



Individual variation in leopard (*Panthera pardus*) prey composition in Namibian farmlands highlights the importance of wild prey over livestock

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Abstract

Human-carnivore conflict, particularly involving livestock depredation, remains a major threat to large carnivore conservation worldwide. To protect their livelihood, farmers often attempt to remove “problem” individuals that specialize in killing livestock, although empirical support for such specialized individuals is limited. Leopards (*Panthera pardus*) are widespread carnivores that are often involved in human-wildlife conflicts, but most studies have focused on protected areas, even though most of their range is unprotected. We tracked 29 leopards for an average of 422 days over ten years on freehold farmlands of central Namibia to investigate their foraging ecology. We investigated 455 clusters of GPS locations (which often indicate prey consumption), and found 375 identifiable prey remains from 20 species. Wild prey constituted 96.8% of identified kills, with gemsbok (*Oryx gazelle*), warthog (*Phacochoerus africanus*), and greater kudu (*Tragelaphus strepsiceros*) representing 77.3% of all identified prey. Livestock (cattle, *Bos* spp., and horses, *Equus ferus*) composed only 3.2% of the kills, with male leopards feeding on livestock three times more frequently than females. While approximately one-third of leopards consumed livestock at least once, no individual exhibited specialization for livestock, although individuals did exhibit specialization for some wild prey. Predation occurred primarily during crepuscular periods, but diel patterns in predation differed between the sexes. These findings challenge assumptions that livestock depredation is driven by habitual livestock-killing leopards and suggest that it may be mostly opportunistic. Our results underscore the value of maintaining wild prey populations and adopting non-lethal management practices to mitigate conflict and promote human-carnivore coexistence across unprotected areas.

Keywords Foraging ecology · Human-wildlife conflict · Livestock · Unprotected areas · Predation · Specialization

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Introduction

Large carnivores are charismatic and conflict-prone species that help maintain biodiversity and ecosystem stability (Ripple et al. 2014; Newsome et al. 2017; Prugh and Sivy 2020), yet are among the most imperiled species on Earth (Ripple et al. 2014; Kropfel et al. 2015). Large carnivores are important due to their disproportionate ecological effects, including regulating prey and competitor populations (Prugh et al. 2009; Ripple and Beschta 2012) and maintaining food webs (Estes et al. 2011; Ripple et al. 2014). The decline of large carnivores is primarily driven by actual or perceived conflicts with humans, most commonly arising from carnivores killing livestock or pets (Kissui 2008; Broekhuis et al. 2017; van Eeden et al. 2017) or directly injuring or killing people (Packer et al. 2005; Bombieri et al. 2019, 2023; Rani et al. 2024). Yet the actual killing of livestock can be overestimated or not fully documented by farmers (Rasmussen 1999; Boulhosa and Azevedo 2014; Grey et al. 2017), sometimes leading to increased retaliatory killing of carnivores.

Although many large carnivores have generalized diets, individuals often exhibit specialization in their diet (Bolnick et al. 2003; Hayward and Kerley 2008; Araújo et al. 2011; Hertz et al. 2024). This pattern accords with the niche variation hypothesis, which holds that broad population niches often emerge because individuals specialize on different subsets of resources rather than every individual being a broad generalist (Bolnick et al. 2003). This individual specialization may be tied to individual differences in behavior (i.e., boldness, level of exploration) that lead to individuals hunting specific animals (e.g., bolder individuals may hunt larger prey or prey riskier to be hunted than less bold individuals; Sih et al. 2004; LaBarge et al., 2024). Comprehensive predation studies focusing on individual carnivores that are conflict-prone are therefore essential for developing effective, evidence-based conservation strategies and mitigating human-wildlife conflict (Ogada et al. 2003; Gusset et al. 2009; Carter and Linnell 2016; van Eeden et al., 2017; Kropfel et al. 2020).

In human-dominated landscapes, livestock farmers frequently attribute livestock depredation to specific “problem individuals” that are perceived to specialize in killing domestic animals and often advocate for the targeted removal of such individuals through lethal control (often trapping or shooting at the remains of killed livestock; Stein et al. 2025). However, empirical evidence supporting the existence individuals that are livestock specialists remains limited and contentious (Linnell et al. 1999). The main exception to this are bears (*Ursus* spp.), where often a few problem individuals cause the majority of all human-bear conflicts and the occurrence of problem bears is often linked to exposure to anthropogenic food (Kropfel et al. 2021). Previous research on felids has shown that males are more often involved with livestock depredation (Linnell et al. 1999). This highlights the need for rigorous, fine-scale studies that investigate individual variation in foraging by large carnivores to provide evidence and develop effective conflict mitigation strategies.

Leopards (*Panthera pardus*) are among the most widespread and ecologically adaptable large carnivores in the world (Ghoddousi et al. 2016; Jacobson et al. 2016). Despite their adaptability, leopards are listed as Vulnerable by the International Union for Conservation of Nature (IUCN; Stein et al. 2025). They currently occupy only 25–37% of their historic range across Africa and Asia, with the majority of extant populations persisting outside protected areas in landscapes shared with humans where antagonistic interactions are common (Jacobson et al. 2016). Leopards are increasingly affected by human-wildlife conflicts over livestock and game species owned by people (Kissui 2008; Athreya et al. 2011; Constant et

al. 2015; Ghoddousi et al. 2016; Rani et al. 2024). Retaliatory killings are the main causes of mortality and population declines for leopards, compounded by unsustainable trophy hunting, poaching, and habitat loss or degradation (Jacobson et al. 2016; Stein et al. 2025).

Leopards can function as apex or subordinate carnivores depending on the presence of dominant competitors (i.e., African lions [*Panthera leo*], spotted hyenas [*Crocuta crocuta*], and tigers [*Panthera tigris*]), and exhibit a high degree of adaptability in their foraging ecology (Hart et al. 1996; Henschel et al. 2005; Hayward et al. 2006; Hayward and Kerley 2008; Balme et al. 2020). Leopards preferentially select medium-sized ungulates (typically between 10 kg and 40 kg), but will also kill larger and smaller prey, including livestock (Hart et al. 1996; Henschel et al. 2005; Hayward et al. 2006; Hayward and Kerley 2008). Other attributes of preferred prey include species that use dense vegetation and have small prey group sizes, characteristics that increase the success of leopard ambush hunting strategies (Hayward et al. 2006; Kittle et al. 2014). Although results of previous studies differ in whether males or females have a broader diet (e.g., Voigt et al. 2018; Balme et al. 2020), it is plausible that leopards have sex-specific patterns in their foraging ecology. Females have reproductive demands (i.e., gestation, lactation, and cub rearing) that can substantially increase their energetic requirements, potentially leading females to target smaller or more accessible prey to balance energy intake and risk (e.g., Voigt et al. 2018; Balme et al. 2020). In contrast, males have larger body size (Hayward and Kerley 2008; Voigt et al. 2018), bolder behavior and greater risk tolerance (LaBarge et al., 2024), and larger ranges and daily movements (Snider et al. 2021; Rodriguez-Recio et al. 2022). Energetic scaling predicts that larger-bodied carnivores are more likely to target larger-bodied prey to meet daily maintenance costs (Carbone et al. 1999), linking male leopards' greater body size to a potential higher frequency of killing large prey. Leopard foraging, prey hoisting, and diel activity also often vary by habitat, prey type, and proximity to human activity. For example, leopards are typically active during crepuscular and nocturnal hours (Martins and Harris 2013; Pitman et al. 2013; Havmøller et al. 2020) but shift their activity to be more nocturnal in areas with human activity (van Cleave et al. 2018; Smyth et al. 2025).

