



Solitary Ethiopian wolves increase predation success on rodents when among grazing gelada monkey herds

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Mixed-species associations generally form to increase foraging success or to aid in the detection and deterrence of predators. While mixed-species associations are common among mammals, those involving carnivorous predators and potential prey species are seldom reported. On the Guassa Plateau, in the Ethiopian highlands, we observed solitary Ethiopian wolves (*Canis simensis*) foraging for rodents among grazing gelada monkey (*Theropithecus gelada*) herds. The tolerant and sometimes prolonged (> 1 h) associations contrasted with the defensive behaviors exhibited by geladas toward other potential predators. Ethiopian wolves spent a higher proportion of time foraging and preyed more successfully on rodents when among geladas than when alone, providing evidence that gelada herds increase the vulnerability of subterranean rodents to predation. Ethiopian wolves appear to habituate gelada herds to their presence through nonthreatening behavior, thereby foregoing opportunistic foraging opportunities upon vulnerable juvenile geladas in order to feed more effectively on rodents. For Ethiopian wolves, establishing proximity to geladas as foraging commensals could be an adaptive strategy to elevate foraging success. The novel dynamics documented here shed light on the ecological circumstances that contribute to the stability of mixed groups of predators and potential prey.

Key words: Afroalpine, *Canis simensis*, Ethiopia, interspecific association, rodents, *Theropithecus gelada*

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Mixed-species associations occur widely among vertebrates, including mammals and birds (Stensland et al. 2003). The ecological benefits of mixed-species associations tend to fall into 2 broad and mutually compatible categories: foraging advantages gained by enhanced access to food and enhanced detection and deterrence of predators (Cords 1987; Bshary and Noe 1997; Stensland et al. 2003; Goodale et al. 2010). The tendency for mixed-species associations to occur depends on several factors, including the diet, social system, and phylogenetic distance between the participating species (Stensland et al. 2003).

Mixed-species associations involving predators and potential prey are rare, and such interactions tend to be opportunistic and fleeting rather than stable (Oommen and Shanker 2010). Predation risk is likely the ecological factor that reduces the stability of such mixed groups, as carnivores generally evoke defensive or flight responses among potential prey (Caro

2005). Perceived predation risk is magnified when the size ratio between the predator and potential prey is large (Stankowich and Blumstein 2005), yet a ratio close to 1 may contribute to stable group formation (Oommen and Shanker 2010).

Primates frequently engage in mixed-species associations, typically with other primates, nonprimate mammals, and birds (Stensland et al. 2003; Cords and Würsig 2014). Associations between primates and nonprimates are typically commensalistic, with the benefits accruing to the nonprimate rather than the primate, and typically involve antipredatory or foraging-related advantages (Heymann and Hsia 2014). In the latter case, primate groups flush prey (i.e., insects) by disturbing vegetation (e.g., King and Cowlshaw 2009) and/or dropping fruits and leaves (e.g., Newton 1989). Few observations of primates associating with their potential predators exist, and those that do typically involve small raptors (e.g., Egler 1991; Heymann

1992). In mixed-species associations involving primates and terrestrial carnivores, the carnivore is typically engaging in facultative frugivory rather than predatory activity (e.g., Newton 1985; Desbiez et al. 2010).

Here we describe nontrophic associations between 2 mammals endemic to the Ethiopian Highlands—Ethiopian wolves (*Canis simensis*) and gelada monkeys (*Theropithecus gelada*—Fig. 1; Supporting Information S1)—at an Afroalpine grassland site called Guassa in north-central Ethiopia. During these sometimes prolonged associations, Ethiopian wolves stalked slowly near or within herds of geladas, repeatedly catching rodents and evoking little to no response from the monkeys. While Ethiopian wolves specialize on rodent prey, they occasionally catch larger prey such as hares, antelope, and sheep (Sillero-Zubiri and Gottelli 1995b). It is, therefore, somewhat puzzling that Ethiopian wolves maintain close proximity to gelada herds without attempting opportunistically to catch juvenile monkeys, which are expected to be the most vulnerable members of the herd, and moreover, that they are permitted to forage among gelada herds, which are normally extremely sensitive to the presence of predatory threats (Iwamoto et al. 1996; Hunter 2001). Our observations suggest that Ethiopian wolves could be gaining a foraging advantage by being among geladas, potentially by capturing rodents flushed out or otherwise made vulnerable by the monkey herd.

