'Wildlife Conservation Society', 17A Aleutskaya street, 690091, Vladivostok, Russia

[5]Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation, University of Kent, Canterbury, CT27NZ, Kent, United Kingdom

*Corresponding author: Taisiia V Marchenkova, Federal State Budgetary Institution Joint Directorate of Kedrovaya Pad' State Bioshere Nature Reserve and Land of the Leopard National Park, Ministry of Resources and Environment of the Russian Federation, 2 Dalzavodskaya street, 690001, Vladivostok, Primorsky Krai, Russia, Email: marchenkova.taisia@gmail.com
Handling Editor: Aliza le Roux

Intraspecific interactions in solitary carnivores are difficult to study and often overlooked, yet they are fundamental to understanding species ecology and informing conservation. Using 11,290 independent photographic events of 358 individually recognized Far Eastern leopards (*Panthera pardus orientalis*) collected over a decade (2014 to 2023), we investigated the drivers of social interactions in this putative formally solitary felid. We tested 3 non-mutually exclusive hypotheses concerning the co-occurrence and temporal activity patterns of different demographic classes: adult males, lone females without cubs, and females with cubs. Applying recurrent event analysis and diel activity overlap analysis, we found that inter-sexual spatial associations were strongly mediated by female reproductive status. Females with cubs consistently avoided locations recently used by adult males, a pattern consistent with infanticide avoidance. Conversely, lone females were significantly attracted to male-occupied areas, likely to maximize mating opportunities. No significant attraction or avoidance was detected between lone females and females with cubs. All demographic groups exhibited predominantly diurnal activity patterns with high temporal overlap, suggesting that spatial avoidance, rather than temporal segregation, is the primary mechanism mediating male-female interactions. Our findings reveal unexpected flexibility in the social behavior of a solitary carnivore and demonstrate that female maternal status is a key driver of these dynamics. This nuanced understanding provides a critical, empirically based framework for evaluating the suitability of different male-female combinations in future translocation and population restoration efforts for this critically endangered felid.

Keywords Amur leopard, camera traps, diel activity, *Panthera pardus*, recurrent event analysis, spatiotemporal interaction

Introduction

Population structure emerges from repeated intraspecific interactions that range along a continuum from avoidance to attraction, with interaction intensity often being density-dependent (Begon et al. 2014; Rockwood 2015; Clutton-Brock 2016). These interactions influence demographic traits—such as reproductive success (Durant 2000), sex-age structure (Semeniuk et al. 2011), and the architecture of social networks (Verschueren et al. 2023)—which are consistently shaped by sex and age, with different classes occupying distinct social roles in terms of connectivity, homophily, and network position (Croft et al. 2008; Makagon et al. 2012; Shizuka and Johnson 2020). While the formation of social networks is well-studied in group-living species, for cryptic or solitary animals this process remains largely unknown.

Many large carnivore species are described as "solitary," implying that individuals move asynchronously from conspecifics and engage in only infrequent, brief social interactions (Logan and Sweanor 2001; Kappeler and van Schaik 2002), with direct contact largely confined to mating or territorial disputes (López-Bao et al. 2008; Mattisson et al. 2013). Nonetheless, recent research has revealed that intraspecific interactions in felids are more complex than previously recognized, with significant implications for cub survival (Packer and Pusey 1983; Jhala et al. 2019), population spatial structure (Liu et al. 2024), and foraging behavior (Elbroch and Quigley 2017).

Despite spending most of their lives in solitude, individuals of solitary species nonetheless experience periodic social encounters with conspecifics, primarily driven competition for resources, contact

Received: August 20, 2025. **Revised:** May 10, 2026. **Accepted:** May 22, 2026.

with related individuals, and reproduction. Competition arises from resource distribution, influencing temporary tolerance or home range overlap depending on population density and territoriality (Ferreras et al. 1997; Macdonald and Johnson 2015). In contrast, contact between relatives is characterized by mutual tolerance among kin, which can enhance inclusive fitness (Hamilton 1964; Macdonald 1983). Reproductive dynamics also create conditions for interaction: in fragmented habitats, for instance, the distribution of potential mates often necessitates extensive home range overlap and a relaxation of strict territorial defense, facilitating contact without persistent aggression and enabling successful mating. Recent studies underscore the complexity of these systems. For example, male pumas (*Puma concolor*) form hierarchical social networks in which tolerance is best explained by direct reciprocity (Elbroch and Quigley 2017), and some male felids form temporary hunting coalitions (Guilder et al. 2015). Such examples demonstrate that behaviors traditionally categorized under competition, kinship, or mating can in fact be dynamic and highly context-dependent.

We addressed this gap by analysing a decade-long intensive camera-trapping survey of the main nucleus of the Far Eastern (Amur) leopard (*Panthera pardus orientalis*) in the Russian Far East (Marchenkova et al. 2026). Recent extensive conservation efforts have led to a remarkable recovery of this population, both in size and geographic extent across the Russia–China borderlands, with an estimated population of ~150 individuals (Stein et al. 2025), a substantial increase from fewer than 40 in the late 1990s (Pikunov et al. 2009). This recovery provides a unique opportunity to investigate the intraspecific interactions in a formerly critically endangered felid population.

Leopards exhibit variable patterns of intraspecific interactions across their range. In Namibia, for example, individuals displayed temporal segregation in both intra- and inter-sexual co-occurrence (Verschueren et al. 2023), yet no evidence of spatial or temporal avoidance of males by lone females or females with cubs was found. Conversely, Persian leopards (*Panthera pardus tulliana*) showed distinct differences in activity timing (Rouse et al. 2021). One key driver of such avoidance is infanticide. Infanticide by males is a well-documented behavior in large felids (Singh et al. 2014; Tortato et al. 2017; Jhala et al. 2019), including leopards, and constitutes a critical factor shaping social organization and spatial patterns. In African leopard populations (*Panthera pardus pardus*), infanticide is a primary cause of cub mortality and is strongly linked to male reproductive strategy (Balme and Hunter 2013). This behavior creates selective pressure for mothers to adopt counter-strategies, including spatial avoidance of potentially infanticidal males, polyandrous mating, and maternal aggression (Palombit 2015). In contrast, lone females without cubs may exhibit neutral spatiotemporal interactions with males or active attraction during the mating period, reflected in changes in spatial behavior, such as expansion of their home range (Lovallo and Anderson 1996; Rozhnov et al. 2015).

Across their global range, leopards are generally described as crepuscular, nocturnal (Odden and Wegge 2005; Martins and Harris 2013; Havmøller et al. 2020), or cathemeral (Rouse et al. 2021), even in the presence of larger apex predators such as tigers (*Panthera tigris*) (Carter et al. 2015) and lions (*Panthera leo*) (Rafiq et al. 2020). However, how temporal activity patterns differ among leopard reproductive groups remain understudied, particularly in populations experiencing low anthropogenic pressure. Moreover, activity patterns may vary with maternal status, as demonstrated in pumas (Allen et al. 2025).

We formulated 3 hypotheses to investigate intraspecific interactions in the Far Eastern leopard (*P. p. orientalis*):

H1: Infanticide avoidance. Given that infanticide is a major source of natural mortality in leopards (Balme and Hunter 2013), we predicted that females accompanied by cubs would exhibit spatial and temporal avoidance of adult males, and potentially also of lone females due to reproductive competition (Clutton-Brock and Huchard 2013).

H2: Breeding attraction. In light of recent conservation efforts across the subspecies' range in Russia and China, the leopard population is currently in a recovery phase (Vitkalova et al. 2018). We therefore anticipated high spatial and temporal co-occurrence between lone females and adult males, particularly during peak breeding months, reflecting mating opportunities in a recovering population.