Previous studies on leopard foraging behavior have often relied on a small number of individual leopards located within protected areas (Balme et al. 2014), both of which can potentially introduce bias in understanding leopard foraging behavior. The limitation of small sample sizes of individuals is particularly important given accumulating evidence that some leopards exhibit individual specialization in prey selection which may not be representative of the broader population (Balme et al., 2019; Voigt et al. 2018). This is also crucial for developing targeted conflict-prevention interventions, as identification of specialized individuals versus population-wide opportunistic behavior determines the most effective management strategies in conflict situations (Linnell et al. 1999; Balme et al. 2020). Moreover, the research focus on protected areas is problematic, since most leopard populations are located outside such reserves in human-dominated landscapes (Jacobson et al. 2016), where human infrastructure and activities can have strong impact on carnivore movements, activity budgets, and prey availability (Rodriguez-Recio et al. 2022; Burton et al. t al. 2024). This spatial bias leads to a mismatch between the areas where leopard research is conducted and areas where applied conservation action is most needed.

In this study, we investigated clusters of GPS locations from collared individuals (hereafter "GPS clusters"; which often indicate prey consumption) to understand leopard foraging ecology for 29 individuals across a ten-year period. We conducted our study on freehold

farmlands in central Namibia, where human-leopard conflicts often result in the removal of “problem individuals” (Stein et al. 2025). We hypothesized that male and female leopards differ in their prey composition and predicted that males would more frequently kill larger prey, including livestock such as cattle, than females. We further hypothesized that some individuals exhibit dietary specialization on particular prey species, either wild or domestic. We predict if there are “problem leopards” that specialize in preying on livestock, these individuals would be primarily males—attributable to adult males having larger size, bolder behavior, and larger ranges and daily movements. We also hypothesized that leopards in our study area avoid hunting during times when humans are more active (e.g., mornings and afternoons). In addition, we report on other characteristics of leopard foraging (e.g., prey hoisting, differences in prey composition among farms) for reference to future studies. By focusing on leopard foraging ecology in a human-dominated landscape outside of protected areas, our research provides critical insights into leopard ecology with direct implications for conflict mitigation and conservation planning.

Materials and methods

Study area

We conducted our study in central Namibia (23°01′–21°26′ S and 16°51′–18°17′ E) (Fig. 1), which comprised a mosaic of plateaus, rugged hills, and mountains up to 2,479 m a.s.l. (Mendelsohn et al. 2022). Mean annual precipitation ranged from 300 to 350 mm, with most rainfall falling during the rainy season from January to April (Mendelsohn et al. 2022). Maximum daytime temperatures reached up to 35 °C in hot dry season (September–December), while nights in the cold dry season (May–August) dropped to frost levels (Mendelsohn et al. 2022). Habitats included predominantly dry riverbeds, camelthorn (*Acacia erioloba*) savannah, high mountains, rocky hills, grasslands and bush-encroached lowlands; with vegetation generally being highland savannah, dominated by arid hook thorn (*Acacia hereroensis*) and a diverse variety of grass species. Common ungulates and potential natural leopard prey species (in decreasing order of body mass) included eland (*Taurotragus oryx*), mountain zebra (*Equus zebra*), greater kudu (*Tragelaphus strepsiceros*), gemsbok (*Oryx gazella*), red hartebeest (*Alcelaphus buselaphus*), warthog (*Phacochoerus africanus*), impala (*Aepyceros melampus*), springbok (*Antidorcas marsupialis*), and steenbok (*Raphicerus campestris*) (Voigt et al. 2018; Melzheimer et al. 2020). In addition to leopards, cheetahs (*Acinonyx jubatus*) and brown hyenas (*Parahyaena brunnea*) inhabited the area, as well as several species of small and mid-sized carnivores. The competitively dominant African lions and spotted hyenas were exterminated several decades ago and occurred only sporadically. Potential avian scavengers included Verreaux’s eagle (*Aquila verreauxii*), lappet-faced vulture (*Torgos tracheliotos*), white-backed vulture (*Gyps africanus*) and marabou stork (*Leptoptilos crumenifer*) (Brown et al. 2017).

The primary land uses in the area were cattle and game farming, horse breeding, hunting, and tourism on privately owned freehold farms (Richmond-Coggan 2022). Livestock (cattle, *Bos* spp., and horses, *Equus ferus*) were widespread across most farms ($n=44$) and their numbers were probably comparable to the most common wild ungulate species (Žagar et al. 2025), although exact abundance data was lacking across the study area. Livestock

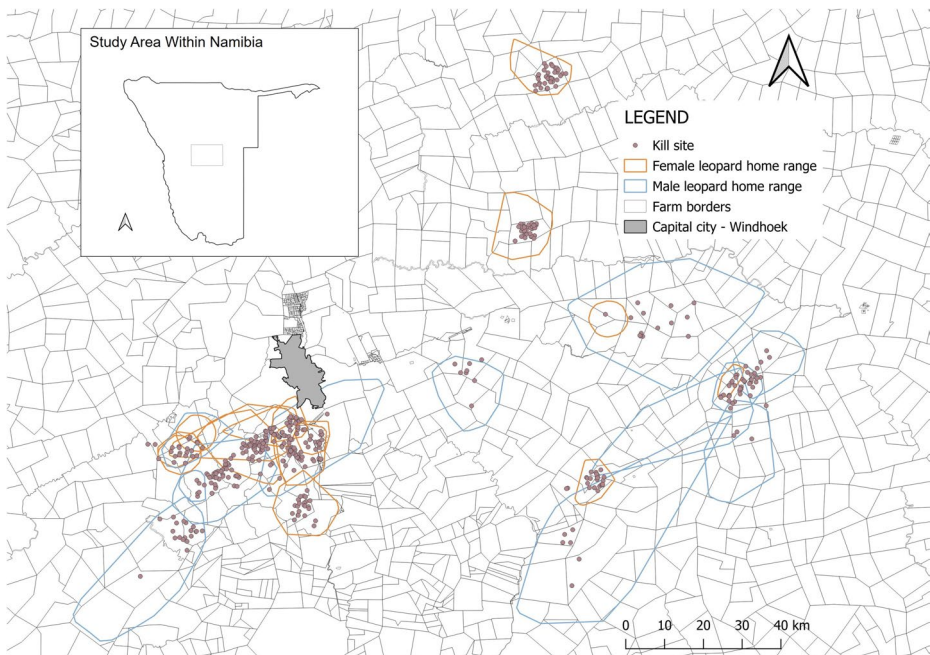


Fig. 1 Map of the study area in central Namibia surrounding the capital city of Windhoek, with the spatial distribution of leopard GPS clusters of identified prey ($n=375$) and the 95% minimum convex polygon home ranges of 29 GPS-collared leopards monitored between 2013 and 2022 and the boundaries of freehold farms in gray