Here, we explore the ecological basis of Ethiopian wolf–gelada interactions by testing the hypothesis that the associations are driven by foraging advantages for the Ethiopian wolves. First, we examined ecological correlates of the associations, including seasonality, time of day, and the herd size of geladas. We expected the frequency of associations to 1) differ between the wet and dry seasons due to temporal fluctuations

in rodent population sizes (Happold and Happold 1989; Sillero-Zubiri et al. 1995a; Sillero-Zubiri and Gottelli 1995b; Ashenafi 2001), which may make foraging more difficult for Ethiopian wolves during a particular season. We also expected the frequency of associations to 2) increase at mid-day during the peak foraging activity of geladas, rodents, and Ethiopian wolves (Sillero-Zubiri et al. 1995a; Sillero-Zubiri and Gottelli 1995b; Ashenafi et al. 2005, 2012) and 3) to increase with herd size of geladas due to greater environmental disturbance by the geladas. Next, we investigated gelada perceptions of risk posed by potential predators by recording behavioral responses to carnivores (e.g., Ethiopian wolves, servals, and feral dogs). Finally, to determine if and how Ethiopian wolves benefit from the associations with geladas, we explored how Ethiopian wolf activity patterns, attempt rate (attempts per hour), foraging efficiency (successful attempts per hour), and foraging success (the likelihood of capturing a rodent) differ in the presence of geladas.

MATERIALS AND METHODS

Study site and subjects.—The present study of Ethiopian wolves and geladas occurred on the Guassa Plateau, a 111 km² Afroalpine, tall-grass ecosystem located along the western edge of the Great Rift Valley (10°15′–10°27′N; 39°45′–39°49′E) at elevations between 3,200 and 3,600 m above sea level (Ashenafi 2001; Fashing et al. 2010). From 2007 to 2012, the average monthly temperature (\pm SD) at Guassa was $11.0 \pm 1.2^\circ\text{C}$ (Fashing et al. 2014). Rainfall averaged $1,650 \pm 243$ mm per year and was strongly seasonal, and more than half of annual rainfall occurred during July and August (Fashing et al. 2014).



Fig. 1.—A) An Afroalpine rodent among geladas (*Theropithecus gelada*); B and C) Ethiopian wolves (*Canis simensis*) foraging for rodents among geladas; and D) an Ethiopian wolf successfully captures a rodent while among geladas (photograph in c reproduced with permission from Malcolm Ramsay).

Protected by an indigenous conservation system dating to the 17th century (Ashenafi and Leader-Williams 2005), Guassa retains an intact large-carnivore community, including Ethiopian wolves (*C. simensis*), African wolves (*Canis aureus lupaster*), spotted hyenas (*Crocuta crocuta*), leopards (*Panthera pardus*), and servals (*Leptailurus serval*—Ashenafi 2001; Ashenafi and Leader-Williams 2005; Rueness et al. 2011). Domestic dogs (*Canis lupus familiaris*) from human settlements adjacent to Guassa were also occasionally present. Notably, cryptic African wolves appeared to forage for rodents among geladas (Supporting Information S2) in a fashion similar to Ethiopian wolves, but this phenomenon occurred with less regularity and has not yet been systematically studied.

Ethiopian wolves are medium-sized (11–19 kg) canids that live in family packs of 2–13 adults, which defend small communal territories through daily patrols (Sillero-Zubiri and Gottelli 1994; Sillero-Zubiri et al. 1995a, 1995b). Their year-round diet consists of ~80% murid rodents, which are abundant in Afroalpine areas (Delany 1972; Yalden 1988; Sillero-Zubiri et al. 1995a, 1995b; Sillero-Zubiri and Gottelli 1995b; Ashenafi et al. 2005). On occasion, they will hunt larger prey (e.g., hares, antelope, or sheep), sometimes in packs (Sillero-Zubiri and Gottelli 1995b). Ethiopian wolves are the most endangered canid in the world, with fewer than 450 individuals distributed throughout the remaining pockets of suitable Afroalpine habitat (Gottelli and Sillero-Zubiri 1992; Sillero-Zubiri and Gottelli 1995a; Marino 2003; Marino and Sillero-Zubiri 2011).

