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Article *in* American Journal of Primatology · January 2020

DOI: 10.1002/ajp.23098

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Received: 17 May 2019 | Revised: 24 October 2019 | Accepted: 20 December 2019

DOI: 10.1002/ajp.23098

RESEARCH ARTICLE

AMERICAN JOURNAL OF PRIMATOLOGY WILEY

Leopard predation on gelada monkeys at Guassa, Ethiopia

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Funding information

Dean Gibson and San Diego Zoo; Leakey Foundation; CSU Fullerton; Margot Marsh Biodiversity Foundation; U.S.-Norway Fulbright Foundation; Gisela and Norman Fashing; French Agence Nationale de la Recherche; Primate Conservation Inc.; Joe and Pat Healey; Anita and Hans-Peter Profunser; Christopher Schroen Memorial Fund

ABSTRACT

Predation is widely believed to exert strong selective pressure on primate behavior and ecology but is difficult to study and rarely observed. In this study, we describe seven encounters between lone wild leopards (*Panthera pardus*) and herds of geladas (*Theropithecus gelada*) over a 6-year period in an intact Afroalpine grassland ecosystem at the Guassa Community Conservation Area, Ethiopia. Three encounters consisted of attempted predation on geladas by leopards, one of which was successful. All three attacks occurred in low-visibility microhabitats (dominated by tussock graminoids, mima mounds, or tall shrubs) that provided leopards with hidden viewsheds from which to ambush geladas. An additional four encounters did not result in an attempted attack but still document the consistently fearful responses of geladas to leopards. In encounters with leopards, geladas typically gave alarm calls ($n = 7$ of 7 encounters), reduced interindividual distances ($n = 5$), and collectively fled towards or remained at their sleeping cliffs ($n = 7$), the only significant refugia in the open-country habitat at Guassa. Geladas did not engage in mobbing behavior towards leopards. Encounters with leopards tended to occur on days when gelada herd sizes were small, raising the possibility that leopards, as ambush hunters, might stalk geladas on days when fewer eyes and ears make them less likely to be detected. We compare the behavioral responses of geladas to leopards at Guassa with those previously reported at Arsi and the Simien Mountains and discuss how gelada vulnerability and responses to leopards compare with those of other primate species living in habitats containing more refugia. Lastly, we briefly consider how living in multilevel societies may represent an adaptive response by geladas and other open-country primates to predation pressure from leopards and other large carnivores.

KEYWORDS

gelada, leopard, microhabitat, open-country, predation, refugia

1 | INTRODUCTION

Predation is considered a major selective pressure on behavior and group-living in many diurnal primates (Shultz, Opie, & Atkinson, 2011; Sterck, Watts, & van Schaik, 1997; van Schaik, 1983). Among predators known to predate upon primates, large felids are especially important, having been implicated in more primate attacks than any other category of predator, including raptors, canids, hyaenids, small carnivores, and reptiles (Hart, 2007). The most widespread of the large felids (Jacobson et al., 2016), leopards (*Panthera pardus*) are known to prey on a wide range of extant catarrhine primates, including Asian and African colobines, guenons, mangabeys, baboons, great apes, and humans (Busse, 1980; D'Amour, Hohmann, & Fruth, 2006; Isbell, 1990; Isbell, Bidner, Van Cleave, Matsumoto-Oda, & Crofoot, 2018; Karanth & Sundquist, 1995; Koziarski, Kissui, & Kiffner, 2016; Matsumoto-Oda, Isbell, & Bidner, 2018; Naha, Sathyakumar, & Rawat, 2018; Tutin & Benirschke, 1991; Zuberbühler & Jenny, 2002). There is also evidence from the fossil record suggesting that leopards preyed on now-extinct hominins (e.g., *Paranthropus robustus*: Brain, 1970; *Homo neanderthalensis*: Camarós, Cueto, Lorenzo, Villaverde, & Rivals, 2016). Thus, leopard predation has probably long played a role in shaping the predator defense and avoidance adaptations of many primate species, including members of the hominin lineage (Isbell et al., 2018; Zuberbühler & Jenny, 2002).

Although a number of studies have investigated leopard predation on primates inhabiting lowland rainforests or savannah-woodland habitats (e.g., Boesch, 1991; Isbell, 1990; Isbell et al., 2018; Zuberbühler & Jenny, 2002), little is known about primate-leopard interactions in more open environments where refugia from predators are scarce. This gap in our knowledge is due to both the rarity of observed predation events in the wild in general (Isbell, 1994a; Miller & Treves, 2011) and the dearth of extant primate species living in open habitats in particular. Geladas (*Theropithecus gelada*) are endemic to Afroalpine grassland habitats in the Ethiopian Highlands, and thus are good candidates for offering insights into the impacts of leopard predation on primate behavior in open-country habitats.

Living at elevations of 1,700–4,600 m above sea level (a.s.l), geladas are medium-sized and sexually dimorphic monkeys that form multilevel societies (Bergman & Beehner, 2013). These multilevel societies are comprised of core social structures, called one-male units (OMUs), that consist of a single dominant leader-male, a number of females and their young, and, occasionally, one or two additional subordinate follower-males (Kawai, Ohsawa, Mori, & Dunbar, 1983; Snyder-Mackler, Beehner, & Bergman, 2012). OMUs that share a common home range are subsequently nested within a band. The OMUs within a band aggregate and separate at irregular intervals, and are sometimes joined by OMUs from other bands, resulting in a modular social grouping system. All the geladas present at a particular time are referred to as a herd (Kawai et al., 1983; Snyder-Mackler et al., 2012). Gelada herds, which can contain up to 1,200 individuals, represent some of the largest aggregations of any primate species (Bergman & Beehner, 2013; Snyder-Mackler et al., 2012).

One function of the aggregations formed by geladas may be to mitigate predation threats (Crook, 1966; Dunbar & Dunbar, 1975). Individuals in a large herd may benefit from both the increased predator detection probability offered by so many eyes and ears and the reduced likelihood during a successful attack that any one individual will be the one captured by a predator (i.e., the dilution effect) (Hamilton, 1971; Isbell, 1994a; Olson, Hintze, Dyer, Knoester, & Adami, 2013). In addition to forming large aggregations, geladas adopt several other antipredator strategies that, like in other primates, may vary depending on the type of predator encountered and the circumstances surrounding each encounter (Cheney & Seyfarth, 1990, Crofoot, 2012). Though occasional cases of active defense towards predators, such as chasing or mobbing behavior, have been observed (leopards: Iwamoto, Mori, Kawai, & Bekele, 1996; domestic dogs, *Canis lupus familiaris*: C. M. Miller, pers. observ.), geladas primarily exhibit less aggressive, more evasive antipredator behaviors. These responses to predators can involve alarm-calling, heightened vigilance, and flight to the safety of sleeping cliffs, the geladas' only significant refugia in their Afroalpine habitats (dogs: Iwamoto, 1993; Iwamoto et al., 1996; leopards: Hunter, 2001).