H3: Temporal segregation. We hypothesized that adult males and lone females would exhibit the diel activity patterns typically reported for leopards across their global range—namely, crepuscular, nocturnal, or cathemeral activity (Odden and Wegge 2005; Martins and Harris 2013; Havmøller et al. 2020; Rouse et al. 2021). In contrast, we predicted that females with dependent cubs would shift their activity toward greater diurnality, thereby reducing spatiotemporal overlap with potentially infanticidal males.

Materials and methods

Study area

This study was conducted in the Kedrovaya Pad State Nature Biosphere Reserve, the Land of the Leopard National Park, and its buffer zone (hereafter, the study area collectively referred to as LLNP) (Fig. 1). Covering a total area of 3,620 km^2, this region is situated in the south-west of Primorsky Krai in the Russian Far East, along the border with the Chinese provinces of Jilin and Heilongjiang (42.54 to 43.73° N and 130.43 to 131.79° E). The terrain is characterized by low mountains with elevations not exceeding 1,000 m, and features frequent and pronounced changes in elevation, resulting in rugged topography. The climate is temperate, influenced by continental winds in winter and eastern monsoons in summer. Winters experience limited snowfall, with southern slopes often becoming snow-free within 2 to 3 d after a snowfall. In the southern portion of the study area, snow cover is frequently entirely absent. Mean annual precipitation is 715 mm, the majority of which falls during the summer months. The mean annual temperature is +5.3 °C.

The landscape is dominated by mixed stands of coniferous, coniferous–deciduous, and broad-leaved forests, interspersed with small patches of woodland and meadows. Dominant tree species include Mongolian oak (*Quercus mongolica*), Korean pine (*Pinus koraiensis*), Manchurian fir (*Abies holophylla*), castor aralia (*Kalopanax septemlobus*), various maple species (*Acer* spp.), and other broad-leaved taxa (Krestov and Verkholat 2003). Alongside the Amur tiger, leopards act as apex predators within the region. Other mammalian carnivores and mesomammals present include the brown bear (*Ursus arctos*), Asiatic black bear (*Ursus thibetanus*), leopard cat (*Prionailurus bengalensis*), yellow-throated marten (*Martes flavigula*), Asian badger (*Meles leucurus*), raccoon dog (*Nyctereutes procyonoides*), and red fox (*Vulpes vulpes*). There are no human settlements within the

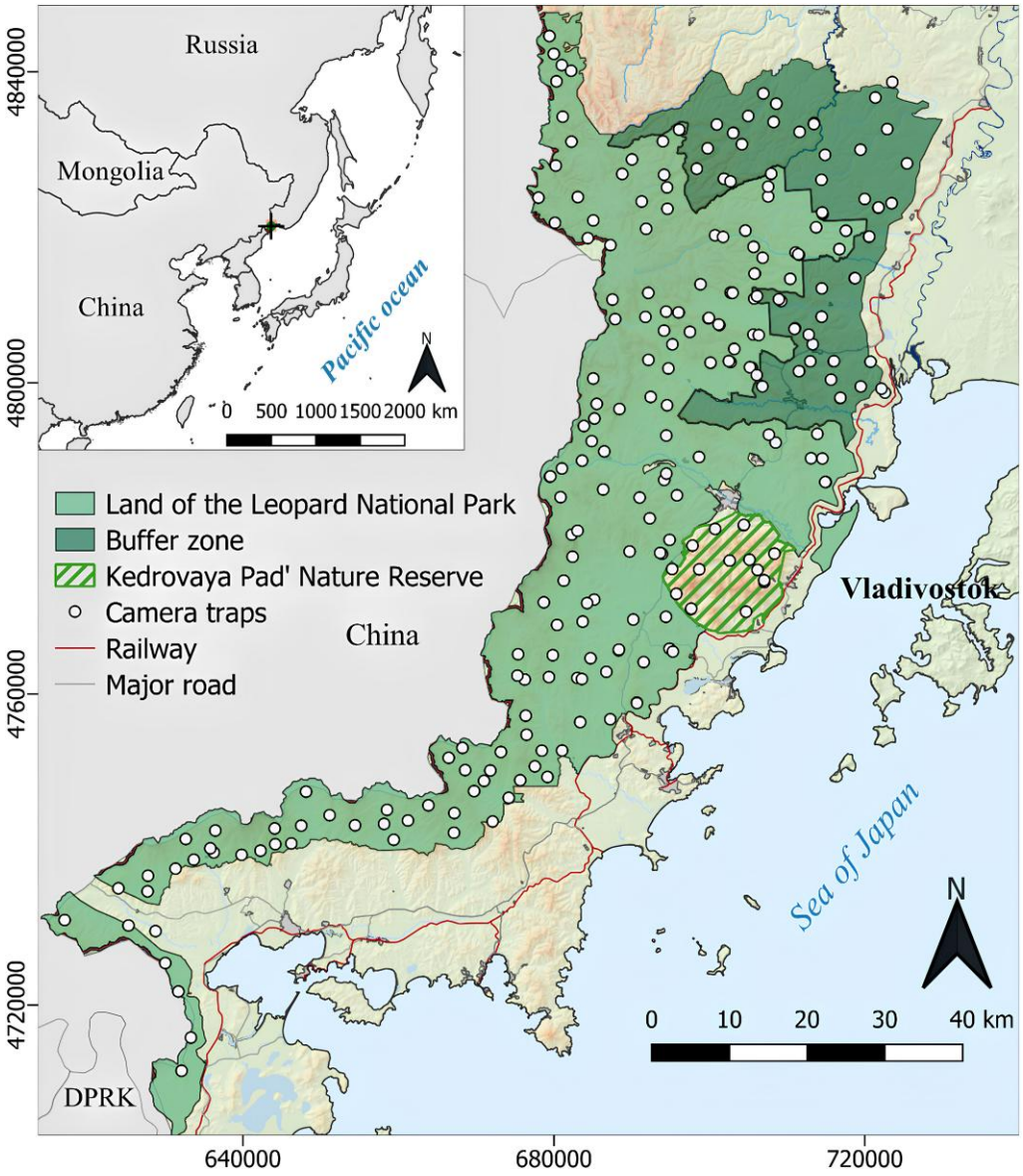

Figure 1 Study area with camera trap network in the Kedrovaya Pad Nature Reserve, the Land of the Leopard National Park, and its buffer zone, Russia (the study area collectively referred to as LLNP).

boundaries of LLNP. Agricultural activity and livestock grazing are absent within the park, with the exception of occasional livestock incursions from border villages.

Data collection

Camera traps were deployed across the LLNP from 2014 to 2023. Monitoring was conducted annually using a permanent network of camera stations distributed throughout the study area. The area is bisected by an international border control fence running parallel to the Chinese border at a distance of 5 to 20 km, creating 2 distinct zones in which camera trap stations operated under different regimes, as described below.

Border zone

This zone comprises the area between the border control fence and the international border with China. Camera traps in this zone operated continuously throughout the year, with batteries and memory cards replaced biannually.

Unrestricted zone

This zone encompasses the remainder of LLNP. Camera traps in this area were deployed only during the winter–spring period. Installation commenced in October within the reserve, in November within the national park, and after mid-January in the buffer zone, following the closure of the hunting season for wild ungulates to minimize disturbance and prevent vandalism. All cameras in this zone were retrieved by May. This schedule ensured simultaneous operation of all cameras in both zones (*Border* and *Unrestricted*) for a minimum of 3 consecutive months (>90 d) each year.