Though their ranges probably overlapped more widely in the past, today Ethiopian wolves and gelada monkeys are sympatric at only a handful of sites (Marino 2003). The gelada monkey is a large (male weight averages ~19.0 kg) terrestrial cercopithecoid primate which subsists mostly on graminoids and forbs and sleeps on cliff sides (Bergman and Beehner 2013; Fashing et al. 2014). Geladas have an unusual multilevel social organization in which the lowest level is the one-male unit (Kawai et al. 1983; Snyder-Mackler et al. 2012). On any given day, many one-male units can be seen traveling together in aggregations called *herds*. Herds can consist of up to 1,200 geladas at some sites (Bergman and Beehner 2013), though the largest recorded herds at Guassa have been 600–700 individuals. Herd composition changes on a regular basis, as one-male units leave and join other herds. One-male units that are regularly seen together and share a common home range are known as *bands* (Kawai et al. 1983; Snyder-Mackler et al. 2012). Our main study band (Steelers Band) at Guassa consists of ~220 individuals. We began studying this band in December 2005 and have monitored it continuously on a near daily basis (typically between the hours 0800 and 1730) since January 2007.

Data collection.—During all-day follows of the study band from January 2006 to February 2006 and from December 2006 to April 2008, we recorded gelada responses to encounters with all carnivores to evaluate differences in gelada responsiveness to different carnivores. During this period, geladas encountered Ethiopian wolves often, feral dogs occasionally, and servals rarely, and did not encounter cryptic African wolves, hyenas,

or leopards. All responses to Ethiopian wolves and dogs were recorded within 100 and 300 m, respectively (due to the geladas' responsiveness to dogs at much greater distances). Movements of geladas were estimated visually to the nearest meter. In cases where geladas and canids re-encountered one another within an hour, we only analyzed data from the initial encounter because we assumed subsequent encounters were probably impacted by the first encounter and thus not independent of one another (cf. Fashing 2001).

To determine how geladas affect Ethiopian wolf activity patterns and predation success upon rodents, we conducted opportunistic focal follows (Altmann 1974) of Ethiopian wolves at distances from 100 to 750 m on 17 days from 2 July to 31 August 2011. Seven of these days included associations with geladas, and all 17 days included solitary foraging data for the Ethiopian wolves. The majority of follows occurred between 1200 and 1700 h. Focals began when an Ethiopian wolf was first sighted and ended when the wolf was out of sight and lasted between 2 min and 2.5 h ($n = 17$ focals). We observed Ethiopian wolves alone for a total of 6.8 h during the study period and observed wolves in association with geladas for 2.7 h.

During focals of wolves, we recorded on a continuous basis all instances of wolf predation attempts along with the outcome of those attempts (success or failure) through time.

In addition, data on the following states were collected on a continuous basis during focals, with time of onset and termination recorded to the nearest second using a digital voice recorder:

- (i) Activity: (a) *foraging* was defined as slow, light-footed walking with ears oriented forward and the belly close to the ground (Ashenafi 2001), (b) *stationary* was defined as lying down, sitting, or standing without movement, and (c) *traveling* was defined as fast walking or running.
- (ii) Microhabitat: we continuously monitored changes in the identities of the dominant plant genera (e.g., *Festuca*, *Hypericum*, *Euryops*, mixed short grasses) in the immediate vicinity of the focal wolf. Microhabitats dominated by shrubs and tall grasses were classified as *complex* and those dominated by short grass and herbaceous growth as *simple*.
- (iii) Association with geladas: associations began when there was a distance of < 50 m between at least 1 gelada and the focal wolf and ended when the distance increased above 50 m.

Our data collection protocols followed the guidelines approved by the American Society of Mammalogists (Sikes et al. 2011).

Data analysis.—To investigate how geladas perceive risk in relation to potential predators, we compared the distances moved by gelada individuals upon detecting Ethiopian wolves and domestic dogs using Mann–Whitney *U*-tests because the data did not conform to the assumptions of normality and homogeneity of variance.