The Afroalpine grasslands of the Ethiopian Highlands provide an excellent ecosystem in which to study predator–prey dynamics. This is due partly to the presence of a variety of microhabitats that could contribute to variation in predator–prey interactions, and partly to the open-country nature of the highlands that allows for observations of behavioral responses of prey to predators when refugia are scarce (Ashenafi, 2001; Fashing, Nguyen, Venkataraman, & Kerby, 2014) (Figure 1). Furthermore, Ethiopian Afroalpine grasslands that have not been heavily degraded by livestock grazing or farming still support diverse carnivore assemblages, including leopards, spotted hyenas (*Crocuta crocuta*), servals (*Leptailurus serval*), African wildcats (*Felis lybica*), Ethiopian wolves (*Canis simensis*), and cryptic African wolves (*Canis aureus lupaster*) (Gutema et al., 2018; Venkataraman, Kerby, Nguyen, Ashenafi, & Fashing, 2015). Although geladas exhibit a range of behavioral responses to canids, from passive tolerance of Ethiopian wolves in their herds to alarm-calling and immediate flight away from domestic dogs (Venkataraman et al., 2015), little is known about how geladas react to wild felids.

In this report, we provide complete accounts of seven encounters between leopards and geladas in an intact Afroalpine grassland ecosystem, the Guassa Community Conservation Area, in north-central Ethiopia. During each leopard sighting, we recorded detailed data on the behavior and location of nearby gelada(s) and the overall herd size, as well as the dominant vegetational characteristics of the habitat in which the encounter occurred. Here, we evaluate gelada responses to leopards by examining a mix of quantitative and anecdotal information on movement and spacing patterns at the time of and after each encounter. We then compare gelada–leopard interactions at Guassa with those at two other sites (Arsi and Simien Mountains National Park) and discuss how gelada vulnerability and responses to leopards compare with those of other primate species living in less open habitats containing more refugia. Lastly, we briefly consider how living in multilevel societies may represent an adaptive

FIGURE 1 Habitats where gelada–leopard encounters occurred at Guassa, Ethiopia. (a) Giant lobelias atop plateau where Attack 1 and Interaction 4 occurred. (b) Mima mounds where Interaction 3 occurred, representative of the habitat where Attack 2 occurred. (c) Field of tussock grass where Attack 3 occurred. (d) Cypress tree plantation near where Attack 3 occurred. (e) Cliffs on which Interaction 2 occurred. (f) Cliffs on which Interaction 1 occurred. Photos by Carrie M. Miller (a,c,d,e) and Iris R. Foxfoot (b,f)

response by geladas and other open-country primates to predation pressure from leopards and other large carnivores.

2 | METHODS

2.1 | Study site and subjects

This study was conducted in the Guassa Community Conservation Area (hereafter Guassa), an intact 111 km^2 Afroalpine grassland ecosystem in the Menz Highlands of north-central Ethiopia (N 10°15′–10°27′; E 39°45′–39°49′). Guassa sits atop a plateau 3,200–3,600 m a.s.l., along the western rim of the Great Rift Valley, and has been protected by an indigenous community conservation system for the past 400 years (Ashenafi, 2001; Ashenafi & Leader-Williams, 2005; Welch, Kerby, & Frost, 2017). Guassa's boundaries are delineated by cliffs along its eastern border and local farmlands everywhere else, and is named after *guassa* (*Festuca macrophylla* Poaceae), a perennial tall grass of up to 1 m in height that is abundant in the region (Ashenafi, 2001; Fashing et al., 2014). In addition to plains dominated by *guassa*, other microhabitats at Guassa include open short graminoid and forb dominated areas, seasonal wetlands dominated by tall tussock graminoids, areas dominated by shrubs or giant lobelias (*Lobelia rynchopetalum* Campanulacaeae), and a small nonnative cypress tree (*Cupressus lusitanica* Cupressaceae) plantation (Ashenafi, 2001; Fashing et al., 2014). At Guassa, tussocks (often the sedge, *Carex monostachya* Cyperaceae) can reach up to 1 m in height, shrubs 1–2 m, giant lobelias 3 m, and cypresses 8–10 m, whereas short graminoids are typically <0.1 m tall (Fashing et al., 2014). Mima mounds, dome-like mounds up to 1.5 m tall and 3 m wide created by rodents (Ashenafi, Leader-Williams, & Coulson, 2012), are also a common feature at Guassa and are often covered with tall graminoids and shrubs (Figure 1b). Only three human structures exist on Guassa: A campsite (Gelada Camp: 10°20′N, 39°49′E, Elev: 3,438 m) consisting of 5–7 closely spaced tents occupied by Guassa Gelada Research Project (GGRP) researchers and staff, a small ecotourist lodge (Wolf Lodge) operated by the local community 5 km south of Gelada Camp, and a small elementary school (School) 1 km south of the Wolf Lodge (Figure 2).

The observations described here are part of the GGRP, an ongoing long-term study of gelada behavioral ecology that began in December 2005 (systematic continuous data collection began in January 2007: Nguyen et al., 2015). Five of the seven gelada–leopard interactions described herein occurred over the course of a single year, from May 2017 to May 2018, and the remaining two were observed before May 2017 (02 October 2012 and 05 February