husbandry practices varied among farms, with most livestock allowed to roam freely within large, fenced game camps, but these fences were not effective for preventing access to leopards or other wildlife. Farmers conducted routine inspections of both the infrastructure and livestock, and vulnerable livestock (breeding cows with suckling calves) were sometimes confined to smaller kraals and moved closer to the farmhouses to facilitate management and provide protection from predators. Lethal removal of predators was generally the main depredation prevention method, although some individual farmers also attempted to use other methods (e.g., livestock guarding dogs, electric fences, protective collars). Lethal removal through shooting was usually conducted using meat-baiting next to a hide or box-trap, while leopards were also killed when returning to feed on killed livestock (often by using gin traps). The exact number of removed leopards across the study area was unknown, but frequency of removal seemed to vary considerably among the farms. The effectiveness of these lethal and non-lethal prevention methods in our study area remains unknown.

Field Methods

We captured 29 leopards (Table 1) between 2013 and 2022 using mechanically or electronically triggered metal box traps. We immobilized leopards with a dart gun using 0.04–0.06 mg/kg medetomidine hydrochloride (Medetomidine 10 mg/mL; Novartis, Johannesburg, South Africa) and 2.5–3.0 mg/kg ketamine (Ketamine 1G; Kyron Laboratories, Johannesburg, South Africa) and reversed them with 2.0–2.4 mg/kg atipamezole (Antise-

Table 1 Identification code of leopards monitored during the study, their sex, average age over the monitored time period, weight at capture, duration of monitoring in days, as well as the total number of GPS clusters, the number of GPS clusters we visited, and the number of kill remains found at the GPS clusters. The individual dietary specialization scores are given as a proportional similarity index (PS_i) and their variation. n/a: not applicable

ID	Sex	Age (avg)	Weight (kg)	Duration of Monitoring	Total GPS Clusters	GPS Clusters Checked	Kills Found	$PS_i \pm$ Variation
F01	Female	6.0	34.0	336	75	20	16	0.66±0.01
F02	Female	5.0	35.5	902	322	26	21	0.72±0.01
F03	Female	7.0	41.5	349	140	19	18	0.75±0.01
F04	Female	6.0	35.5	398	183	20	16	0.89±0.01
F05	Female	3.0	37.5	823	343	30	21	0.75±0.01
F06	Female	4.0	35.0	323	272	39	24	0.86±0.01
F07	Female	2.0	38.0	310	268	34	28	0.81±0.01
F08	Female	3.0	31.0	494	211	27	23	0.74±0.01
F09	Female	1.8	30.5	906	376	22	20	0.71±0.01
F10	Female	5.0	34.0	446	191	20	18	0.63±0.01
F11	Female	3.0	31.0	556	274	25	21	0.61±0.01
F12	Female	2.6	35.0	342	144	2	2	n/a
F13	Female	5.5	40.0	60	31	4	4	n/a
F14	Female	4.0	37.0	478	209	1	1	n/a
F15	Female	2.5	27.5	299	114	2	2	n/a
F16	Female	5.0	35.5	251	54	11	11	n/a
M01	Male	4.5	63.0	755	267	24	22	0.69±0.01
M02	Male	3.0	34.5	406	150	20	20	0.81±0.01
M03	Male	7.5	68.5	605	189	22	20	0.85±0.00
M04	Male	5.5	68.5	246	65	20	20	0.67±0.01
M05	Male	6.0	58.0	451	139	12	10	0.75±0.02
M06	Male	4.5	69.0	266	61	5	4	n/a
M07	Male	6.5	67.5	339	86	14	11	n/a
M08	Male	6.0	56.0	312	89	6	6	n/a
M09	Male	3.0	54.5	56	30	3	3	n/a
M10	Male	3.5	49.0	370	17	6	6	n/a
M11	Male	5.0	52.5	453	62	4	4	n/a
M12	Male	3.5	48.0	459	75	8	7	n/a
M13	Male	4.0	50.0	232	29	9	9	n/a

dan; Novartis, Johannesburg, South Africa) (Voigt et al. 2018, Šabeder et al. 2026). All capture and immobilization procedures were approved by the Internal Ethics Committee of the Leibniz Institute for Zoo and Wildlife Research (IZW, Berlin, Germany; permit number: 2002-04-01) and the Ministry of Environment, Forestry and Tourism of Namibia (MEFT; permit numbers: 1689/2012, 1813/2013, 1914/2014, 2067/2015, 2194/2016, 2208/2017 and RCIV000822018 for 2018–2022). We fitted leopards with GPS collars equipped with either remote (e-obs GmbH, Germany) or satellite downloads (Vectronic Aerospace GmbH, Germany, and Followit Wildlife, Lindsberg AB, Sweden) and three-axes accelerometers. We programmed remote download collars to take positions every 15 min and programmed satellite collars to take positions every 4 h. We weighed each leopard and estimated their age by wear of teeth and other morphological characteristics following Stander (1997) and

Voigt et al. (2018). We report ages as the average age for the individual over the course of the time we monitored them (Table 1).

To find prey remains we field-checked GPS clusters (e.g., Martins et al., 2013; Pitman et al. 2013) from 2013 to 2022. We generated GPS clusters for leopard activity that had at least three GPS locations within 100 m in a 24 h window. We considered cases when two GPS clusters were apart by > 100 m but within the same temporal window (i.e., the start of cluster_{*n*+1} was within the cluster duration of cluster_{*n*}) as one GPS cluster (Pitman et al. 2013). The main factors influencing our decision about which GPS clusters to check was the time since the start of the cluster when we received the GPS data, the current capacity of the team for fieldwork, and the total sample size of confirmed kills for the given individual. When more GPS clusters were available than we could visit in the field, priority was given to fresher and longer clusters (i.e., > 12 h with at least one location during nighttime) and to individuals with lower sample sizes. Our search of GPS clusters started at the center of the cluster and gradually extended to the search perimeter (up to approximately 50 m from the outermost locations of the cluster). We spent a minimum time of 30 person-minutes searching for prey remains at each GPS cluster. This searching time was prolonged when the GPS cluster was located in habitat with low visibility (e.g., due to dense vegetation or rugged terrain).