Next we examined the ecological correlates of encounters. First, we examined the hourly patterns of encounters between Ethiopian wolves and geladas by plotting the

temporal distribution of encounters by hour of the day. Second, to test whether wolf encounters with the study band of geladas increased during the dry season, we adjusted the observed number of wolf encounters to our sampling effort (number of all-day follows per month) and visually examined the curve. Low sample sizes precluded statistical analysis for this portion of the study. Third, we used logistic regression to examine the possible effect of gelada herd size on the likelihood of encounter between Ethiopian wolves and geladas.

To evaluate whether Ethiopian wolves derive a foraging advantage from their associations with geladas, we compared the proportion of time wolves spent foraging while in the presence and absence of geladas using a Welch *t*-test. For this section of the analysis, we employed a simulation approach to account for possible repeated observations of wolves (see below).

We also examined whether the attempt rate (attempts per hour) and foraging efficiency (successful attempts per hour) of Ethiopian wolves were higher among geladas using matched-pairs *t*-tests on the data that included only those instances in which we definitively observed the same individual wolves both in the presence and absence of geladas ($n = 7$).

We examined the relative impact of microhabitat, associations with geladas, and the interaction between the 2 variables on the predation success of Ethiopian wolves by comparing 5 generalized linear mixed models using an information theoretic approach. In addition to wolf association with geladas, we included microhabitat as a predictor variable in our models as habitat type may affect predation success because rodent densities vary among Afroalpine habitat types (Sillero-Zubiri and Gottelli 1995a, 1995b; Ashenafi et al. 2005) and because habitat types differ in their physical structure, a trait that can influence prey detection and catchability (Birney et al. 1976; Grant et al. 1982; Kotler 1984). Predation attempt outcome was the response variable, modeled according to a binomial distribution (1 = success, 0 = failure), and descriptive models were formulated according to specific predictions about the effect of association and microhabitat upon predation attempt outcome. These models were combinations of microhabitat (simple/complex), association (yes/no), and the interaction between the two as fixed effects, and individual wolf ID was included as an intercept-only random effect in all 5 models to explicitly account for repeated measures (Table 2). We also incorporated a random intercept-only model (model 5) which corresponds to the null hypothesis of no effect (Burnham et al. 2010). To compare model fit, we used the corrected Akaike information criterion (AIC_c) due to low sample size and calculated model weights (w_i) in addition to evidence ratios, which indicate strength of evidence based on the ratio between pairs of model weights (Anderson 2008). Lower AIC_c values indicate a better-fit model to the data among the candidate set (Burnham and Anderson 2002; Burnham et al. 2010).

We were unable to identify (to individual or age/sex class) the focal wolves because (a) there is little sexual dimorphism in this species (Sillero-Zubiri and Gottelli 1994) and (b) Ethiopian wolves at Guassa are not well habituated to human observers

and focals were conducted at distances of > 75 m in mountainous terrain. Because Ethiopian wolves at Guassa have relatively stable (but overlapping) territories, the wolf population at Guassa is small (~21 individuals—Ashenafi et al. 2005), and our wolf focal follows occurred in a limited geographic region, we suspect that we observed ≥ 2 but ≤ 10 focal individuals. Accordingly, we quantified how our *t*-test and model selection results could be biased by repeated sampling of the same individuals within our data set. For each number n such that $2 \leq n \leq 10$, we randomly assigned (with replacement) individual wolf IDs to each observation date (only 1 wolf was followed per day). This assignment was performed 100 times to create 100 data sets for each value of n , then *t*-tests and model selection procedures were performed for each data set. Results for the *t*-test were nominally different according to the degree of repeated sampling (see “Results”). We found that model rankings for Ethiopian wolf predation success were identical for each data set, with ΔAIC_c values between each candidate model differing little (< 0.1 in each case). Similarly, when we compared model rankings between data sets with different values of n , the results were again identical, and ΔAIC_c values between each candidate model differed only slightly (< 0.2 in each case). From these diagnostic sensitivity evaluations, we conclude that our results for the model selection portion of the analysis were not affected by our inability to recognize individual Ethiopian wolves, nor by the number of wolves considered for the analysis. Accordingly, for the sake of clarity in presenting the results of our analysis, we assumed that 4 wolf individuals were observed during the study, and each ID was then randomly assigned to observation dates.