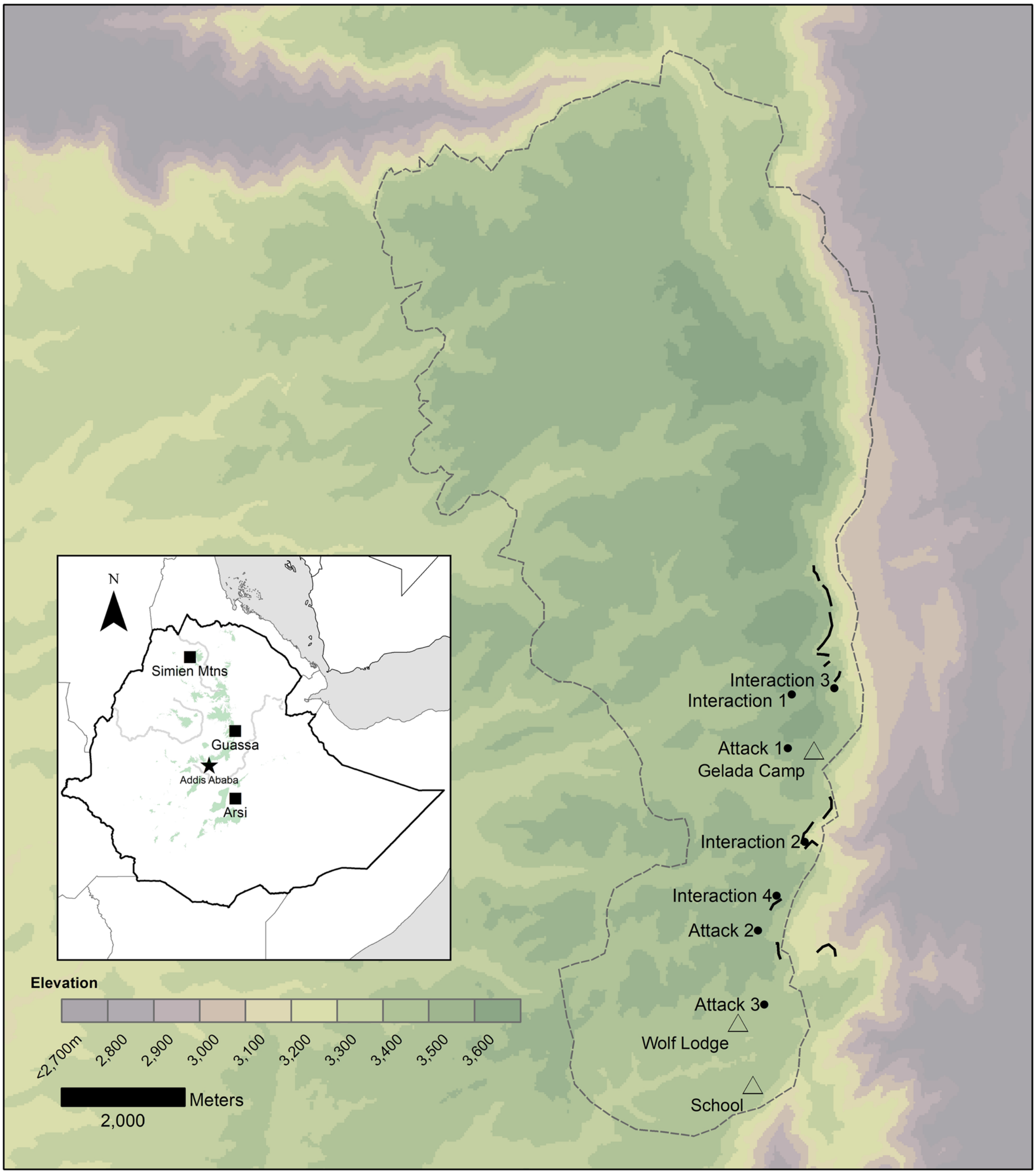

FIGURE 2 Map of Guassa depicting the locations where gelada herds encountered lone leopards and the locations of nearby sleeping cliffs (depicted with solid black lines) at Guassa, Ethiopia between 2012 and 2018

2015). Researchers have collected data on geladas belonging to the "Steelers Band" (totaling ~220 individuals in 15 OMUs in January 2007 and ~150 individuals in 13 OMUs in May 2018) on 2 of every 3 days on average since the start of continuous data collection in January 2007. All geladas in the study band are individually recognizable and well-habituated to the presence of researchers. Their mean daily travel distance is 3,496 m, with a mean annual home range of 9.3 km^2 (95% fixed kernel estimate; $n = 5$ years; Moua, 2015). The fluidity of gelada social organization (Snyder-Mackler et al., 2012) means that on any given day, not all Steelers Band OMUs were necessarily present together, and that non-Steelers OMUs often traveled with the band for hours, days, weeks, or even months at a time. As such, herd counts, conducted at least once per observational day, typically consisted of both Steelers and non-Steelers individuals.

2.2 | Behavioral data collection

As part of the regular data collection protocol of the GGRP, researchers obtained GPS points at 30-min intervals to track the gelada herd's daily movement patterns, beginning between 0700 and

0800 hr and ending between 1730 and 1800 hr (Moua, 2015). In the event of a leopard sighting, other data collection was abandoned and all leopard and gelada behaviors and interactions were recorded on an ad libitum basis (Altmann, 1974). Data gathered during these encounters included a count of the number of geladas present in the herd, a description of the vegetation in which the encounter occurred, an estimate of the distance between the leopard and the nearest gelada and researcher, an estimated range of interindividual spacing between geladas before and after the leopard sighting, any observed gelada vigilance behavior including alarm-calling, and all other interspecific interactions between the leopard and the geladas. Researchers also recorded the age class, sex, and where possible, identity, of the closest gelada to the leopard (adults were designated to be of "prime-age" if they appeared to be in early- to mid-adulthood and showed no signs of advanced aging, Nguyen et al., 2015). Finally, where possible, researchers also recorded GPS points at the locations of the researcher, the leopard, and the closest gelada to the leopard in each encounter.

All protocols for this study were reviewed and approved by the Ethiopian Wildlife Conservation Authority and the IUCAC at California State University Fullerton. All research reported here also adhered to the legal requirements of Ethiopia and to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates.

3 | RESULTS

During the first 5.75 years (January 2007–September 2012) of continuous observation by members of the GGRP, no encounters between leopards and geladas were recorded. Over the subsequent 5.75 year period (October 2012–May 2018), seven gelada–leopard encounters were observed (Figure 2). We do not believe this difference in leopard sightings between the periods relates to changes in gelada habituation over time (by mid-2008, they were already habituated to within 5–10 meters of observers) and our rates of gelada observation have not changed over the course of the study (except in 2017–18 when an extra observer was in the field enabling more frequent monitoring than 2 of every 3 days).

Six of the seven encounters with leopards occurred on days when geladas were in herds smaller than their average size that month and year (Table 1). On average, gelada herd sizes during leopard encounters were 22% smaller than the average herd counts for the months, and 27% smaller than the average herd counts for the years, when these encounters occurred. Furthermore, four of the seven encounters with leopards occurred during 2018, when geladas formed much smaller average herds than in any previous year.

In encounters with leopards, geladas typically gave alarm calls ($n = 7$ of 7 encounters), decreased their interindividual distances ($n = 5$), and collectively fled towards or remained at their sleeping cliffs ($n = 7$). Geladas did not engage in mobbing behavior towards leopards. Below, we provide detailed descriptions of each encounter's environmental context and the behavioral interactions between leopards and geladas in each instance, starting with the three leopard attacks on geladas (see Table 2 for a summary).