Whenever possible we identified the prey species, its sex, and age class; which we categorized as juveniles (individuals < 1 year old), sub-adults (animals > 1 year but not yet at full body size), and adults (animals at full body size, generally > 2 years old). We based age determination on tooth eruption and growth, body size and shape, horn morphology and ossification in epiphyses of the long bones (Schaller 1976). We based our sex determination on the morphology of genitalia (when visible) and/or horns. We also recorded whether the prey was dragged, hoisted into a tree, or cached. When prey was dragged, we measured the distance in meters from where the kill was made to where the leopard dragged it to feed. We also noted whether a tree suitable for hoisting prey (i.e., diameter > 15 cm) was present in the 50 m radius around the kill site.

We acknowledge that the GPS cluster method is inherently biased against detecting small prey species (i.e., birds and small mammals), which are often quickly and entirely consumed (Oliveira et al. 2023). We accepted this limitation, since the aim of this study was not to analyze the entire diet of leopards (for which scat or stomach content analysis would be needed; Pitman et al. 2014), but instead to focus on the consumption of large (ungulate) prey. Potential bias among detection of wild and livestock could be more problematic for this study, since use of livestock by predators is sometimes shortened due to human disturbance (Tallian et al. 2023). For this reason, we tested for differences in the feeding times (GPS cluster duration) of kills we found of wild prey and domestic ungulates. We did not detect significant differences (median \pm IQR = 3.30 ± 2.35 days for domestic prey and 2.20 ± 2.00 days for wild prey; Wilcoxon rank sum test, $W = 2201$, $p = 0.08$), indicating that the potential for bias is low.

Statistical analyses

We first summarized characteristics of individual leopards and assessed the data. We used Mann-Whitney U tests to determine whether male and female leopards varied in age, body mass, or duration of monitoring. We used a Wilcoxon rank sum test with continuity correc-

tion to evaluate whether the time that had elapsed since the start of a GPS cluster affected our likelihood of locating prey remains when we investigated it.

To evaluate variation in prey composition, we first compared the relative percentages of wild prey and livestock consumed by leopards to understand the prevalence of livestock in leopard diet and determine the most frequent prey species. We then aggregated kills into a series of contingency tables and used Fisher's exact tests (when counts were <5) and chi-square tests to test whether classes or categories of prey varied significantly. To limit Type I errors in these analyses, we used Monte Carlo simulations ($n=2000$) in Fisher's exact tests, and the Yates continuity correction in chi-square tests. To determine whether the proportion of the main prey varied on individual farms (using farms with at least 10 documented kills) we compared the total prey on each farm to the number of each of the three main prey species using Fisher exact tests. To determine whether male and female leopards varied in their consumption of the three main prey species and livestock, we compared the proportion each sex consumed compared to the total number of other prey consumed, using chi-square tests for the three main prey and Fisher's exact test for livestock. To determine whether male and female leopards varied in the proportions of age classes (juveniles, sub-adults, and adults) they consumed for the three most frequent prey species, we used Fisher's exact tests for each species.

To quantify the difference in prey composition between an individual and the rest of the leopards in the study population (for the 16 individuals with ≥ 10 documented kills of known prey), we used a proportional similarity index (PS_i ; Bolnick et al., 2003), following the methods used in previous leopard research (Balme et al. 2020). In the assessment, the diversity of prey in an individual's diet will range from 0 (its diet is completely different from the rest of the leopard study population) to 1 (its diet is the same as the rest of the leopard study population). We estimated the individual PS_i index using the package *RInSp* (v1.2.5; Zaccarelli et al. 2013), along with the estimated variance, by applying Monte Carlo resampling procedures with 999 replicates. We used the proportion of five classes of prey in the analysis (each of the three most frequent prey, livestock, and a combined category for all other wild prey species), and report the average individual PS_i specialization scores and prey classes for individual leopards. We considered specialists to be leopards that were $\geq 20\%$ different ($PS_i \leq 0.80$) from the rest of the leopard study population (Balme et al. 2020). We used a Mann-Whitney U test to determine whether individual specialization scores varied among male and female leopards.

To understand variation in male and female foraging ecology, we estimated the diel activity of when leopards killed prey. We used the first point of GPS clusters as the time of kill and assumed that the leopards feeding on prey remains that we found had killed the prey and were not scavenging. We considered crepuscular times to be within an hour before and after sunrise and sunset. We fit the temporal data from the GPS collars for all individuals to a circular kernel density to estimate the distribution of temporal activity for leopards using the *overlap* package (Meredith and Ridout 2017).

We conducted all statistical analyses with R version 4.4.0 (R Core Team 2024), considering results statistically significant when $p \leq 0.05$.

Results

Overview

We collected foraging data from 29 GPS-tracked individual leopards ($n_{\text{male}} = 13$, $n_{\text{female}} = 16$) for an average of 421.5 days (± 212.5 SD) (Table 1). Male and female leopards did not vary in age ($df=28$, $U=75$, $z=1.25$, $p=0.21$) or duration of monitoring ($df=28$, $U=87$, $z=0.72$, $p=0.47$), but males ($\bar{x} \pm \text{SD} = 56.8 \pm 10.3$ kg) were significantly heavier than females ($\bar{x} \pm \text{SD} = 34.9 \pm 3.6$ kg; $df=28$, $U=10$, $z=4.10$, $p < 0.0001$).

We investigated 455 GPS clusters from the collared leopards ($n_{\text{male}} = 163$, $n_{\text{female}} = 292$); an average of 36.8% (± 0.18 SD, range=4.6–86.5%) GPS clusters for each individual. We found prey consumed by leopards at 388 (85.3%) of the GPS clusters, including two GPS clusters with two prey species (for which we treated each kill separately in the subsequent analyses). At 15 GPS clusters we were unable to identify the prey species that had been consumed. The GPS clusters we investigated averaged 2.53 days (± 1.67 SD, range=0–12) in duration. We checked an average of 15.7 GPS clusters (± 10.6 SD, range=1–39) per individual leopard and 9.9 GPS clusters (± 13.6 SD, range=1–47) per farm. We investigated the GPS clusters on average 59.0 days (± 61.5 SD, range 0–403) after the leopard left the prey. The time elapsed since the start of a GPS cluster did not have a significant effect on our likelihood of locating prey remains when we investigated the GPS cluster ($W=13110$, $p=0.91$). For the 353 kill sites that we measured exact researcher searching time, we found the kill remains on average after 3.3 min (± 7.9 SD, range 0–80) of searching.

The resulting 375 identified prey items consumed by leopards included 20 different prey species. Overall, wild prey composed 96.8% ($n=363$) of identified prey, while livestock composed 3.2% ($n=12$). The percentage of the three main leopard prey species killed on individual farms varied significantly among gemsbok (range=13.3–81.8%; Fisher exact test, $p=0.04$) and greater kudu (range=0.0–34.6%; Fisher exact test, $p=0.03$), but not warthog (range=7.7–46.2%, $p=0.52$) (Table 2).