We used RStudio for data analysis (RStudio 2012). We used the package lme4 (Bates et al. 2012) for the mixed-modeling portion of the analysis and the bbmle (Bolker and R Development Core Team 2011) and AICcmoavg (Mazerolle 2013) packages to compute ΔAIC_c and Akaike weights for all candidate models. We estimated conditional and marginal R^2 values using the MuMIn package in R (Barton 2011).

RESULTS

Time of day and seasonality of encounters.—Encounters between Ethiopian wolves and geladas usually occurred between late morning and late afternoon (Fig. 2). The distribution of encounter times was normal (Shapiro–Wilk normality test: $W = 0.98$, $P = 0.28$) and centered at a mean occurrence time of 13:21h (Fig. 2). The encounter rate between Ethiopian wolves and geladas was at its highest from January to April 2008 (Fig. 3) which were 4 unusually dry months (mean rainfall = 26.3 mm per month; $n = 4$ months—Fashing et al. 2014).

Gelada herd size.—Larger gelada herd sizes marginally increased the likelihood of an encounter between Ethiopian wolves and the study band of geladas (mean herd size: wolf presence = 321.3, wolf absence = 295.8; logistic regression: $P = 0.19$). When we analyzed data for the wet season and dry season separately using logistic regression, the results were similar (wet season, mean herd size: wolf presence = 199.1,

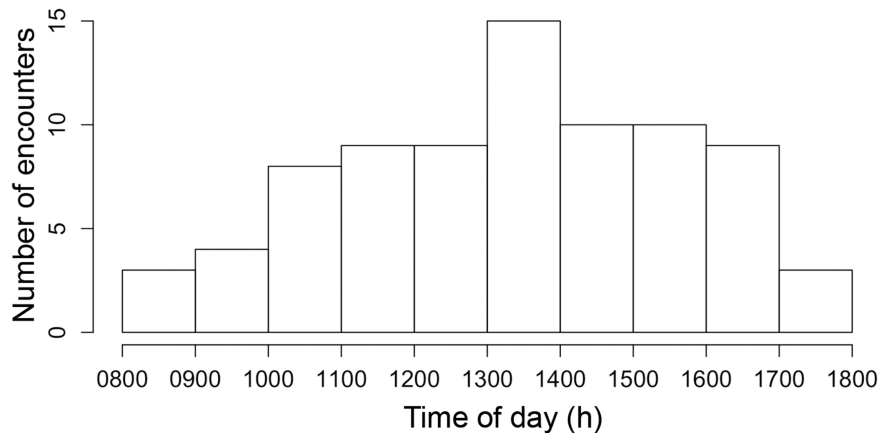


Fig. 2.—Histogram of encounter times between Ethiopian wolves (*Canis simensis*) and geladas (*Theropithecus gelada*) from January 2007 to April 2008. Encounters peaked during the mid-day ($\bar{X} = 1328$ h) and coincide with the peak aboveground activity of rodents and the foraging activity of geladas and Ethiopian wolves.

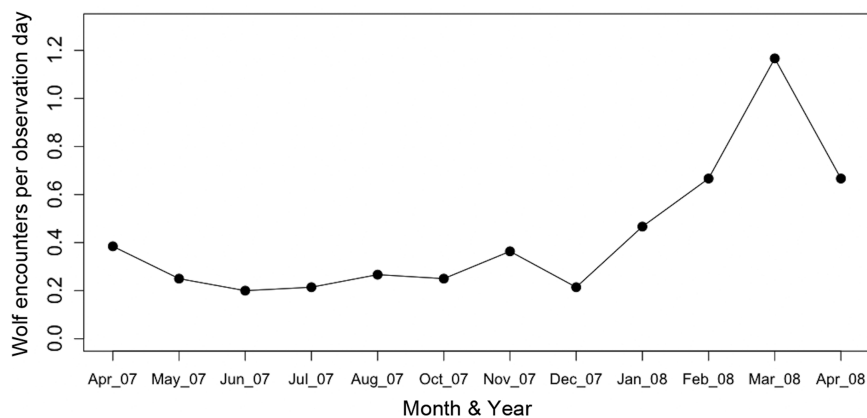


Fig. 3.—Monthly counts of encounters between Ethiopian wolves (*Canis simensis*) and geladas (*Theropithecus gelada*) from April 2007 to April 2008. Data were adjusted for observation days per month and September 2007 was excluded due to low sample size.

wolf absence = 225.9, $P = 0.26$; dry season, mean herd size: wolf presence = 342.6, wolf absence = 321.8, $P = 0.36$).