A variety of camera trap models were used, including Reconyx PC900 and HF2 (Holmen, USA), Seelock Spromise S108 and S308 (Alexandria, Australia), Bushnell NatureView and Aggressor (Kansas,

Table 1 Summary of camera trap monitoring data in the the Kedrovaya Pad State Nature Biosphere Reserve, the Land of the Leopard National Park, and its buffer zone (total area referred to as LLNP), Russia, 2014 to 2023.

N	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	Total
# Camera trap stations	151	173	136	170	183	200	190	199	206	202	244
# Camera trap nights	30,552	32,455	29,397	37,418	42,594	44,485	44,703	45,423	45,989	45,562	398,578
# Camera trap stations with leopards	107	118	93	143	153	160	156	163	172	163	227
# Leopard photos	4,699	2,528	7,837	9,981	11,153	12,761	13,386	17,342	16,275	12,713	108,675
# Leopard independent captures	877	548	664	958	1,188	1,316	1,275	1,508	1,618	1,338	11,290

USA), ScoutGuard SG560K-8M and SG968K-10M (London, UK), and Browning BTC-7A and BTC-8E-HP4 (Alabama, USA). Detailed information on camera settings is provided in the Supplementary material S1. Most stations were equipped with 2 cameras positioned facing one another; the few exceptions were located in the border zone along forest roads. Cameras were attached to trees at a height of 45 to 50 cm and positioned 3 to 3.5 m from animal trails, ensuring that the infrared sensors were optimally placed. Trail sites along ridges and spurs, where the probability of animal detection was highest, were preferentially selected for installation. To ensure homogeneous spatial coverage of the entire study area, at least 1 camera station was placed within each 5 × 5 km grid cell (Fig. 1)—a cell size corresponding to the minimum estimated home range of a female leopard with cubs (Pikunov et al. 2003). The mean distance between neighboring camera stations was 2.9 km (±1.9 km SD).

The monitoring network expanded from 160 stations in 2014 to 210 stations in 2023 (Supplementary material S2). However, stations that were stolen, damaged by fire, or operational for less than 3 mo (in the unrestricted zone) or 9 mo (in the border zone) were excluded from the analysis. Consequently, the number of active stations ranged from 151 in 2014 to 202 in 2023, with the number of photographs obtained varying accordingly (Table 1).

Individual identification

For each capture, defined as an instance in which an individual or a group of individuals was photographed at a specific location and time—the clearest image was selected for individual identification. All captures were recorded in a Microsoft Access database. Each entry included the date and time of capture, station number and coordinates, estimated age of the individual, photographs of the right and left flanks, and any additional comments.

Age was estimated based on the individual's status at first sighting. If an individual was first recorded as a cub, its age was determined by comparison with a reference database of photographs of captive leopards of known age. For individuals first recorded as adults, age at first sighting was conservatively set to a minimum of 1 yr.

Individual identification was performed using ExtractCompare software (http://conservationresearch.org.uk/), which operates on data stored in the Microsoft Access database. For each photograph, key points on the animal's silhouette were manually marked—namely, the withers, the base of the tail, and the attachment points of the left and right shoulders and hips. A grid was then applied, and the spot pattern on the animal's flank was highlighted for subsequent comparison. ExtractCompare employs a semi-automated algorithm to compare these patterns against those of previously identified individuals, generating a list of the most similar candidates for final confirmation by a specialist.

For each identified individual, we compiled a comprehensive capture history that included the date, time, and location (station number and coordinates) of each sighting, along with the animal's sex, age, name, distinctive markings, and any joint detections with conspecifics. Sex was determined primarily by the presence of external genitalia or, for females, by the presence of dependent cubs. All captured leopards were classified into 5 categories: adult male, lone female, female with cubs, subadult, and unknown (the latter reserved for individuals for whom photograph quality precluded reliable classification). Females photographed alone but known to have cub(s) on the basis of images obtained before or after the capture in question were assigned to the "female with cubs" class, recognizing that cubs may have been present nearby but not detected by the camera. Subadult status was assigned only to individuals that had been previously recorded as cubs.

Analysis

All statistical analyses were performed in the R environment (R Core Team 2020). We assumed that leopard presence within the study area was unaffected by anthropogenic disturbance or prey availability, given that the site is characterized by minimal human impact—including an absence of major roads and settlements (see "Study area")—and supports sufficient prey resources for both leopards and tigers (Petrov et al. 2025). Accordingly, our analyses focused exclusively on intraspecific interactions among leopards.

We employed recurrent event analysis (Ferry et al. 2024) and diel activity analysis (Meredith and Ridout 2014) to investigate intraspecific interactions and their optimal spatiotemporal scales among 3 demographic classes of leopards: adult males, lone adult females, and females with cubs. Compared with other widely used approaches for assessing species interactions, such as multi-species occupancy modeling (Rota et al. 2016) or time-to-event analysis (Niedballa et al. 2019), recurrent event analysis offers several advantages. It is less sensitive to variation in relative abundance, incorporates multiple observations beyond the first detection of an animal, provides greater statistical power, and enables the analysis of non-linear temporal dynamics.

Intraspecific interactions

We implemented recurrent event analysis using piece-wise exponential additive mixed models (PAMMs; Bender et al. 2018; Ramjith et al. 2022; Ferry et al. 2024) to quantify how the occurrence of 1 leopard class influenced the subsequent occurrence of another. This framework allowed us to characterize the spatiotemporal scale of interactions using 2 complementary metrics: effect strength and effect duration, thereby capturing the directional nature of interactions.

All captures were categorized to estimate the dynamics of the visitation rate of 1 leopard class (hereafter, the "secondary species" in the

model) following the detection of another class (the "primary species"). Additional leopard classes not focal to a given model—including subadults, unclassified individuals, and whichever female class was not the target—were assigned to a "tertiary species" category to control for potential confounding effects from conspecifics. Captures of Amur tigers (*Panthera tigris altaica*) were also included in the "tertiary species" group, given their potential to influence leopard occurrence at a site. The specific recurrent event pairs analyzed for each combination are listed in Supplementary material S3. Capture data were transformed into a piece-wise exponential format using the "pammtools" package (Bender and Scheipl 2018), and models were fitted with the "ctrecurrent" package (Ferry et al. 2024). To identify a biologically meaningful time scale over which intraspecific interaction persistence could be detected, we tested a series of survey duration windows: 30, 20, 14, 10, 7, 5, and 3 d (Supplementary material S4). These durations were selected based on the initial period adopted by Ferry et al. (2024), with sequential reductions of approximately one-third until the minimum feasible data volume (3 d) was reached. For analyses involving lone females and females with cubs, a 5-d window was used, as insufficient data were available for shorter periods for these pair combinations.

From each fitted hazard function, we extracted 2 key metrics. Effect strength was calculated as the ratio of the peak hazard to the baseline hazard, where peak hazard represents the maximum estimated hazard during the interaction period, and baseline hazard was estimated as the mean hazard during the asymptotic phase (defined as the final quartile of the observation window). Effect duration was defined as the time required for the hazard to stabilize within 5% of the baseline level, providing an estimate of the temporal persistence of the interaction. All metrics were extracted automatically from PAMM outputs using custom R functions.

We fitted 3 sets of PAMMs, corresponding to the following dyadic combinations: (i) adult males and females with cubs, (ii) adult males and lone females, and (iii) lone females and females with cubs. For each combination, models were fitted in both directions, yielding 6 models in total:

(A-M1) Effect of adult males on the visitation rate of females with cubs.
(A-M2) Effect of females with cubs on the visitation rate of adult males.
(B-M3) Effect of adult males on the visitation rate of lone females.
(B-M4) Effect of lone females on the visitation rate of adult males.
(C-M5) Effect of lone females on the visitation rate of females with cubs.
(C-M6) Effect of females with cubs on the visitation rate of lone females.