Wild prey composition

Ungulates made up 96.7% ($n=351$) of the 363 wild prey items we identified, with other wild prey species consisting of helmeted guinea fowl (*Numida meleagris*, $n=5$, 1.3%), chacma baboon (*Papio ursinus*, $n=2$, 0.6%), common ostrich (*Struthio camelus*, $n=1$, 0.3%), Cape hare (*Lepus capensis*, $n=1$, 0.3%), and Cape porcupine (*Hystrix africae australis*, $n=1$, 0.3%), as well as two leopard cubs (0.6%). The leopard cubs were killed and partly consumed on two separate occasions by the same male leopard after he took over a new territory.

Leopards predominantly fed on three prey species (77.4%; 290 of 375 identified prey): gemsbok ($n=139$, 37.1% of all identified prey), warthog ($n=82$, 21.9%), and greater kudu ($n=69$, 18.4%). These were followed in frequency by steenbok ($n=29$, 7.7%) and impala ($n=10$, 2.7%) (Fig. 2). Male and female leopards did not vary in their consumption of gemsbok (Chi-square test, $df=1$, $\chi^2=0.01$, $p=1.00$), warthog (Chi-square test, $df=1$, $\chi^2=2.67$, $p=0.10$), or greater kudu (Chi-square test, $df=1$, $\chi^2=0.02$, $p=0.88$) (Fig. 2).

The three primary ungulate prey species varied by age class, and male and female leopards sometimes varied in the age classes they preyed upon. The majority of gemsbok with an assessed age class ($n=114$) were juveniles (64.0%), while adults made up 24.6% and

Table 2 Variation in the percentage of the 5 main prey categories (gemsbok, greater kudu, warthog, livestock, all other prey, and prey we were unable to identify) among individual farms

Farm ID	Gemsbok	Greater Kudu	Warthog	Livestock	Other Prey	Not Identified
Farm 1	0.0	0.0	100.0	0.0	0.0	0.0
Farm 2	0.0	0.0	0.0	0.0	100.0	0.0
Farm 3	25.0	50.0	0.0	0.0	0.0	25.0
Farm 4	25.0	25.0	25.0	0.0	0.0	25.0
Farm 5	0.0	0.0	100.0	0.0	0.0	0.0
Farm 6	0.0	0.0	0.0	50.0	0.0	50.0
Farm 7	20.0	20.0	0.0	0.0	60.0	0.0
Farm 8	56.8	9.1	4.6	2.3	15.9	11.4
Farm 9	100.0	0.0	0.0	0.0	0.0	0.0
Farm 10	0.0	66.7	0.0	0.0	33.3	0.0
Farm 11	66.7	0.0	0.0	0.0	33.3	0.0
Farm 12	26.5	5.9	35.3	0.0	14.7	17.7
Farm 13	25.0	0.0	0.0	25.0	25.0	25.0
Farm 14	0.0	0.0	100.0	0.0	0.0	0.0
Farm 15	0.0	0.0	0.0	0.0	100.0	0.0
Farm 16	26.7	33.3	6.7	6.7	20.0	6.7
Farm 17	67.9	7.1	14.3	3.6	7.1	0.0
Farm 18	0.0	0.0	0.0	0.0	100.0	0.0
Farm 19	81.8	0.0	0.0	0.0	18.2	0.0
Farm 20	66.7	0.0	0.0	33.3	0.0	0.0
Farm 21	0.0	0.0	100.0	0.0	0.0	0.0
Farm 22	100.0	0.0	0.0	0.0	0.0	0.0
Farm 23	37.8	26.7	0.0	2.2	31.1	2.2
Farm 24	0.0	0.0	0.0	0.0	100.0	0.0
Farm 25	0.0	0.0	0.0	0.0	100.0	0.0
Farm 26	27.6	6.9	3.5	1.7	32.8	27.6
Farm 27	0.0	100.0	0.0	0.0	0.0	0.0
Farm 28	0.0	16.7	0.0	0.0	50.0	33.3
Farm 29	15.4	34.6	3.9	3.9	19.2	23.1
Farm 30	20.6	5.9	20.6	0.0	11.8	41.2
Farm 31	0.0	0.0	0.0	0.0	100.0	0.0
Farm 32	0.0	100.0	0.0	0.0	0.0	0.0
Farm 33	18.9	27.0	0.0	2.7	43.2	8.1
Farm 34	50.0	0.0	0.0	0.0	50.0	0.0
Farm 35	0.0	66.7	0.0	0.0	0.0	33.3
Farm 36	0.0	0.0	0.0	0.0	100.0	0.0
Farm 37	100.0	0.0	0.0	0.0	0.0	0.0
Farm 38	13.3	13.3	13.3	6.7	26.7	26.7
Farm 39	27.8	11.1	11.1	0.0	22.2	27.8
Farm 40	0.0	100.0	0.0	0.0	0.0	0.0
Farm 41	66.7	33.3	0.0	0.0	0.0	0.0
Farm 42	0.0	0.0	0.0	12.5	87.5	0.0
Farm 43	0.0	0.0	25.0	0.0	0.0	75.0
Farm 44	25.0	0.0	0.0	0.0	0.0	75.0

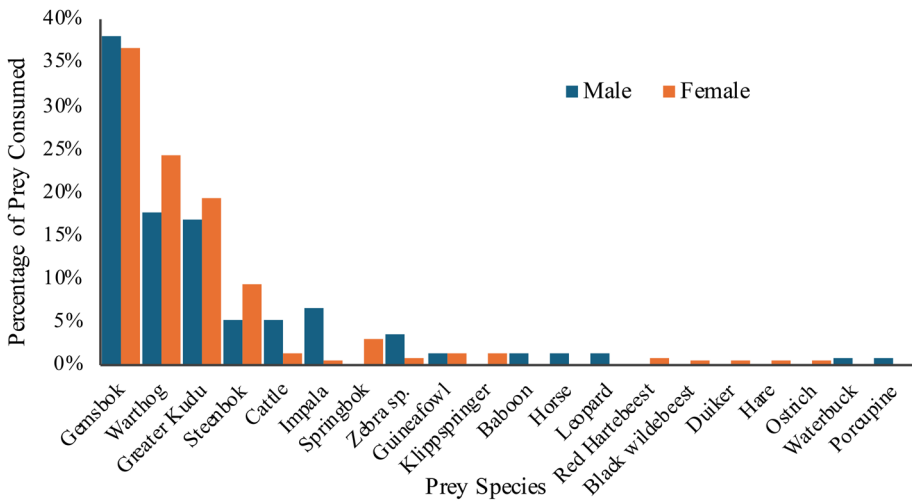


Fig. 2 Percentage of identified prey species killed by male (blue; $n=142$) and female (orange; $n=246$) leopards in freehold farmland in central Namibia

sub-adults 11.4%. Male and female leopards did not vary in their consumption of gemsbok age classes (Fisher's exact test, $p=0.87$). Most warthogs with an assessed age class ($n=69$) were adults (76.8%), while juveniles made up 17.4% and sub-adults 5.8%. Male and female leopards had a marginally significant difference in the age classes of warthogs consumed (Fisher's exact test, $p=0.08$), with females eating 91.7% of the juveniles consumed by leopards. The majority of greater kudus with an assessed age class ($n=54$) were juveniles (63.0%), while adults made up 29.6% and sub-adults 7.4%. Male and female leopards varied significantly in the age classes of greater kudus they consumed (Fisher's exact test, $p=0.05$) with females eating 73.5% of the juveniles consumed by leopards and males eating 62.5% of the adults consumed.