3.1 | Attack 1. The unsuccessful pursuit of members of a gelada herd by a leopard

At 1430 on 05 February 2015, a herd of 224 geladas were traveling north up a ridge to a plateau dominated by patches of giant lobelias, *guassa*, and other tall graminoids, occasionally stopping to feed. The geladas were widely distributed (spaced 2–20 m apart), with the leaders of the OMUs crossing the plateau 500 m ahead of the bachelor males, who had yet to ascend the ridge at the back of the herd. The remaining geladas were spread out approximately 100 m across the face of the ridge, making their way up to the plateau. Shortly after ascending the ridge, the ~80 geladas at the front of the herd turned around and started running south, past the researcher (EKB), towards the bulk of the herd, which was still ascending the ridge. At this time, EKB heard several alarm calls, and an adult leopard emerged from a stand of giant lobelias, chasing a group of geladas. The leopard was 5 m away from the closest gelada in the herd, likely an adult female, but after an ~8 m pursuit, the leopard noticed the researcher 30 m away and immediately discontinued the chase and ran back into the stand of giant lobelias from which it had emerged. The chase and retreat by the leopard

TABLE 1 Gelada herd counts at the time of leopard encounters relative to the mean (± *S.E.*) herd count for each encounter month and year

			Comparision to herd count that month		Comparision to herd count that year	
Date	Time	Herd count during encounter	Mean ± *S.E.*	% Difference	Mean ± *S.E.*	% Difference
02OCT12	1300	135	186 ± 25	↓ 27%	156 ± 5	↓ 13%
05FEB15	1430	224	220 ± 18	↑ 2%	205 ± 7	↑ 9%
28SEP17	0840	50	76 ± 18	↓ 34%	167 ± 9	↓ 70%
20FEB18	0949	72	126 ± 16	↓ 43%	92 ± 8	↓ 22%
19MAR18	0925	50	63 ± 10	↓ 21%	92 ± 8	↓ 46%
03APR18	1631	73	89 ± 25	↓ 18%	92 ± 8	↓ 21%
12APR18	1345	80	89 ± 25	↓ 10%	92 ± 8	↓ 13%

TABLE 2 Summary of key characteristics of the seven encounters between gelada herds and lone leopards at Guassa, Ethiopia between 2012–2018

Gelada–leopard encounter	Date	Time	Location[1]	Weather[2]	Microhabitat[3]	# Geladas present[4]	Gelada nearest to leopard: Age class	Gelada nearest to leopard: Sex	Gelada nearest to leopard: Min. distance to leopard (m)	Gelada interindividual spacing (m)[5]: Before encounter	Gelada interindividual spacing (m)[5]: After encounter	Did leopard pursue gelada (s)?[6]	Distance from nearest sleeping cliff (m)[7]	Distance geladas ran (m)[8]	Did gelada(s) alarm-call?	Did gelada(s) mob leopard?	Min. distance between observer (s) and leopard (m)[9]	Obser-ver(s)
Attack 1	05FEB15	1430	N10°20.05458′ E039°48.42882′	Sunny, no fog	Mima mound, mixed shrub, and giant lobelia	224*	Adult	♀	5	2–20	1–5	Y	1014	n/a	Y	N	30	EKB
Attack 2	20FEB18	0949	N10°18.459′ E039°48.168′	Partly cloudy, light fog	Mima mound & tall graminoid	72	Adult	♂	2	5–10	0–5	Y	352	50	Y	N	15	BL & IRF
Attack 3	03APR18	1631	N10°17.809′ E039°48.223′	Partly cloudy, no fog	Tall graminoid	73	Adult	♂	0	4–15	0–2	Y	774	100	Y	N	100	BL
Interaction 1	02OCT12	1300	N10°20.52636′ E039°48.46344′	Sunny, no fog	Tall graminoid & mixed shrub	135	Adult	♂	100	unk	unk	N	714	100	Y	N	200	BSK
Interaction 2	28SEP17	0840	N10°19.235′ E039°48.578′	Sunny, no fog	Mixed shrub	50	Adult	♂	60	0–10	0–10	N	50	n/a	Y	N	200	CMM
Interaction 3	19MAR18	0925	N10°20.581′ E039°48.836′	Cloudy, light fog	Short graminoid	50	Adult	♂	40	5–10	0–2	N	102	n/a	Y	N	150	CMM
Interaction 4	12APR18	1345	N10°18.763′ E039°48.331′	Cloudy, light to medium fog	Mima mound & tall graminoid	80	Juve-nile	♂	40	2–5	0–2	N	86	n/a	Y	N	40	CMM

[1]GPS coordinates (latitude, longitude) of the leopard when first detected by observer(s).
[2]Weather at time of encounter: No fog = no fog present; light fog = fog present but observers can still see objects >100 m in the distance.
[3]General categories of plants that predominate in the habitat where the encounter occurred.
[4]Approximate number of geladas present at the time of the encounter.
[5]Estimated range of interindividual distances (in meters) between members of the gelada herd shortly before and immediately after a leopard encounter; "unk" indicates that this value is unknown.
[6]Were any geladas actively pursued by the leopard? Y = yes, N = no.
[7]The distance to the nearest sleeping cliff from where the geladas were located at the time of their encounter with the leopard.
[8]The distance the majority of the gelada herd ran (continuously traveled without stopping) after the leopard was first detected.
[9]The minimum distance between the leopard and the nearest observer(s).
*Although the total herd size count at this time was 224 geladas, the leading contingent of ~80 geladas were the only ones to encounter the leopard.

lasted ~10 s. Following the attack, the geladas remained in place and continued to alarm-call for several minutes, at estimated interindividual distances of 1–5 m, before travelling east towards a sleeping cliff. Several hundred meters east of where the attack occurred, the geladas again reached the top of the plateau, where they remained, 1–2 m apart, to graze, groom, and rest. After the attack, the geladas spent the night at a different sleeping cliff than the one they had slept on the previous day, though these cliffs are spaced only a few hundred meters apart.

3.2 | Attack 2. The unsuccessful pursuit of an adult male gelada by a leopard

At 0833 on 20 February 2018, a herd of 72 geladas departed from their sleeping cliff and gradually ascended 500 m up a steep rise and onto a short grass meadow plateau covered with mima mounds. Individual geladas, spaced 5–10 m apart, foraged as they made their ascent.

At 0915, several adult males moved northwest up a gradual rise consisting of several rock outcrops, briar root shrubs (*Erica arborea* Ericaceae) and tall graminoids, and disappeared from sight. At 0949, the males (~40 m from the closest herd members) bounded down the rise towards the bulk of the herd, emitting loud alarm calls that the rest of the herd quickly emulated. A few seconds later, Logan (LOG), the large, prime-age adult leader-male of a study OMU (K-unit), was seen leaping off a rocky outcrop towards the main herd, pursued by an adult leopard, ~2 m in length. The leopard was only 1–2 m behind LOG, but after a short pursuit (5–10 m), it saw the observers and immediately aborted the chase, turned around, and fled back up the rise and out of sight.