In addition to the PAMM framework, we described patterns of joint detections, defined as instances where a lone female and an adult male were recorded at the same location within 10 min of one another on the same day. For each such event, we recorded the time and month to define the period of highest number of joint intersexual detections.

Diel activity patterns

We categorized the 24-h cycle into 3 distinct periods—twilight, daytime, and night—based on mean sunrise (07:02) and sunset (19:20) times specific to our study area. These times were derived from longitude and latitude coordinates using the "bioRad" package (Dokter et al. 2019). Twilight was defined as the 1-h intervals immediately preceding and following both sunrise and sunset. Consequently, daytime was designated as the period between 08:02 and 18:20, and night-time as the period between 20:20 and 06:02.

Diel activity patterns of leopards were classified according to the scheme proposed by Gomez et al. (2005): diurnal (<10% of detections at night), mostly diurnal (10% to 29% at night), crepuscular (50% of detections during dawn or dusk), nocturnal (≥90% at night), mostly nocturnal (70% to 89% at night); patterns falling outside these thresholds were classified as cathemeral.

To assess the relative use of each time period given its availability, we calculated Manly's selection ratio w_i (Manly et al. 2002):

$$w_i = o_i/\pi_i$$

where w_i is the selection ratio for the period i; o_i is the observed proportion of detections occurring in period i; π_i is the proportional length of period i relative to the total 24-h cycle. Values of $w_i > 1$ indicate selective use greater than expected by chance, whereas $w_i < 1$ indicates avoidance (Manly et al. 2002).

To examine seasonal variation in activity, we partitioned the data into 2 seasons: warm (April–October) and cold (November–March). These divisions were based on the average timing of sustained drops in daily temperature below freezing, the onset of persistent snow cover, and associated changes in day length.

Subadult individuals and those of unknown sex were excluded from all diel activity analyses. Activity distributions were estimated for the 3 demographic leopard classes (adult males, lone females, and females with cubs) using circular kernel density analysis (Meredith and Ridout 2014; Ogurtsov 2025). Capture times were first converted to radians, and a probability density curve was generated for each group.

Temporal overlap between activity distributions was quantified using the coefficient of overlapping Δ_4 (Meredith and Ridout 2014), with 95% confidence intervals (CIs) obtained from 1,000 bootstrap resamples. In addition, we applied Watson's 2-sample U^2 test to assess the homogeneity of circular distributions between pairs of leopard demographic classes (Jammalamadaka et al. 2021). All calculations were performed using the R packages "overlap" (Meredith and Ridout 2014), "circular" (Lund et al. 2017), and "chron" (James et al. 2020) packages.

Results

A total of 11,290 independent leopard captures were recorded within the LLNP between 2014 and 2023, with annual totals ranging from 548 to 1,618 (Table 2). Overall, we identified a total of 358 unique individuals (297 with both flanks, 31 with right and 30 with left, subsequently), including 110 males, 153 females, and 55 individuals of unknown sex. Among the identified females, 54 were documented with cubs. A total of 98 unique litters were recorded; in 83 of these cases (85.6%), the mother could be identified. In all remaining instances, cubs were photographed alone without the presence of the mother.

Of the 789 captures involving females with cubs, only 2 instances were recorded in which multiple families were detected at the same camera station within a 1-mo interval. Lone females were frequently detected at stations where a female with cubs had been photographed, with an average of 1.36 ± 0.62 (SD) lone females per station (range = 1

Table 2 Summary of captures and identified individuals of leopards from camera trap monitoring data for each year from 2014 to 2023 at the the Kedrovaya Pad State Nature Biosphere Reserve, the Land of the Leopard National Park, and its buffer zone (total area referred to as LLNP), Russia.

N		2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	Total
Leopard captures	Total	877	548	664	958	1,188	1,316	1,275	1,508	1,619	1,338	11,290
	Male	613	364	403	629	658	865	783	987	1,071	868	7,241
	Lone female	170	114	139	186	279	344	349	313	322	245	2,460
	Female with cubs	49	39	73	94	139	56	62	102	92	83	789
	Subadults	19	4	33	19	49	23	32	60	63	40	342
	Unknown	26	27	16	30	63	28	49	46	71	102	458
Identified individuals	Total	71	70	77	96	125	115	131	157	164	147	[a]
	Male	25	23	22	31	37	36	36	53	57	52	110
	Female	33	33	32	47	59	62	69	71	74	67	153
	Unknown	2	2	0	1	4	2	3	16	18	10	55
	Subadult	7	2	8	7	13	10	14	26	15	16	[a]
	Cub	11	10	18	15	22	12	16	13	17	15	[a]
	Families	6	6	10	8	13	9	10	11	12	13	98

[a]The total number of identified individuals of all ages, including separately for cubs and subadults across all years, is not provided. This omission is to prevent double-counting of individuals over the entire study period, as some animals transitioned between categories from 1 yr to the next (eg an individual first recorded as a cub would be registered as a subadult in the following year, and as an adult in the third year).

to 4). The number of males per camera trap station was 1.53 ± 0.62 (SD) (range = 1 to 5).

Intraspecific interactions

Across the full study period, the proportion of deviance explained by survey duration ranged from 0.02% to 8.58%, with the maximum explanatory power and the highest effect strength both observed for the 3-d survey window (Supplementary material S4: Table S1, Models S1 to S7; Fig. S2). Due to insufficient detection numbers for the male–female with cubs dyad, we were unable to fit yearly models for survey durations shorter than 20 d.

For females with cubs, co-occurrence with males was significantly reduced during the first 2 d following a male's visit (effect strength = 3.33, Table 3, Model A-M1). This indicates that the daily number of events per camera station was ~3 times higher on the second day following a male sighting compared with baseline (Table 3, Model A-M1; Fig. 2a). Lone females exhibited the opposite pattern: their visitation rate increased markedly within 1 d following a male detection, with an effect strength of 15.83, meaning the daily event rate per station was 15 times higher immediately after a male sighting relative to baseline (Table 3, Model B-M3; Fig. 2c). This pattern of attraction remained consistent across years (Supplementary material S4: Table S1, Models S10 to S19; Fig. S2).

In models where the male was treated as the secondary species (Models A-M2 and B-M4), a significant effect of time on male occurrence rate was detected following detections of both lone females (Table 3, Model B-M4; Fig. 2d) and females with cubs (Table 3, Model A-M2; Fig. 2b). This suggests that males are attracted to females irrespective of maternal status, although the effect strength was greater following lone female sightings (effect strengths: 14.87 and 39.35 for females with cubs and lone females, respectively). No significant effect was detected in either direction between lone females and females with cubs (Table 3, Models C-M5 and C-M6; Fig. 2e and f).

A total of 71 paired male–female detections were recorded. The temporal interval between lone female and male captures for paired detections ranged from 1 to 10 min in 76% of cases ($n = 54$), with the remaining 24% ($n = 17$) being simultaneous detections. In most paired captures (77.4%), the male was photographed before the female; in 22.6% of cases, the female preceded the male. Paired male–female detections occurred throughout the year, with a higher proportion recorded in winter ($n = 47$, 66%) compared with summer ($n = 24$, 34%). Within the border zone, where year-round monitoring provided a longer observation period, paired detections peaked between January and March, with a secondary, smaller peak in October (Fig. 3).

Eleven individuals were detected in association with multiple opposite-sex conspecifics within a 2-mo period. These included 2 females each photographed with 2 different males, 8 males each photographed with 2 different females, and 1 male photographed with 3 different females. We also documented 5 mating events in front of camera traps, comprising captures in November ($n = 2$), January ($n = 1$), February ($n = 1$), and April ($n = 1$) (Supplementary material S4: Fig. S3).