Behavioral responses of geladas to wolves and domestic dogs.—Gelada responses to Ethiopian wolves and domestic dogs differed strikingly (Table 1). While at least 21% of encounters with Ethiopian wolves resulted in at least 1 alarm call by geladas, only 11% (9/80) of encounters resulted in a movement of > 10 m (mean flight distance = 4 m) and 68% (54/80) of encounters resulted in no movement by geladas. Conversely, geladas always (10/10) moved upon encountering domestic dogs. The distance geladas fled upon encountering dogs (323 ± 101 m [SE]; $n = 10$) was significantly higher than for Ethiopian wolves (4 ± 1 m [SE]; $n = 80$; Mann–Whitney U : $n_{\text{dog}} = 7$, $n_{\text{wolf}} = 77$, $Z = -5.063$, $P < 0.0001$). Dogs hunted geladas in packs of up to 3 individuals, and 3 geladas were killed during the 10 dog encounters from 2006 to 2008. Ethiopian wolves hunted among geladas almost exclusively solitarily, with 2 wolves being present among geladas on only 3 of 80 occasions from 2006 to 2008.

Time budgets of Ethiopian wolves.—Ethiopian wolves exhibited a trend toward spending more time foraging when among geladas than when alone (Welch 2-sample t -test: P -values ranged from 0.04 to 0.11 depending on the extent of simulated

repeat sampling). Although our inability to identify individual wolves in the field may weaken this portion of our analysis, our results are unlikely to be biased by sampling effort because median focal duration on Ethiopian wolves was comparable when wolves were in association with geladas (7 min) versus when they were solitary (5.2 min).

Attempt rates and foraging efficiency.—The attempt rates of Ethiopian wolves did not significantly differ in the presence and absence of geladas (mean attempts per hour: gelada presence = 18.9, gelada absence = 26.3, matched-pairs t -test: $t_6 = -0.99$, $P = 0.36$), nor did their foraging efficiency (mean catches per hour: gelada presence = 10.3, gelada absence = 12.0, matched-pairs t -test: $t_6 = -0.48$, $P = 0.65$).

Foraging success of Ethiopian wolves.—Ethiopian wolves had greater foraging success in the presence of geladas (proportion of successful foraging bouts: $16/24 = 66.7\%$) compared to when wolves foraged solitarily ($15/61 = 25\%$; Fig. 4). The best-ranking model predicting predation success contained only the variable *association* and had an AIC_c weight of 0.58, indicating that this model has a 58% chance of being the best model among the candidate set (Table 2). The evidence ratios indicate that this model is between 2.6 and 580 times more likely than the other competing models. The log-likelihood and AIC_c

Table 1.—Responses of geladas to encounters with Ethiopian wolves (*Canis simensis*) and domestic dogs (*Canis lupus familiaris*) during the 2006–2008 study period.

	<i>n</i>	Distance of association	Distance fled upon encounter ($\pm SE$)	Notes
Ethiopian wolf	80	100 m	4 m (± 1 m)	No movement by geladas in 68% of encounters; 77/80 (96%) associations involved solitary wolves
Domestic dog	10	300 m	323 m (± 101 m)	30% of encounters resulted in a gelada death; dog attacks occurred in packs of up to 3 individuals