At its closest, the leopard was 15 m away from the observers (BL, IRF) and remained in sight for <10 s. During the pursuit, the main gelada herd fled 20 m, pausing ~50 m away from the leopard's closest point, and 10 m from the edge of a steep downgrade that eventually gave way to sheer sleeping cliffs 500 m below. The geladas continued to alarm-call for 5 min after the attack, and when LOG was seen in the herd shortly after, he had a fresh 1 × 3 cm wound above his left brow that was likely incurred while fleeing from the leopard.

At 0959, the herd began traveling east, back towards their sleeping cliffs, moving in tight formation with all individuals ≤5 m apart. After their descent from the plateau, at 1052, the gelada herd ventured onto farmlands below their sleeping cliff, and subsequently out of sight. The geladas were located at 0949 the next day (21 February 2018) at a sleeping cliff 2 km north of their original cliff.

3.3 | Attack 3. The ambush capture of an adult male gelada by a leopard

At 1630 on 03 April 2018, a herd of 73 geladas was grazing in a sedge-dominated (*Carex monostachya* Cyperaceae) tussock habitat 200 m east of the Wolf Lodge, dispersed 2-15 m apart (Figure 1c). At this time, You-Know-Who (YOU), a prime-age follower-male in a study OMU (V-unit), was obscured from view in the ~1 m tall tussocks. The next closest individual, an unidentified subadult male, was ~10 m away. At 1631, many members of the herd suddenly emitted intense alarm calls and sprinted ~100 m west, out of the tussocks and into a short graminoid dominated habitat, in the opposite direction of their sleeping cliffs. The geladas clustered together, ≤2 m apart, and faced the tussocks as they continued to alarm-call and display vigilance behavior, with a few individuals standing bipedally.

From 1631–1633, YOU's body was seen being moved but was almost entirely obscured from view by the tall tussocks. During this time, the gelada herd ran east back towards the sleeping cliffs and out of sight, passing within 150 m of YOU's location in the tussocks. A few moments later, YOU's body moved past the edge of the tussocks and into the short grass, and the adult leopard carrying it, ~2 m in length, was clearly seen for the first time.

The leopard continued walking northeast along the edge of the tussocks, intermittently carrying and dragging YOU's body by the neck towards the nearby cypress plantation (Figure 3). At 1634, having moved ~30 m from the attack site, the leopard stopped,

FIGURE 3 (a) A leopard carrying an adult male gelada, YOU, at Guassa, Ethiopia during Attack 3. (b) The same leopard during the same attack, standing over YOU and turning its gaze towards the observer. Photos by Bing Lin

turned around, and upon seeing the observer (BL) ~100 m away, immediately abandoned YOU's body and fled into the cypress plantation. There were no other geladas in sight by this time.

By the time BL approached YOU's body at 1640, YOU was already dead and children from the school south of Wolf Lodge had begun gathering around YOU's body, probably because they heard the geladas' alarm calls. As a result, BL decided to carry YOU back to Gelada Camp for a postmortem examination. The next day, the geladas were found at a different sleeping cliff, a few kilometers north of the one from the day before.

On 04 April 2018, BL and IRF dissected YOU. Bloodstains were noted on YOU's muzzle and anus, and his body was in *rigor mortis* with bloating around his midsection. YOU weighed 17.75 kg and his presumed cause of death was a broken neck. Six additional injuries attributed to the leopard attack were also present: A scratch on his left breast, and puncture wounds on his right breast, under his chin, in the middle and below his throat, and on the left side of his lower jaw (Figure 4). YOU also had a parasitic swelling (10 × 8 × 5 cm in size) on his right breast caused by the tapeworm *Taenia serialis* (Nguyen et al., 2015), which had not seemed to impede his movement or behavior before his death. After the postmortem was completed, YOU was buried at Gelada Camp for future excavation and donation to the Comparative Mammalogy Lab at the National Museum of Ethiopia.

In addition to the three leopard attacks, we witnessed four additional gelada interactions with leopards that did not culminate in attempted predation.

3.4 | Interaction 1. Gelada–leopard encounter in a valley

At 1300 on 02 October 2012, a herd of 135 geladas, most of whom had been foraging moments earlier, began issuing loud alarm calls and looking across the small valley where they were located. Following their gaze, one of the two observers (BSK) saw a single unidentified adult male gelada ~200 m away. Spotting movement ~100 m below the unidentified male, BSK looked through binoculars to see a leopard moving rapidly up the valley slope, away from both the lone gelada male and the gelada herd. The leopard paused behind a bush and then disappeared into tall graminoids. Based on the location where it was first spotted and its direction of movement, the leopard probably emerged from a dense microhabitat of giant lobelias and shrubs located between the gelada male and the herd shortly before the first alarm call was uttered. After the leopard sighting, the gelada herd reversed their direction of travel, moving away from the leopard's last location and back towards their sleeping cliffs.

3.5 | Interaction 2. Gelada–leopard encounter at a cliff

At 0803 on 28 September 2017, four gelada OMUs (~50 geladas) were ascending from their sleeping cliff onto the plateau above. Half were resting or feeding on the cliff edge, dominated by rocks and *guassa*, and half were resting on large boulders ~300 m below the cliff edge, dispersed over 40 m with individuals 0–10 m apart. At the base of the cliff were large boulders, tall shrubs, giant lobelias, and large succulents.

At 0840, geladas at the base of the cliff began alarm-calling, followed shortly by the geladas at the top of the cliff. Following the geladas' gazes, the observer (CMM) sawan adult leopard (~2 m in length) traveling across the boulders, passing within 60 m of the closest gelada, an unidentified adult male, near the cliff base. The leopard paused briefly and looked in the direction of the alarm-calling geladas, but did not alter its course and remained in view as it headed south, away from the geladas, from 0842 to 0845. The leopard did not seem to notice CMM at any point during the encounter, and once it was out of sight, the geladas continued to