Diel activity patterns

Overall, 54.5% of adult leopard captures occurred during daytime ($n = 5,716$), followed by twilight (26.9%, $n = 2,818$) and night (18.6%, $n = 1,956$). All 3 demographic classes, adult males, lone females, and females with cubs, exhibited broadly similar diel activity patterns, with daytime activity ranging from 51.9% in males to 66.4% in females with cubs (Table 4). For all groups, the Manly selectivity index w_i exceeded 1 for daytime and twilight periods, indicating preferential use, and fell below 1 for night-time, indicating avoidance (Table 4). This predominantly diurnal pattern was consistent across both warm and cold seasons, although daytime activity was more pronounced during the summer months (Fig. 4).

Lone females and males each displayed 2 distinct activity peaks: 1 shortly after sunrise and another just before sunset. In contrast, females with cubs exhibited a single major peak spanning the period between sunrise and midday (Fig. 5). This general pattern remained stable across seasons (Fig. 5) and years (Supplementary material S4: Fig. S4).

Pairwise temporal overlap between activity distributions was high for all demographic combinations. The coefficient of overlapping Δ_4 between lone females and males was 0.93 (95% CI: 0.91 to 0.94), although Watson's 2-sample test indicated a significant difference between their activity curves ($U^2 = 1.38$, $P < 0.01$). Overlap between females with cubs and males was also high ($\Delta_4 = 0.84$, 95% CI: 0.79 to 0.86), with a significant difference detected between their distributions ($U^2 = 0.85$, $P < 0.01$). In contrast, the activity curves of lone females and

Table 3 Summary of recurrent event analysis using PAMMs output results for different pairwise combinations of leopard demographic classes based on overall data from 2,014 to 2,023 camera trap survey in the the Kedrovaya Pad State Nature Biosphere Reserve, the Land of the Leopard National Park, and its buffer zone (total area referred to as LLNP), Russia. Bold values highlight statistically significant results ($P < 0.05$).

Set	*N*	Direction			Survey duration (days)	No. of obs.	Peak hazard value	Baseline hazard value	Effect strength	Effect duration	Model output				
		Primary group	Secondary group	Tertiary group							Estimate	SE	edf	*P*-value	Deviance explained (%)
A	M1	Male	Female with cubs	Lone female; subadults; unknown individuals; tigers	3	26	0.11	0.04	3.33	2.94	−2.56	0.20	6.87	**<2e−16**	**8.58**
	M2	Female with cubs	Male	Lone female; subadults; unknown individuals; tigers	3	35	0.56	0.04	14.87	2.13	−2.60	0.17	5.28	**0.001**	**5.79**
B	M3	Lone female	Male	Female with cubs; subadults; unknown individuals; tigers	3	298	1.25	0.08	15.83	0.65	−2.58	0.06	8.60	**<2e−16**	**4.14**
	M4	Male	Lone female	Female with cubs; subadults; unknown individuals; tigers	3	228	1.78	0.04	39.35	0.18	−2.92	0.07	8.77	**<2e−16**	**6.76**
C	M5	Female with cubs	Lone female	Males; subadults; unknown individuals	5	17	0.21	0.03	7.06	4.71	−2.52	0.26	1.75	0.11	2.18
	M6	Lone female	Female with cubs	Males; subadults; unknown individuals; tigers	5	25	0.10	0.04	2.66	2.02	−2.99	0.32	1.53	0.38	2.80

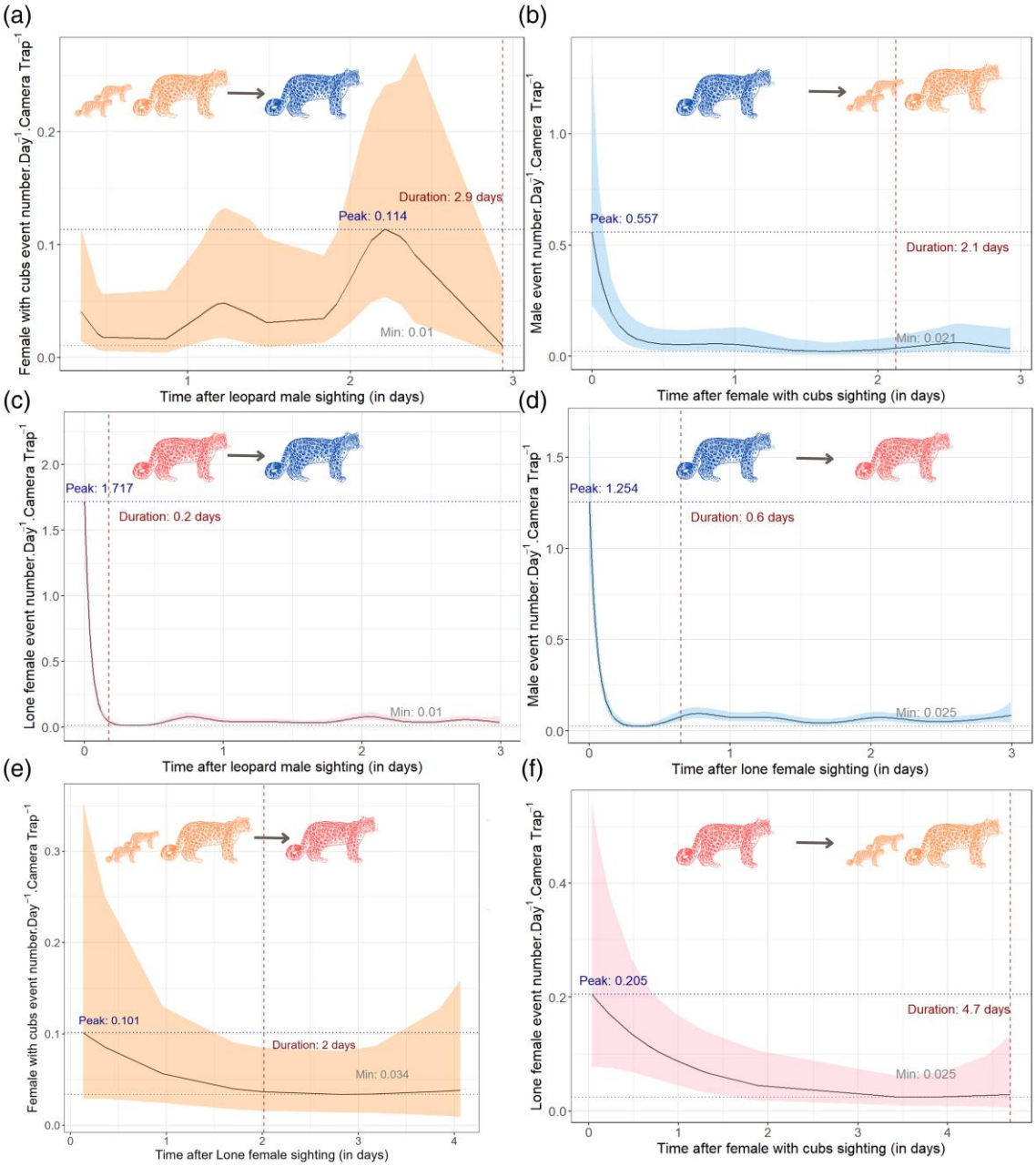

Figure 2 Temporal dynamics of the visitation rate of different classes of Far Eastern leopards based on overall study period in the Kedrovaya Pad State Nature Biosphere Reserve, the Land of the Leopard National Park, and its buffer zone (total area referred to as LLNP) for 2014 to 2023 by recurrent event analysis using PAMMs predictions: (a) female with cubs visitation rate after adult male sighting, (b) adult male visitation rate after female with cubs sighting, (c) a lone female visitation rate after the male sighting, (d) adult male visitation rate after lone female sighting, (e) female with cubs visitation rate after lone female sighting, (f) a lone female visitation rate after female with cubs sighting. (3-d survey duration for a to d, 5-d survey duration for e and f). Vertical dashed line shows duration of interaction effect, horizontal dashed line—peak of visitation rate. Graphical representation of leopards with arrow indicates follow after some time of individual after another.

females with cubs did not differ significantly ($U^2 = 0.15$, $P > 0.05$), and their overlap was similarly high ($\Delta_4 = 0.90$, 95% CI: 0.86 to 0.93).