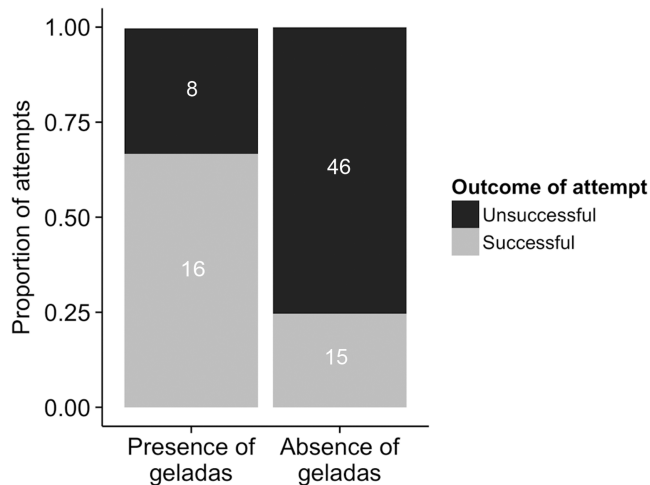


Fig. 4.—Stacked barplot depicting proportions of successful and unsuccessful predation attempts by Ethiopian wolves (*Canis simensis*) on rodents observed during July and August 2011. Wolves had more successful attempts catching rodents in the presence of geladas (16/24 = 66.7%) than when alone (15/61 = 25%). White numbers represent counts.

values in Table 2 indicate that microhabitat is a pretending variable (Anderson 2008) in model 2 in this analysis, and thus any weight attributed to this model is due to the inclusion of association as a factor. Likewise, the interaction model (model 1) has only a slightly improved log-likelihood compared to the best fitting model (model 3). As indicated by the marginal and conditional R^2 values for our mixed-effects models (representing the variance accounted for by the fixed effects and by both fixed and random effects, respectively—Nakagawa and Schielzeth 2013), the full model (model 1) incorporating the microhabitat and association variables and their interaction accounted for 23% of the variance in the data set (Table 2). When we reduced our data set to the 7 observation days in which Ethiopian wolves were observed both in association with geladas and alone, the results were identical, indicating that interindividual differences in wolf foraging expertise did not confound the analysis.

DISCUSSION

Mixed groups of predators and their potential prey items tend to be opportunistic and fleeting due to predation risk (Boinski and Scott 1988; Oommen and Shanker 2010). While associations between geladas and Ethiopian wolves could result from chance encounters, the temporal stability of the associations

(up to 68.1 min per encounter—cf. Newton 1985) and the tolerance of the geladas toward nearby wolves are particularly notable. Several ecological factors appear to contribute to the peaceful and stable nature of this association.

We found striking differences in how geladas perceive and act upon risk in relation to potential predators at Guassa. Geladas clearly differentiate between Ethiopian wolves (a non-threatening stimulus) and domestic dogs (a threatening stimulus) even from considerable distances, probably because of the starkly divergent hunting tactics of these 2 canids (Table 1). At Guassa, geladas immediately flee great distances to the safety of cliff sides upon encountering (usually) overtly aggressive domestic dogs, and encounters with unfamiliar humans also evoke a flight response, whereas encounters with servals ($n = 2$) result in intense alarm calling but not flight (J. T. Kerby, R. Burke, and S. Jones, pers. obs.). Iwamoto et al. (1996) noted that geladas at Arsi in southern Ethiopia mobbed leopards and fought domestic dogs. By contrast, geladas at Guassa tolerate individual Ethiopian wolves within the middle of herds and rarely flee, suggesting that geladas do not perceive Ethiopian wolves as threatening despite similarities in size and color with domestic dogs.

It is intriguing that Ethiopian wolves do not opportunistically attack immature geladas. Young geladas are expected to be the most vulnerable members of the herd to opportunistic predation attempts, but in more than 8 years of study at Guassa, only 1 unsuccessful predation attempt by an Ethiopian wolf upon a (small juvenile) gelada has been documented (Supporting Information S3). This episode resulted in dozens of geladas (mostly adult males) repeatedly mobbing the wolf, the wolf dropping the gelada unharmed from its mouth while running away. Predation attempts by Ethiopian wolves thus appear to induce a mobbing response, resulting not only in a lost feeding opportunity and possible injury but also loss of the occasion to forage for rodents among the herd. The presence of large adult male geladas (mean weight = 19.0 kg—Bergman and Beehner 2013) may play a fundamental role in shaping the restraint of Ethiopian wolves, which would further affirm the key role of body size differences in the dynamics of mixed-species associations involving predators and potential prey (Boinski and Scott 1988; Oommen and Shanker 2010).