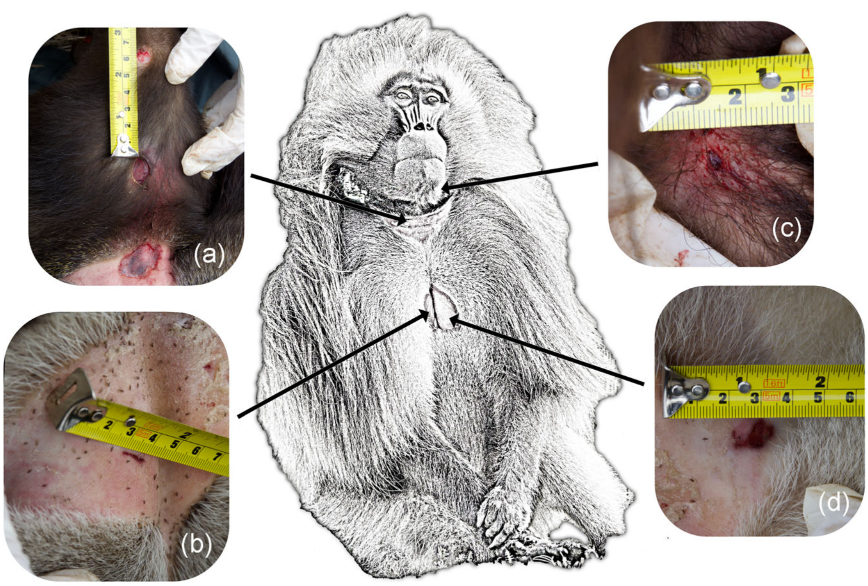

FIGURE 4 Postmortem injuries found on YOU, the adult male gelada killed by a leopard in Attack 3. (a) 1.0 × 1.0 cm puncture wound under the chin (top), 1.5 × 1.0 cm puncture wound to the center of the throat (middle), 4.0 × 2.0 cm puncture wound in the flesh below the neck (bottom). (b) 1.0 cm scratch on the right side of the chest. (c) Puncture wound on the lower left side of the jaw. (d) 1.0 × 3.0 cm puncture wound on the left side of the chest. Photos by Bing Lin

alarm-call for 5 min until 0850, when they resumed ascending the cliff and began their day's ranging on the plateau above. During the interaction, geladas exhibited no noticeable change in interindividual spacing.

3.6 | Interaction 3. Gelada–leopard encounter below a cliff

At 0900 on 19 March 2018, a herd of ~50 geladas was grazing at the bottom of their sleeping cliff, dispersed over ~80 m, spaced 5–10 m apart. This habitat consisted of thick vegetation, a mix of shrubs, short graminoids, and giant lobelias, which transitions into private farmlands ~100 m east from the cliff base. *Guassa* and other tall graminoids predominated higher up on the cliff.

At 0925, the geladas began alarm-calling and looking towards the north side of the cliff, which drops into a V-shaped canyon. An unidentified adult male gelada ran in the direction in which the herd was alarm-calling, followed closely by a medium-sized juvenile ~5 m behind. At this point, an adult leopard (~2 m in length) was seen ascending the cliff along a nearly vertical gradient (see Figure 1e), about 150 m away from the observer (CMM).

The leopard was ~40 m from the nearest adult male gelada (previously seen running towards the leopard), who continued to alarm-call and follow the leopard at this distance, sprinting a short distance while intermittently stopping and looking back at the other herd members. Although the leopard looked in the direction of the alarm-calling geladas, it did not react in any other way. The leopard continued to ascend the cliff and was lost from view at 0933 amidst the tall graminoids towards the clifftop. The geladas alarm-called for several minutes and reduced interindividual spacing to ≤2 m. By 0945, the geladas ascended the south side of the cliff, traveling in the opposite direction, away from where the leopard was last seen traveling.

3.7 | Interaction 4. Gelada–leopard encounter on the plateau

At 0830 on 12 April 2018, a herd of ~80 geladas was traveling away from their sleeping cliffs in a southerly direction to a small valley covered by mima mounds and dominated by tall graminoids. Conditions were foggy, resulting in poor visibility. The geladas moved in tight formation, dispersed over ~50 m with individuals spaced 2–5 m apart. By 1330, the geladas reached a rocky outcropping at the upper, southern edge of a valley, and they began grooming and huddling for warmth.

At 1345, the geladas began alarm-calling and looking in a northerly direction, back towards the valley, and at 1355, the observer (CMM) saw an adult leopard's head briefly appear above a mima mound and the tall graminoids growing atop it (together ~1.5 m in height) before disappearing from view. The leopard was ~40 m away from the observer and the nearest gelada, an unidentified large juvenile male from a bachelor unit. After the leopard's disappearance at 1356, a small group of individuals, including the large juvenile male, alarm-called for several minutes spaced ≤2 m apart. At 1405, the gelada herd began traveling east, towards their sleeping cliffs and in the opposite direction from where the leopard was seen. The herd descended to the farmlands below the cliffs at 1515. The next morning (13 April 2018) at 1151, the herd was found 1.5 km to the south of their sleeping cliff from the previous day.

4 | DISCUSSION

4.1 | Behavioral responses of geladas to leopards at Guassa

Here we provide some of the most detailed accounts to date of primate responses to leopards, offering insights into the strategies geladas use to cope with leopard predation risk in open grassland habitats, where (often distant) cliffsides constitute the only source of refuge (Hunter, 2001; Moua, 2015). Upon encountering a leopard, geladas at Guassa typically engaged in a sequence of three behaviors: alarm-calling, group clustering, and fleeing towards or remaining at refugia (i.e., sleeping cliffs).

Geladas emitted alarm calls in all seven encounters with leopards and reduced interindividual spacing during at least five of these encounters. According to Hamilton's (1971) “selfish herd hypothesis”, each individual possesses a “domain of danger”, the unoccupied space around which they are at risk of random attack, so clustering should decrease this unoccupied space and subsequently lower each individual's predation risk (Stankowich, 2003). After alarm-calling and clustering, geladas generally fled in unison towards their sleeping cliffs, sites they do not usually return to until 1800 or later on a typical day. In the two instances when this flight did not occur, the geladas were already close to their sleeping cliffs. In all other observations, early cliff returns constituted a significant deviation from the herd's normal ranging patterns, likely resulting in decreased foraging times and subsequent reductions in daily caloric intake. This suggests that geladas may at least temporarily avoid areas in the landscape with high perceived risk of predation (e.g., where leopards were most recently seen). Several savanna-woodland dwelling primates have also been shown to alter their behavior or ranging patterns in response to the potential presence of predators (e.g., grivets, *Chlorocebus aethiops*: Coleman & Hill, 2014; vervets, *Chlorocebus pygerythrus:* Willems & Hill, 2009; patas monkeys, *Erythrocebus patas*: Burnham & Riordan, 2012).

Our findings suggest that microhabitat variability contributes to variation in predation risk for geladas at Guassa. Even in an open-country habitat, areas dominated by low-visibility vegetation (e.g., tussocks, mima mounds, shrubs, giant lobelias) likely provide hidden viewsheds for ambush predation. This would increase predation risk (cf., Loarie, Tambling, & Asner, 2013) and may create a “landscape of fear” (cf., Laundré, Hernández, & Ripple, 2010; Willems & Hill, 2009) effect of leopards and other predators (e.g., hyenas, servals) for geladas. All three of the leopard attacks observed in this study occurred in low-visibility microhabitats, a pattern consistent with reports of predation on other primates, including by leopards (baboons, *Papio spp.*: Cowlishaw, 1994; chimpanzees, *Pan troglodytes*: Boesch, 1991).