Discussion

Our findings reveal a distinctive pattern of inter-sexual co-occurrence in Far Eastern leopards, partially mediated by the presence of adult males. Females with cubs consistently avoided locations recently visited by adult males, whereas lone females exhibited a clear attraction to those same locations. These contrasting responses underscore the importance of maternal status in shaping female social interactions and highlight the flexibility of social behavior in a species traditionally described as solitary. Equally important, Far Eastern leopards exhibited predominantly diurnal activity throughout the years and across seasons, a pattern that contrasts with the crepuscular, nocturnal, or cathemeral activity reported for other leopard subspecies (Odden and Wegge 2005; Carter et al. 2015; Van Cleave et al. 2018).

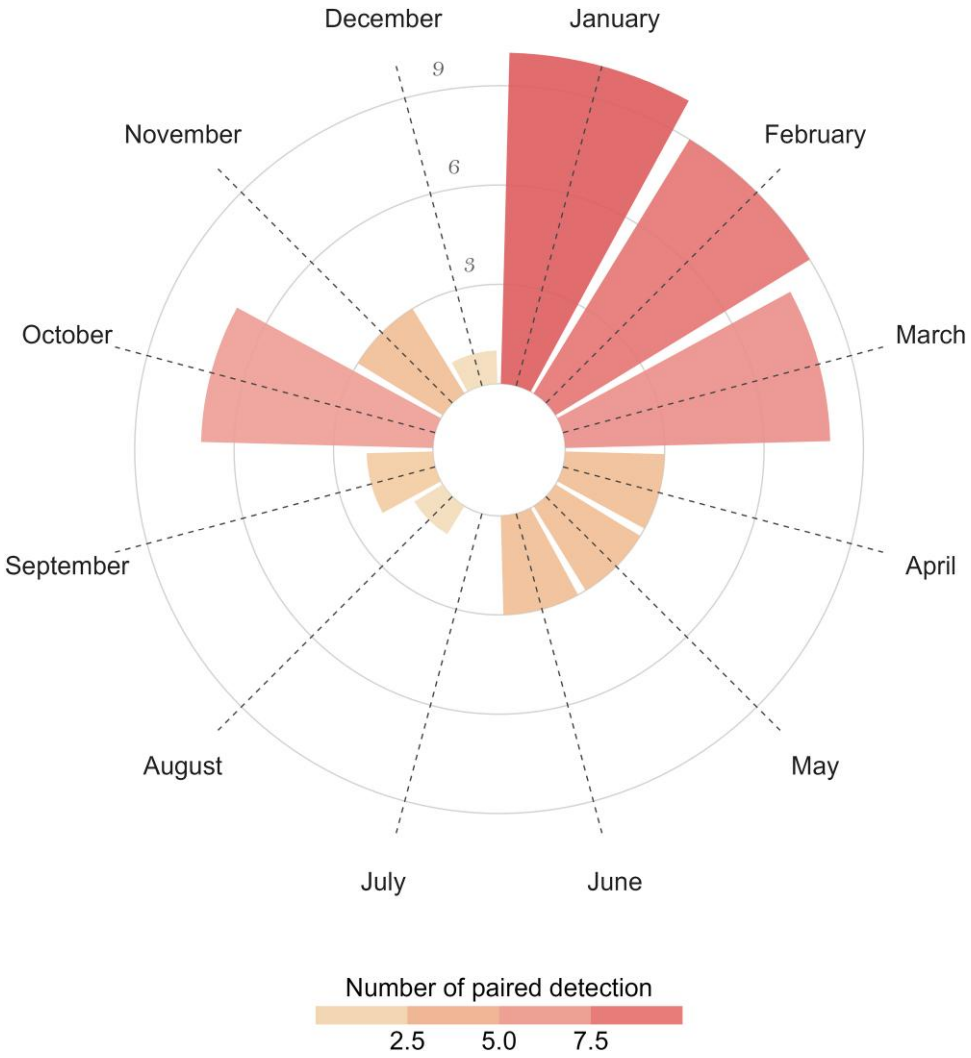

Figure 3 Distribution of pair detections in different months, ie simultaneous capture of lone females and males of Far Eastern leopards, in border zone of the Land of the Leopard National Park across the year based on camera trap data from 2014 to 2023.

Infanticide avoidance in females with cubs

Consistent with our first hypothesis, females with cubs exhibited significant spatial avoidance of adult males, particularly during the 3-d period immediately following a male's visit to the same camera site. This behavior is likely an adaptive strategy to minimize the risk of encountering potentially infanticidal males, a phenomenon well documented in large felids (Packer and Pusey 1983; Balme and Hunter 2013), although infanticide has never been directly observed within our study area. Notably, the avoidance was temporally constrained: females resumed baseline levels of co-occurrence after 3 d. The 3-d avoidance window closely matches the typical duration that a leopard remains near a large kill to defend it from scavengers and conspecifics (Odden and Wegge 2005; Balme et al. 2007; Farhadinia et al. 2018; Hernandez-Blanco et al. 2024; Rozhnov et al. 2024), suggesting a sophisticated risk-assessment strategy, whereby females gauge the likelihood of male presence based on recent activity cues and adjust their space use accordingly.

The lack of significant attraction or avoidance between lone females and females with cubs suggests that these 2 classes do not perceive one another as either a threat or an opportunity, consistent with the absence of direct reproductive competition or infanticidal risk between them.

Table 4 Number of captures for different leopard demographic classes within 3 time periods from camera trap surveys in the Kedrovaya Pad State Nature Biosphere Reserve, the Land of the Leopard National Park, and its buffer zone (total area referred to as LLNP) (2014 to 2023).

Group	Total captures	Time period	*N*	%	Selectivity index (w_i)	Activity pattern
Female with cubs	789	Twilight	164	20.8	1.3	Mostly diurnal
		Daytime	524	66.4	1.6	
		Night	101	12.8	0.3	
Lone female	2,460	Twilight	648	26.3	1.4	Mostly diurnal
		Daytime	1,428	58.0	1.6	
		Night	384	15.6	0.4	
Male	7,241	Twilight	2,006	27.7	1.7	Mostly diurnal
		Daytime	3,764	51.9	1.3	
		Night	1,471	20.3	0.5	

Activity patterns defined according to Gomez et al. (2005).