Livestock prey composition

Livestock prey was primarily cattle ($n=10$, 83.3% of livestock consumed and 2.7% of identified prey items). Of the seven cattle with assessed age classes, four were juveniles, two were sub-adults, and one was an adult. We also documented an adult and a juvenile horse killed (16.7% of livestock and 0.5% of overall prey items), both of which were consumed by male leopards. On average, livestock made up 2.8% of prey consumed by individual leopards, with percentages ranging from 0.0 to 20.0% (female range=0.0–4.5%, male range=0.0–20.0%). We documented 11 of 29 individual leopards feeding on livestock. Nearly all leopards feeding on livestock were only documented doing so once ($n=10$), while one leopard was documented feeding on cattle twice.

There was some variation in the patterns of livestock used by male and female leopards, but less by individual leopard or farm. Males consumed a significantly higher percentage of livestock (6.4% of identified prey, $n=9$) than females (1.3% of identified prey, $n=3$) (Fisher's exact test, $p=0.003$) (Fig. 2). The percentage of livestock among the identified prey on

individual farms did not vary significantly (Fisher's exact test, $p=0.41$), ranging from 0.0 to 25.0%, but with a maximum of one livestock prey item on any given farm.

Individual variation in prey composition

Individual leopard PS_i specialization scores averaged 0.74 ± 0.08 SD ($n=16$, range=0.61–0.89), indicating specialization in the population. Male and female leopards did not vary significantly in their specialization scores (Mann-Whitney test, $df=15$, $U=24.5$, $z=0.28$, $p=0.78$). Two leopards (female F01 and male M01) fed on substantially more ($\geq 20\%$) gemsbok than the rest of the leopard population, while three individuals (females F10 and F11, and male M05) feed on less gemsbok than the rest of the leopard population. Two leopard females (F05 and F07) fed on substantially more warthog than the rest of the population, and two individuals (females F09 and F10) fed on substantially more greater kudu than the rest of the population. Further, two leopards (female F11 and male M04) fed on substantially more other wild prey species than the remaining population, while one individual (female F03) feed on less wild prey species. No individual we analyzed specialized in livestock, with the highest specialization score for livestock being 0.07.

Among the 16 leopards with at least 10 documented kills of known prey species, most individuals ($n=10$, 62.5%) had at least 80% of their diet composed of the main three prey species (gemsbok, warthog, and greater kudu), and another four leopards had at least 70% of their diet composed of these three prey species (Fig. 3). Gemsbok on average represented 35.8% (range=10.0–73.3%) of the known prey consumed, with the similar average percentages among males (34.4%) and females (35.7%) (Fig. 3). Warthogs on average represented 23.8% (range=5.0–45.0%), with similar average percentages among females (25.6%) and males (19.9%). Greater kudu on average represented 19.7% (range=0.0–55.6%), with four

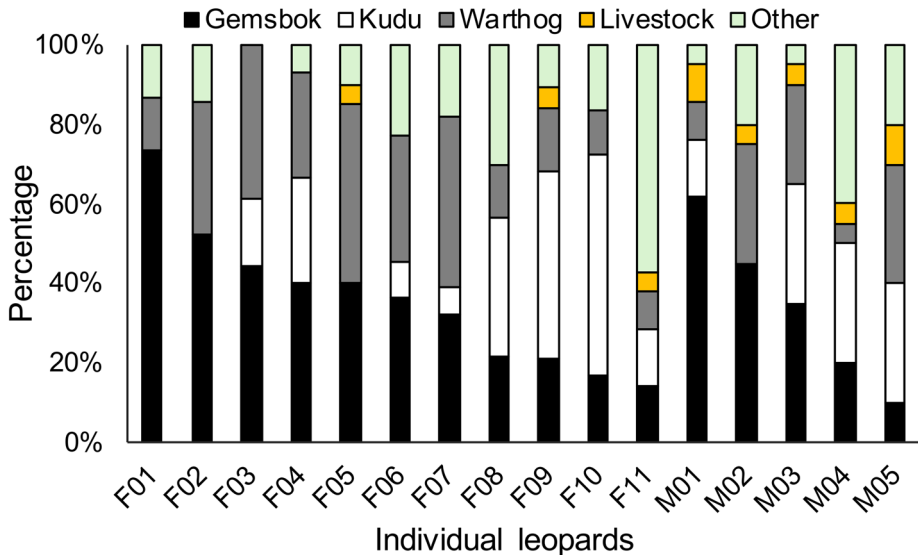


Fig. 3 Individual variation in composition of prey classes among the 16 individual leopards with at least 10 kills of identified prey. Prey classes consisted of gemsbok, warthog, greater kudu, livestock, and all other wild prey species

individual leopards never documented killing one, with similar average percentages among males (20.9%) and females (19.2%) (Fig. 3).

Foraging behaviors

Leopards exhibited a crepuscular pattern of temporal activity when killing prey (Fig. 4a), with females killing prey more often around sunset and males killing prey more often around sunrise (Fig. 4b). Leopards dragged prey ($n=21$ observations) from the kill site to the feeding site for an average of 28.0 m (\pm SD 32.2 m, range: 2–120 m). All prey we documented having been dragged from the site of the kill were wild ungulates. We found only 2.6% ($n=10$) of prey hoisted into trees, despite 20.2% of kill sites ($n=72$) having a tree suitable for hoisting prey within the 50 m radius of the kill site. Males ($n=3$, 2.1%) and females ($n=7$, 2.9%) did not vary in how often they hoisted prey (Fisher exact test, $df=1$, $p=0.75$). We did not observe prey being cached with leaves, dirt, or other material. Instead, leopards often placed carcasses under bushes ($n=299$, 80.2%), but also between rocks ($n=19$, 5.1%) or in caves ($n=2$, 0.05%). Among the remaining kills, 7.2% ($n=27$) were found in open areas and 7.0% ($n=26$) in riverbeds.