Our results also suggest that leopards, as ambush hunters, preferentially stalk geladas in smaller aggregations, where fewer eyes and ears make them less likely to be detected. Though our sample size is small, six of the seven encounters with leopards occurred on days when geladas were in herds smaller than their average size that month and year (Table 1). On the one encounter day (05 Feb 2015) when herd size (224 individuals) slightly exceeded the averages for that month (220) and year (205), the herd was spread over ~500 m and it was only the ~80 geladas that crested a hill ahead of the others that encountered and fled from the leopard. These results are consistent with the long-held notion that the tendency of gelada OMUs to aggregate in large numbers is aimed at reducing predation risk given their extreme vulnerability while foraging far from the refugia of their sleeping cliffs (Crook, 1966; Dunbar & Dunbar, 1975). Although it has been suggested that for primates in forested habitats, beyond a certain group size threshold, additional individuals do not enhance predator detection (Grueter & Van Schaik, 2010; Janson, Monzón, & Baldovino, 2014), we posit that for geladas in open-country habitats, more eyes and ears may make a real difference in reducing the risk of predation from leopards and other large carnivores. This reasoning has long been applied to explain why ungulates living in open habitats form much larger aggregations than those inhabiting forests (Brashares, Garland, & Arcese, 2000; Jarman, 1974). However, how a leopard hiding nearby might actually estimate the number of geladas present is unclear, though geladas are very vocal primates and produce many and varied vocalizations (Gustison, Johnson, Beehner, & Bergman, 2019), providing one possible means by which to assess herd size.

Finally, it should be noted that in all three observed leopard attacks, the presence of researchers, once seen by leopards, resulted in an abrupt cessation of predatory behavior and immediate flight of the leopard. Consistent with observations at other research sites (vervets at Amboseli, Kenya: Isbell, 1994b; olive baboons (*Papio anubis*) at Laikipia, Kenya: Isbell et al., 2018; chacma baboons (*Papio ursinus*) at Moremi, Botswana: Busse, 1980; chimpanzees at Tai Forest, Côte d'Ivoire: Boesch, 1991), large terrestrial predators may be discouraged from pursuing potential primate prey by the presence of researchers, which would affect predation rate and bias predation events towards nonstudy days (i.e., “the Nairobi effect”: Isbell, 1994b). Further, in the two instances in which researchers were spotted by a leopard in close pursuit of a gelada, the natural outcomes of these interactions may have been altered. As such, the use of GPS collars on both predators and prey (e.g., Isbell et al., 2018) and other noninvasive data collection methods (camera trapping, fecal surveys, etc.) are promising avenues for supplementing direct observations of predator–prey interactions.

4.2 | Behavioral comparisons across gelada populations in Ethiopia

Although a comparison of this study with previous work on canid-gelada interactions at Guassa (Venkataraman et al., 2015) suggests that behavioral responses differ partly by the type of potential predator, a comparison of gelada–leopard encounters at Guassa and at other gelada study sites suggests that variable responses to the same predator species also occur. At Arsi, which contains the only gelada population south of the Rift Valley, Iwamoto et al. (1996) observed male geladas mobbing an adult leopard. Adult and adolescent males emitted loud barks and bluff-charged to within 3 m of a leopard while females and smaller juveniles sheltered in trees and bushes nearby. No incidents of such mobbing occurred throughout the seven gelada–leopard encounters observed at Guassa. While we observed gelada males alarm-calling without immediately fleeing in four encounters with leopards, including one case in which an adult male followed a departing leopard, this only occurred when the leopard was first spotted at a safe distance and never culminated in any further defensive action. In Simien Mountains National Park, the only observed gelada–leopard encounter resulted in alarm-calling and the gelada herd fleeing 700 m, the greatest recorded distance the geladas fled from any predator during a one-year study period (Hunter, 2001).

Habitat variation across sites may explain some of the observed differences in gelada responses to leopards among populations. Arsi is significantly smaller (~30 km^2: Abu, Mekonnen, Bekele, & Fashing, 2018) than either Guassa (111 km^2: Fashing et al., 2014) or the Simien Mountains (169 km^2: Hunter, 2001), and offers fewer sleeping cliffs and less expansive and undisturbed plateau areas for foraging (Arsi farmlands begin just 20-200 m inland from the geladas' sleeping cliffs: Iwamoto et al., 1996). As such, flight to distant cliffs is not as viable an option for predator avoidance at Arsi as it may be at Guassa and the Simiens, and Arsi geladas may have no option but to confront leopards directly. This would be especially relevant if escape to nearby cliffs did not fully protect geladas from leopards. Indeed, on one occasion, we observed a leopard traversing a nearly vertical section of a gelada sleeping cliff at Guassa. Thus, because geladas spend most of their time near their sleeping cliffs at Arsi, geladas may be compelled to adopt a “fight rather than flight” strategy of active defense at this site.

4.3 | Leopard predation on geladas and other primates

As in several other primates, adult male geladas appear to be particularly susceptible to leopard attacks. This may be because males, rather than females, are more likely to physically confront predators in an encounter (geladas: Iwamoto et al., 1996; chacma baboons: Busse, 1980; Campbell's monkeys, *Cercopithecus campbelli*: Ouattara, Lemasson, & Zuberbühler, 2014; proboscis monkeys, *Nasalis larvatus*: Matsuda, Tuuga, & Higashi, 2008; chimpanzees: Boesch, 1991). In addition, males, particularly bachelor males, often forage at the periphery of the herd (patas monkeys: Burnham &

Riordan, 2012; geladas: Pappano, Snyder-Mackler, Bergman, & Beehner, 2012), thereby increasing their vulnerability to predation, especially by ambush predators. In our observations at Guassa, for example, gelada males were nearly always found on the herd's periphery and were the targeted prey of leopards in at least two of the three cases of attempted predation. Similarly, an adult male was the victim in the leopard attack on a gelada reported at Arsi (Iwamoto et al., 1996).