Relative to lone females, those with cubs also exhibited a modest but significant reduction in temporal overlap with males. The activity overlap coefficient (Δ_4) between females with cubs and males was

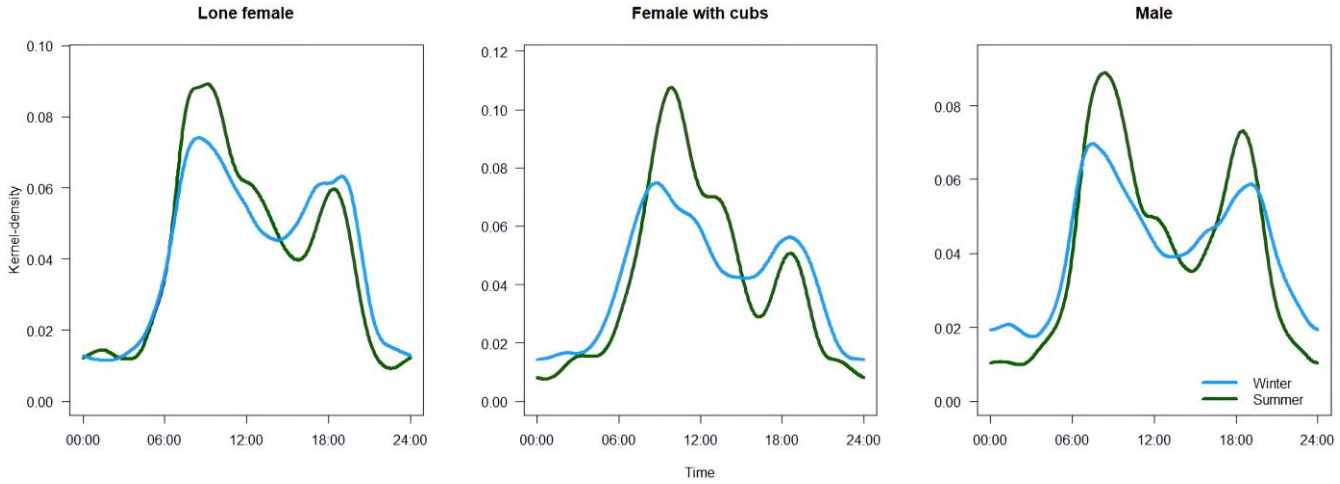

Figure 4 Seasonal diel activity of lone females, females with cubs, and males Far Eastern leopards in the border zone the Land of the Leopard National Parkbased on camera trap data from 2014 to 2023.

0.84, ~9% lower than that observed between lone females and males. This subtle shift toward greater diurnality is consistent with a risk-avoidance strategy aimed at reducing encounter rates with males during the vulnerable period of cub rearing, a pattern documented in other felids (Di Bitetti et al. 2010; Allen et al. 2025). Although modest, this temporal adjustment may complement spatial avoidance, further reducing the likelihood of an aggressive encounter.

Over the decade of monitoring, we recorded 98 unique litters. With the exception of 2 instances, multiple families were never detected at the same camera station within a 1-mo period. In contrast, lone females were frequently photographed at locations recently used by families. This pattern suggests that females with cubs actively avoid not only adult males but also other reproductive females. Such mutual avoidance among breeding females may reduce competition for resources and minimize the risk of potentially aggressive encounters, thereby facilitating coexistence within a shared landscape.

Breeding attraction in lone females

In contrast to females with cubs, lone females exhibited a strong tendency to visit locations recently used by males, with co-occurrence peaking within the first day following a male visit. This pattern aligns with our second hypothesis and is consistent with studies of other leopard populations that have documented high spatial co-occurrence between males and lone females (Rouse et al. 2021; Verschueren et al. 2023). Similarly, we found a high degree of temporal overlap in diel activity between these 2 classes. The pronounced co-occurrence over short temporal scales is likely driven by reproductive opportunities, as lone females without dependent cubs are more inclined to engage in mating activities (Balme and Hunter 2013; Andrews et al. 2019).

Males did not discriminate between female classes based on maternal status; they visited locations occupied by both lone females and females with cubs at broadly similar rates, although the effect of co-occurrence was stronger following lone female sightings. This pattern may reflect the fact that male movements are driven by multiple factors, including patrolling home ranges, seeking resources, and seeking mating opportunities, rather than by female reproductive status alone (Bailey 2005). However, our data cannot distinguish the specific motivations underlying male visitation patterns.

The current pattern of paired male–female detections, with a distinct peak in winter and a secondary small peak in October, contrasts sharply with historical accounts of the Far Eastern leopard population. Historically, when the population was critically low (eg fewer than 30 individuals in the 1980s), it was assumed that leopards bred year-round (Pikunov and Korkishko 1992), reflecting a prolonged, aseasonal "breed when a mate is found" strategy (Naidenko 2019). The emergence of clear seasonal peaks alongside ongoing population recovery likely reflects a change in breeding phenology driven by increasing population density. As the population steadily returns to its natural state, this shift toward a spring–summer birth concentration is consistent with the seasonal breeding patterns observed in other leopard subspecies at higher densities, including African (*P. p. pardus*) and Indochinese (*Panthera pardus delacouri*) populations (Owen et al. 2010; Balme et al. 2013), even if year-round detections persist at lower levels.

In leopard populations with higher densities than that at LLNP (Marchenkova et al. 2025), multiple males are frequently detected at locations used by females (Farhadinia et al. 2019), potentially enabling females to mate with multiple partners and thereby confusing paternity as a strategy to reduce the risk of infanticide (Balme and Hunter 2013). In our study, however, most paired male–female detections involved a single male photographed with multiple females, rather than multiple males with a single female. This pattern may reflect the relatively low density of leopards at the LLNP, where opportunities for females to encounter multiple males within a short period are limited.

Notably, in most paired detections (77.4%), the male was photographed before the female, suggesting that lone females may actively approach areas recently visited by males. This pattern aligns with observations from other leopard populations, where females have been reported to initiate copulatory behavior by approaching and soliciting males (Owen et al. 2010). In a recovering population such as that of LLNP, where encounter rates between potential mates may still be relatively low, such female-driven attraction to male-occupied areas could be an important mechanism for ensuring breeding opportunities.