Discussion

Our study investigated the foraging ecology of leopards in the unprotected freehold farmlands of central Namibia, where human-leopard conflict often leads to the removal of “problem individuals” that are perceived as livestock specialists. Using GPS cluster methods across a ten-year period for 29 leopards, we examined prey composition, as well as individual specialization, foraging behaviors, and intersexual differences. Leopards mainly consumed wild ungulates (96.8%), with most of their prey across the farmlands being three wild ungulate species: gemsbok, warthog, and greater kudu. Livestock constituted only a small percentage (3.2%) of consumed prey and was limited to a maximum of one livestock prey item detected per farm and a maximum of two livestock for one leopard. However, even this limited consumption from the perspective of individual leopards can result in substantial economic losses for individual farmers when considering the value of cattle and horses, farm size (average >40 km²; Melzheimer et al. 2020) and leopard densities (3.5/100 km², Richmond-Coggan 2022). Due to the value of cattle and horses, these losses of livestock to leopards remain a key driver of antagonism toward leopards across their range (Kissui 2008; Athreya et al. 2011; Constant et al. 2015). As predicted, males killed more livestock than females, but prey species composition did not differ between sexes, although females preyed on younger age classes of large prey such as greater kudu. While we did find some individuals exhibited specialization for specific prey, we did not find any evidence for individuals specializing in livestock. Together, these findings advance our understanding of leopard ecology in human-modified landscapes and can be used to facilitate human-carnivore coexistence.

Overall, we documented 20 species of prey consumed, yet three wild ungulates (i.e., gemsbok, warthog, and greater kudu) accounted for 77% of all identified prey items consumed by leopards. This indicated a certain degree of population-level specialization, although this was not as evident as in some other felids, where majority of diet at the pop-

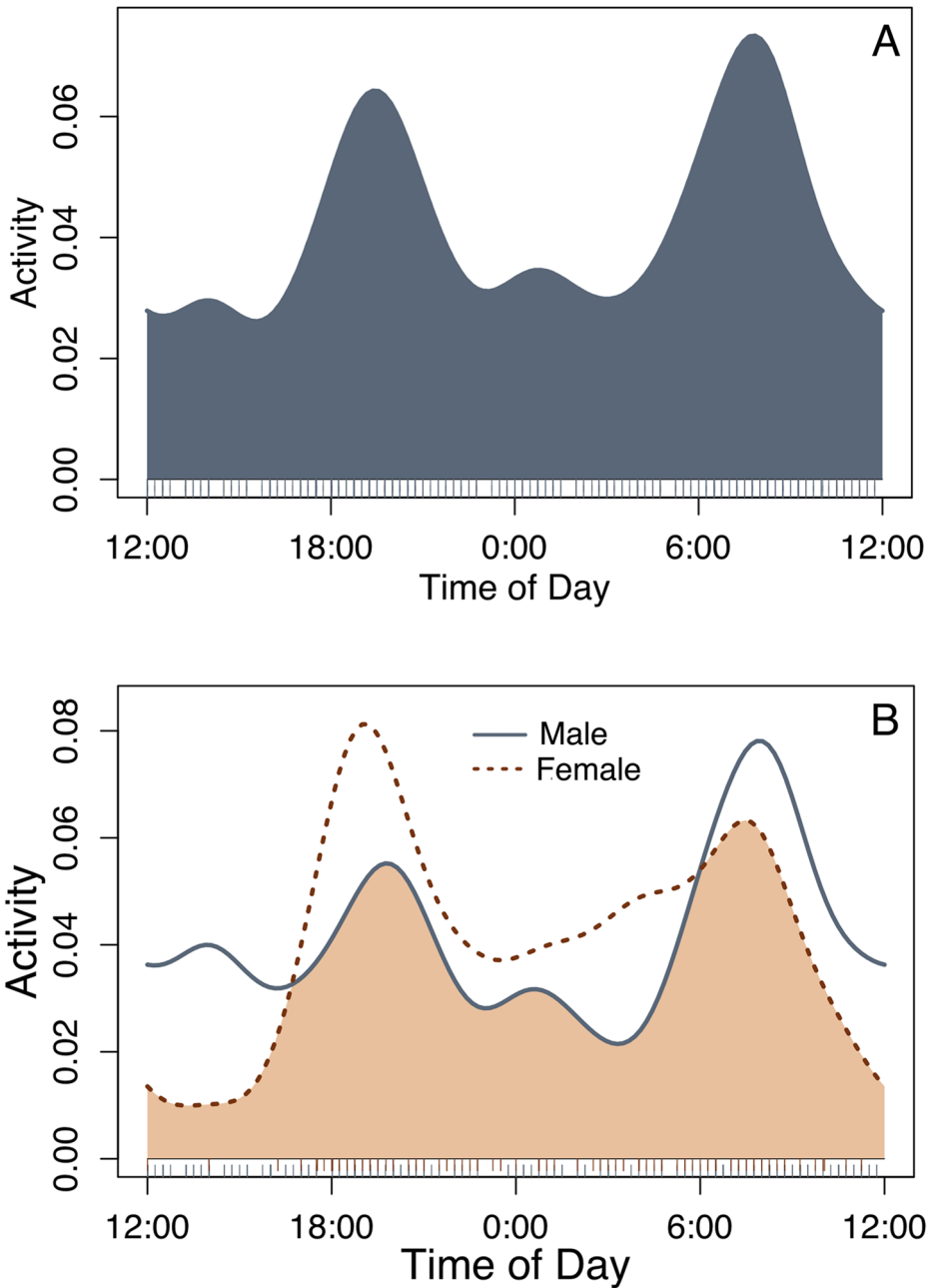


Fig. 4 Kernel density estimates of diel timing of leopard kills, based on the first GPS location recorded at confirmed kill clusters, in local Namibian time for **A**) all leopards combined, and **B**) sex-specific patterns for male and female leopards. In panel B, male and female activity curves are shown in distinct colors, with the shaded area representing the period of overlap in timing of kills

ulation-level is limited to a single prey species (e.g., Allen et al. 2015; Kortello et al. 2007; Krofel et al. 2011). Our findings support the niche variation hypothesis by showing that the population-level diet of leopards is likely based on the specialization of many individuals (Bolnick et al. 2003). Although adult gemsbok and greater kudu often exceed the typical prey size range reported in earlier literature, the majority of prey items of these two species in our study were juveniles. This finding shows that leopards can mediate their body size preferences by selecting individuals of larger prey in younger age classes. Juvenile prey are also more naïve in assessing predator risk, potentially making them easier for leopards to kill. The predominance of gemsbok, warthog, and greater kudu likely reflects a combination of availability and catchability, given that leopards often feed on the most abundant prey available (Stein et al. 2015). However, we were unable to formally assess prey preferences due to the absence of reliable, spatially-explicit data for prey abundance across the study area and because smaller prey items (e.g., birds and smaller mammals) are more difficult to detect using GPS telemetry due to short feeding times (Pitman et al. 2014; Oliveira et al. 2023). Nevertheless, our results provide evidence that leopards inhabiting unprotected, human-modified landscapes predominantly prey on wild species rather than livestock. This suggests there may be value in maintaining robust wild prey populations to lessen potential predation on livestock and encourage human-wildlife coexistence.