Leopards are capable of remaining hidden nearby for long periods before attacking or being detected by their primate prey (Zuberbühler, Jenny, & Bshary, 1999). However, once they have detected a leopard, many primates use alarm calls to deter or thwart leopard attacks (Zuberbühler et al., 1999). In our study, geladas always uttered alarm calls during encounters with leopards. These calls may have served to alert one another that a leopard was nearby or to alert the leopard that it had been seen (cf., Price et al., 2015; Zuberbühler et al., 1999). In the one instance where we observed a leopard capture and kill a gelada, alarm calls were uttered only after the attack had already occurred, raising the possibility that the geladas were unaware of the leopard's presence nearby before the attack. Whether leopards and other predators are actually deterred by gelada alarm calls may depend on the distance of the predator from the nearest gelada at the time of the call and the specific features of the habitat in which the encounter occurs.

If, as we suspect, concealment is important to a leopard's predatory success on geladas, then the microhabitat occupied by geladas should influence their risk of predation. Indeed, many primate species are known to increase vigilance rates in high-risk areas or avoid these areas altogether (olive baboons: Matsumoto-Oda, 2015; white-faced capuchins, *Cebus capucinus*: Campos & Fedigan, 2014; patas monkeys: Burnham & Riordan, 2012; red-tailed monkeys, *Cercopithecus ascanius*: McLester, Sweeney, Stewart, & Piel, 2019). Additional observations of gelada-predator interactions are needed to evaluate whether geladas alter their vigilance behavior in high-risk microhabitats or their ranging patterns after encounters with predators.

4.4 | Evolution of multilevel societies in geladas, hamadryas baboons, and hominins

We have shown previously that geladas do not exhibit signs of fear towards some large carnivores like Ethiopian wolves, with whom they appear to form commensal interspecific associations (Venkataraman et al., 2015). In contrast, in this study we document strong fear responses by geladas towards leopards and establish that leopards prey on geladas. These results highlight how important the threat of leopard predation (though a rarely observed phenomenon) remains in the lives of modern geladas, who are unusual among nonhuman primates in forming multilevel societies. We suggest that this evidence supports the hypothesis that predation, particularly by large felids, has been a selective factor for the formation of multilevel societies in geladas, as it may also have been for their close hamadryas baboon relatives, as well as their more distant hominin relatives.

The formation of multilevel societies in geladas likely represents an adaptation to balance the conflicting pressures of feeding competition and predation. Geladas form large aggregations that can disperse in modular subgroups to range and feed (Bergman & Beehner, 2013; Crook, 1966). Grouping facilitates predator detection (van Schaik, 1983) and diminishes individual predation risk (Hamilton, 1971; Olson et al., 2013), so the high vulnerability of geladas to predation in the open grassland habitats they occupy may favor the formation of very large aggregations in this species. In contrast, feeding competition, especially when food is scarce, favors smaller, more dispersed groups (Koenig, 2002; Wrangham, 1980). This competition probably accounts for the frequent fissioning that occurs within gelada herds, particularly during the dry season when food is less abundant (Hunter, 2001).

Evidence of a similar trade-off between vulnerability to predation and feeding competition also exists for another open-country primate living in multilevel societies: hamadryas baboons (Schreier & Swedell, 2012; Swedell, 2006). Aggregations formed by hamadryas do not reach the enormous sizes of gelada herds, suggesting that their reliance on patchier, higher-quality food items provokes feeding competition at much smaller sizes (Schreier, 2010; Swedell & Plummer, 2012). Still, given that both geladas and hamadryas occupy open-country habitats in which refugia are scarce, their modular social systems—which enable the formation of large aggregations of hundreds of individuals—suggest that predation was and remains a powerful selective pressure on their lives.

Several million years ago, both hominins and the theropith ancestors of modern geladas transitioned from living in woodland-dominated habitats to more open-country environments, an environmental shift that likely presented them with novel challenges (Bedaso, Wynn, Alemseged, & Geraads, 2013; Cerling, Chritz, Jablonski, Leakey, & Manthi, 2013; deMenocal, 2011; Foley & Gamble, 2009; Isbell et al., 2018; Jolly, 1970; Pickford, 1993). These presumed challenges included a reduction in the availability of refugia (Isbell et al., 2018) and an increased reliance on resources in more seasonal, open-country habitats, putatively including grasses and sedges (Cerling et al., 2011, 2013; Paine et al., 2018; Shapiro, Venkataraman, Nguyen, & Fashing, 2016). As a result, hominins and theropiths are both hypothesized to have adopted a fission-fusion way of life—dispersing and re-aggregating at irregular intervals as dictated by changing ecological conditions—ultimately resulting in the formation of multilevel societies (Chapais, 2013; Dunbar, 1993; Grove, Pearce, & Dunbar, 2012; Grueter, Chapais, & Zinner, 2012; Swedell & Plummer, 2012). Perhaps if, as some scholars have suggested, early hominins were constrained by similar foraging pressures to those of geladas and their ancestors (Cerling et al., 2011, 2013; Paine et al., 2018), then the evolution of multilevel societies in hominins may have provided a viable solution to handle predation risk in larger aggregations while still offering the flexibility of smaller unit foraging to cope with variations in the food supply.

ACKNOWLEDGMENTS

We thank the Ethiopian Wildlife Conservation Authority, Amhara Regional Government, and Mehal Meda Woreda for permission to conduct this study. We are grateful for the generous support that the long-term gelada research project at Guassa has received from Dean Gibson and the San Diego Zoo, CSU Fullerton, the Leakey Foundation, Margot Marsh Biodiversity Foundation, Primate Conservation Inc., Gisela and Norman Fashing, Joe and Pat Healey, Anita, and Hans-Peter Profunser, and the Christopher Schroen Memorial Fund. CMM thanks the Leakey Foundation and the Department of Anthropology, UMN Block Grants for funding her work at Guassa. VVV gratefully acknowledges funding from the French Agence Nationale de la Recherche (under the Investissement d'Avenir program, ANR-17-EURE-0010). NN thanks the U.S.-Norway Fulbright Foundation and NN and PJF thank CSU Fullerton and the University of Oslo for their financial and/or logistical support during the preparation of this manuscript. BL thanks Princeton University for the support, David Wilcove for the guidance, and Taili Ni for the edits throughout the manuscript preparation process. We thank Metikay Basasen, Badiloo Muluyee, Bantilka Tessema, Shofera Tessema, Tasso Wudimagegn, and the many field assistants of the Guassa Gelada Research Project for the logistical and research support they provided. We thank Elisa Neves for her helpful analyses of gelada herd sizes over time at Guassa. Lastly, we thank Anthony Di Fiore and two anonymous reviewers for their helpful comments on an earlier draft of this manuscript. This study was entirely noninvasive and adhered to the legal requirements of Ethiopia.

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How to cite this article: Lin B, Foxfoot IR, Miller CM, et al. Leopard predation on gelada monkeys at Guassa, Ethiopia. *Am J Primatol*. 2020;e23098. https://doi.org/10.1002/ajp.23098