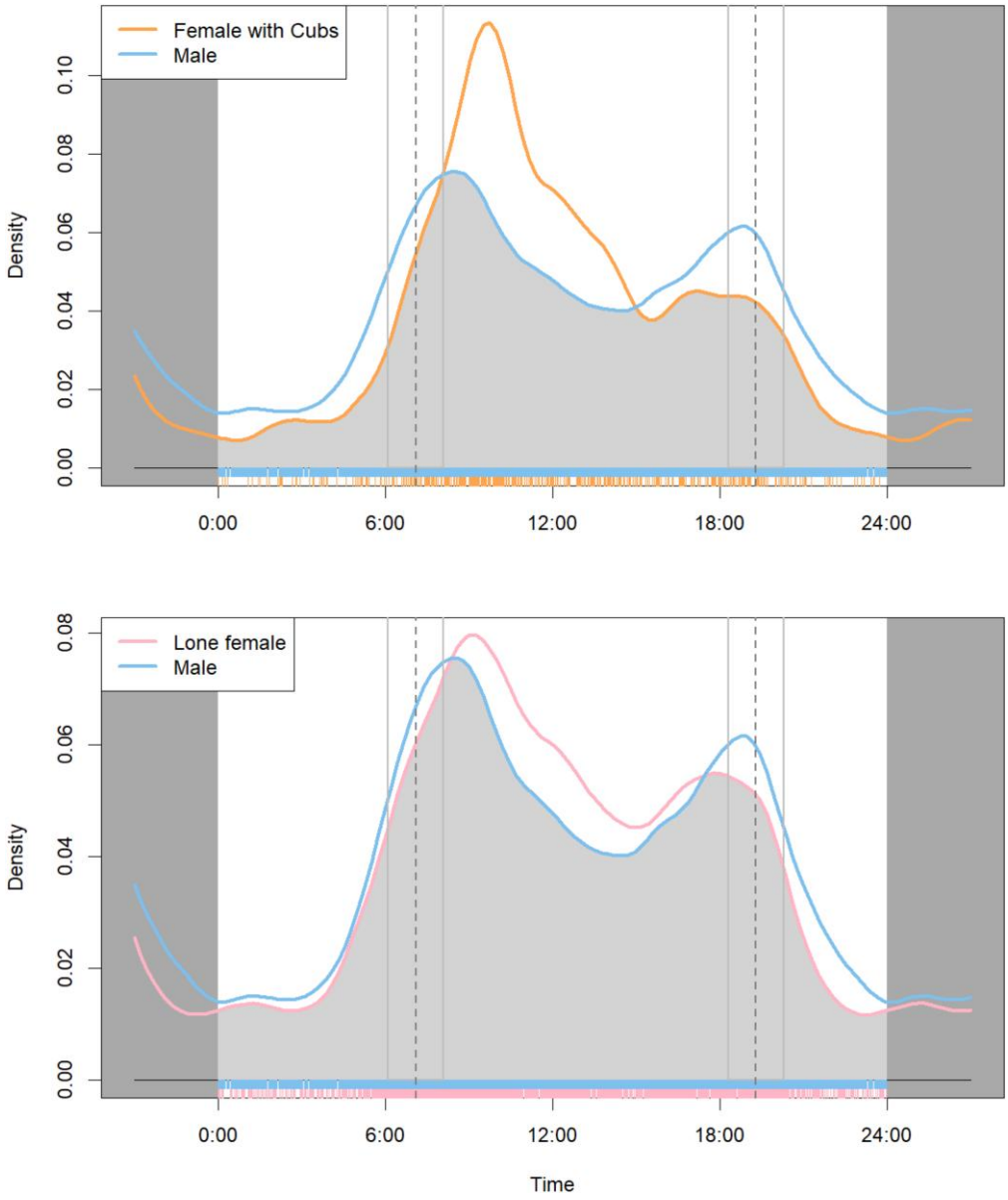

Figure 5 Temporal overlap plot of Far Eastern leopard demographic classes based on camera trap data in the Kedrovaya Pad State Nature Biosphere Reserve, the Land of the Leopard National Park, and its buffer zone (total area referred to as LLNP) from 2014 to 2023: (i) (top) male leopards and females with cubs, and (ii) (bottom) males and lone females. Dashed lines show average time for sunset and sunrise, gray lines—average time for twilight. Gray area under density curves represents the coefficient of overlap (Δ_4).

Temporal segregation

Contrary to our third hypothesis, all leopard demographic classes in this study exhibited predominantly diurnal activity patterns. This finding contrasts with most previous research, which has generally described leopards as crepuscular, nocturnal (Odden and Wegge 2005; Martins and Harris 2013; Havmøller et al. 2020; Rozhnov et al. 2024), or cathemeral (Rouse et al. 2021). The pronounced diurnality observed in the Far Eastern leopard population may reflect the unique ecological and environmental conditions of the Russian Far East. In particular, the study area is characterized by minimal human disturbance, with no permanent settlements, limited infrastructure, and strictly regulated access. The absence of anthropogenic pressure may reduce the need for leopards to adopt nocturnal habits as an avoidance strategy, a pattern commonly observed in areas with high human activity (Athreya et al. 2013; Van Cleave et al. 2018).

In addition, the study area supports a high density of sympatric Amur tigers (*P. t. altaica*) relative to other parts of their range (Darman and Matiukhina 2026). Tigers in this region are known to exhibit crepuscular or nocturnal activity patterns (Yang et al. 2018). Although previous camera-trap analyses in the same area found no evidence of fine-scale spatial avoidance between leopards and tigers (Matiukhina 2020), the temporal niche partitioning observed here, with leopards active during daytime and tigers during twilight and night (Yang et al. 2018), may reflect a broader strategy to reduce interference competition. A parallel can be drawn with Kanha National Park in India, where high tiger densities have forced leopards into suboptimal peripheral habitats (Kumar et al. 2019), underscoring

the need for continued monitoring of these predator–predator interactions. As the populations of both predators continue to recover within the limited available habitat, the potential for future spatial or temporal avoidance may increase.

Limitations

This study had a few limitations. First, the use of a 3-d survey window limited our ability to capture finer temporal dynamics of interactions; higher-frequency or continuous monitoring would provide greater resolution. Second, although we detected significant patterns of attraction and avoidance, model explanatory power was low (<10% deviance explained), indicating that additional factors, such as prey distribution, tiger presence, kinship, and seasonal variation, likely influence leopard interactions. Finally, our focus on broad demographic classes did not account for individual-level social variation, which may play an important role in shaping interaction patterns (Pastorino et al. 2021).

Conclusion

Our study revealed dynamic intraspecific interactions in the Far Eastern leopard, providing insights into interactions within the solitary life of leopards. Our findings demonstrated that social behavior in this population is partially mediated by sex and, critically, by female reproductive status. Females with cubs tended to employ a risk-sensitive strategy, spatially avoiding locations recently visited by adult males for a period of ~3 d. This behavior is consistent with an infanticide avoidance mechanism, highlighting a fundamental cost that shapes female space use during cub rearing. In addition, these mothers exhibit mutual spatial avoidance, suggesting that intrasexual competition as one of the drivers of social organization. In contrast, lone females are attracted to male-visited locations, a pattern best explained by mate-searching behavior and the maximization of breeding opportunities. Contrary to patterns reported for most other leopard populations, all demographic classes in our study area exhibited predominantly diurnal activity. This unique temporal niche is likely facilitated by the low levels of anthropogenic disturbance characteristic of the region and may also represent an adaptive response facilitating coexistence with the sympatric Amur tiger (*P. t. altaica*), which is active primarily during twilight and night. Overall, these findings highlight that Far Eastern leopard social organization is context-dependent and more complex than traditionally assumed, shaped by reproductive strategies, risk trade-offs, and ecological conditions.

Acknowledgments

We sincerely thank all colleagues who participated in the camera trap monitoring and data collection: T. Petrov, G. Sedash, A. Vikalova, M. Mazur, Y. Darman, E. Nikolaeva, R. Nazarenko, G. Kovach, K. Borodulina, and A. Krutikov. The authors also thank WildCRU researchers for their advices and University of Oxford for the possibility to conduct this study.

Author contributions

Taisiia V. Marchenkova (Conceptualization, Validation [equal], Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing—original draft [lead]), Alexander N. Reebin (Data curation, Writing—review & editing [equal], Methodology, Software, Validation [supporting]), Anna A. Yachmennikova (Investigation, Supervision [supporting], Validation [supporting], Writing—review & editing [equal]), Dina S. Matiukhina (Data curation, Resources, Validation, Writing—review & editing [equal], Methodology [supporting]), Ekaterina Y. Blidchenko (Data curation, Resources, Validation, Writing—review & editing [equal]), Darya A. Maksimova (Data curation, Validation, Writing—review & editing [equal]), Viktor B. Storozhuk (Data curation, Project administration, Resources, Writing—review & editing [equal]), Alexey S. Titov (Data curation, Project administration, Resources, Writing—review & editing [equal]), Claudio Sillero-Zubiri (Conceptualization, Writing—review & editing [equal], Project administration, Writing—original draft [supporting], Supervision [lead]), and Mohammad S. Farhadinia (Conceptualization, Project administration, Writing—original draft, Writing—review & editing [equal], Formal analysis [supporting], Supervision [lead])

Supplementary material

Supplementary material is available at *Behavioral Ecology* online.

Funding

This work was carried out as a part of a state assignment from the Ministry of Natural Resources and Ecology of the Russian Federation, with financial support from the ANO “Far Eastern leopards.” TVM was supported by a WildCRU scholarship funded by Panthera and a Joanna Hitchcock Post-Diploma scholarship by from Lady Margaret Hall, University of Oxford. MSF was supported by Research England’s Expanding Excellence in England (E3) Fund, UK Research and Innovation.

Conflicts of interest

The authors declare no competing interests.

Data availability

Analyses reported in this article can be reproduced using the data provided by Marchenkova et al. (2026).

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