One of our key findings was that we found no evidence of individuals that specialized in killing livestock. This supports the idea that the number of livestock killed by individual leopards might sometimes be overestimated by farmers (e.g., Grey et al. 2017). Although approximately one-third of our monitored leopards consumed livestock at least once, only one leopard killed livestock on two occasions during the tracking period. While our hypothesis for individual specialization was supported, we found no individual leopard that exhibited specialization in livestock, and specialist individuals instead consumed specific wild prey species. This illustrates how individuals may exploit distinct dietary niches within shared ecological contexts (Bolnick et al. 2003). These findings do not support the prevailing assumptions among farmers that livestock depredation is driven by a small subset of specialized “problem individuals” (e.g., Boulhosa and Azevedo 2014). We acknowledge the possibility that problem individuals exist but were not included in our sample; for example because these leopards could be killed in retaliation soon after they become specialized in preying on livestock or learn to avoid traps, and thus our probability of capturing them might have been low.

Given the disproportionate effect that even occasional livestock losses can have on farmer attitudes and retaliatory behavior (Grey et al. 2017), our results underscore the need for evidence-based conflict mitigation strategies. Rather than focusing on removal of individual predators, our results suggest that management should prioritize systemic interventions such as improved livestock husbandry, protection of vulnerable age classes (e.g., calves), and the proactive management of wild prey populations. For example, in our study area, cattle were the main livestock prey (2.7% of identified prey killed), with calves being most frequently killed—suggesting that prevention measures in similar leopard-inhabited areas should be focused on cattle herds with calves. Lethal removal targeted at individuals may be unlikely to yield sustained benefits without evidence of repeated depredation by the individual, and in some systems can increase losses by disrupting the social structure and creating opportunities for more problematic individuals to move into the area (Wielgus et al. 2013; van Eeden et al. 2018). However, further research is needed to better understand

effectiveness of both lethal and non-lethal methods for preventing livestock depredation by large carnivores in general (McManus et al. 2015; van Eeden et al. 2018). In human-dominated landscapes, coexistence is likely best achieved through limiting losses to within socially tolerable bounds rather than attempting to eliminate all losses (Carter and Linnell 2016). Tolerance can potentially be increased through providing compensation for verified depredations to buffer economic losses, as well as providing incentives to improve husbandry practices (Dickman et al. 2011; Ravenelle and Nyhus 2017). Predators can also be sources of income through wildlife tourism, and performance-based payments for their presence could be used to increase tolerance in human-dominated landscapes (Zabel and Holm-Müller 2008). Ultimately, maintaining wild prey populations and promoting non-lethal mitigation tools may be most effective for fostering long-term coexistence between people and leopards in shared landscapes.

Our study also provides nuanced information on leopard foraging behavior. We found little difference in the wild prey species consumed by male and female leopards (Fig. 2), but males consumed three times more livestock than females. In human dominated landscapes, shifting hunting behavior towards nocturnal periods likely reduces encounters with humans, and our results support this hypothesis. Both sexes had crepuscular patterns in killing prey, but males more frequently killed prey around sunrise, while females killed prey around sunset. This might suggest female temporal avoidance of male activity peaks which may serve to reduce the risk of infanticide or aggressive encounters (e.g., Balme and Hunter 2013), although our analysis did not account for the presence of cubs. These results are consistent with the behavior of other solitary felids (e.g., Allen et al. 2025) and are similar to a previous study that also noted females having a peak of hunting activity at sunset (Pitman et al. 2013). Also of interest is that only 2.6% of kills were hoisted into trees by leopards, despite frequent availability of trees suitable for hoisting in the vicinity of kills. This is the lowest reported percentage in the literature to date, with previous studies ranging from 6.7 to 51.0% of kills hoisted (de Ruiter and Berger 2001; Pitman et al. 2013; Stein et al. 2015; Balme et al. 2017; Kittle et al. 2017). Instead, leopards frequently dragged prey from kill sites to concealed locations, primarily under bushes and occasionally between rocks or into caves. Dragging to concealed locations may be more common in habitats with abundant vegetation, especially where leopards are persecuted and hoisting prey on trees could make them more exposed. In addition, the low frequency of hoisting may reflect a reduced need for hoisting due to relatively low competition from other large carnivores in our study area. These nuanced temporal and spatial patterns in predation underscore the importance of considering intrasexual differences when studying leopard behavioral ecology and developing effective conservation planning.

While the breadth of our long-term dataset provides strong inferential power and gives us confidence in the robustness of the observed patterns, several methodological limitations warrant consideration. Although we have no evidence of systematic bias in the subset of clusters we examined, it is possible that including all of the clusters could have influenced the composition of prey identified, especially for smaller prey. Additionally, there was often a substantial delay between a leopard generating a cluster and our field investigation (averaging 59 days). Although our analyses revealed no significant effect of time lag on our probability of finding prey, carcass decomposition and scavenger activity may have hindered the identification of small prey. These are inherent limitations of GPS cluster methodology, which is less likely to detect brief feeding bouts and small prey items (e.g., birds and small

prey; Pitman et al. 2014; Oliveira et al. 2023). Large carnivores may also spend less time feeding on domestic animals, likely due to the increased risk from people at these kills (Talian et al. 2023). However, this was not the case in our study (with no significant difference between leopard feeding times at kills of livestock and wild prey), likely due to relatively large size of livestock in our study area (cattle and horses) compared to wild prey. Furthermore, killed livestock has high chance of being discovered by farmers in this area (who search for missing domestic animals), which makes it more likely for us to be informed of livestock kills. As a result of the inherent bias of the methodology we used, our study likely underestimates dietary diversity and may be biased toward larger and more detectable prey species (i.e., wild ungulates and livestock). To address these limitations and provide a more comprehensive understanding of large carnivore foraging ecology, especially in human-modified landscapes where dietary flexibility may facilitate the persistence of populations, future research focused on foraging ecology could integrate complementary methods such as scat analysis (Pitman et al. 2013).

Our long-term study on freehold farmlands in central Namibia offers a nuanced understanding of large carnivore foraging ecology and challenges some common assumptions about livestock predation. While we documented individual specialization in foraging behavior among leopards living in farmlands, livestock depredation appeared to be largely opportunistic rather than driven by a few persistently problematic individuals. This calls for further investigation into the occurrence of livestock-specialized predators and their role in human-carnivore conflicts across their ranges where livestock predation and wild prey abundance can vary considerably (Athreya et al. 2011; Kissui 2008). Our study highlights the value of fine-scale, individual-level data for informing conservation strategies for wildlife and importance of conducting research across the gradient of protected and non-protected areas with variable human impact and predator persecution. Our results also underscore the need for evidence-based management approaches that account for individual behavioral variation and suggest the maintenance of wild prey populations and non-lethal prevention of livestock depredation may be a key to coexistence with large carnivores in agricultural landscapes. This highlights the need for coexistence strategies that are grounded in local ecological realities, particularly in human-dominated landscapes.

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Equal, Supervision—Lead, Resources—Supporting, Visualization—Supporting, Writing—original draft—Supporting, Writing—review & editing—Equal.

Data availability The data is available for any reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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