Our data suggest that wolves may be foregoing foraging opportunities upon geladas in order to feed more effectively on rodents. By consistently exhibiting nonthreatening behavior, Ethiopian wolves may have habituated gelada herds to their presence (cf. Stankowich and Blumstein 2005). For example, in

Table 2.—Results of generalized linear mixed model selection procedure (K = number of estimated parameters; LogL = log-likelihood; w_i = Akaike weights; ER = evidence ratio; R^2 (M, C) = marginal and conditional R^2 values).

Model ^a	Rank	Fixed effects	K	LogL	AIC _c	Δ AIC _c	w_i	ER	R^2 (M, C)
4	1	Association	3	-49.3	104.9	0	0.58	—	0.17, 0.17
2	2	Association + microhabitat	4	-49.28	107.1	-2.2	0.22	2.6	0.17, 0.17
1	3	Association + microhabitat + association \times microhabitat	5	-48.38	107.4	-2.5	0.20	2.9	0.22, 0.23
5	4	None (random intercept only)	2	-55.77	115.7	-10.8	0.003	193.3	0, 0
3	5	Microhabitat	3	-55.49	117.1	-12.1	0.001	580	0.008, 0.008

^aIndividual ID was incorporated as a random intercept in all models.

our study, when near geladas Ethiopian wolves rarely formed groups (3/80 encounters), and engaged in slow stalking rather than rapid movements such as trotting or running in a zig-zag pattern across the landscape, behaviors they normally engage in to stimulate rodent movement and/or catch rodents unaware (Sillero-Zubiri and Gottelli 1995b; Ashenafi 2001). Such context-dependent behaviors may be prerequisites for establishing trust with predator-wary geladas.

Despite the low likelihood of attack by Ethiopian wolves, geladas did occasionally move away from nearby wolves or reorient their body position to see more clearly (32% of encounters; Table 1). The tolerance of the gelada herd toward foraging wolves may indicate that behavioral defenses such as heightened vigilance and awareness sufficiently reduce perceived predation risk by vulnerable geladas. Aside from the presumably minor energetic and physiological costs of such behaviors, there is no discernible cost or benefit to geladas from the presence of Ethiopian wolves, suggesting a commensal or weakly parasitic relationship between the species at Guassa.

Our study demonstrates that the presence of gelada herds predictably and consistently alters the behavior and foraging success of Ethiopian wolves. While in association with geladas, Ethiopian wolves spent a higher proportion of their time foraging but did not exhibit elevated attempt rates. This may indicate that wolves perceive a potential foraging benefit but do not put more effort into capture attempts. Moreover, Ethiopian wolves exhibited higher rates of predation success on rodents, suggesting an indirect effect between geladas and subterranean rodents that increases the likelihood of capture by Ethiopian wolves. Although we did not find that wolves consume more rodents per unit time when among geladas, our sample sizes were small here and additional data on the topic would provide a more robust test of this hypothesis. Taken together, our present results suggest that the primary benefit of being among geladas is avoiding the energetic costs of failed predation attempts.

Geladas are not alone in eliciting stalking behavior by Ethiopian wolves. Researchers have observed Ethiopian wolves stalking near grazing herds of livestock (Sillero-Zubiri and Gottelli 1995b; Ashenafi 2001; Ashenafi et al. 2005), perhaps implying that interactions between grazers and subterranean rodents may be of a more general nature and that establishing proximity to large herbivore commensals may be an adaptive strategy for Ethiopian

wolves to elevate foraging success, perhaps especially during the dry season (Fig. 3). Several mechanisms could account for the elevated rates of foraging success on rodents in the presence of geladas. Geladas could elicit a “flushing effect” by disturbing vegetation and driving rodents to the surface. Alternatively, some researchers have proposed mechanisms of visual or auditory interference by larger grazers upon rodent sensory systems that make it more difficult for prey to detect nearby predators (Sillero-Zubiri and Gottelli 1995b; Ashenafi 2001). Consistent with both hypotheses is our finding that Ethiopian wolves appear to coordinate the timing of their foraging among geladas to the peak aboveground activity by their rodent prey (Sillero-Zubiri et al. 1995a; Sillero-Zubiri and Gottelli 1995b; Ashenafi et al. 2005, 2012). Whatever the mechanism, these patterns highlight complex community dynamics operating between large herbivores, subterranean rodents, and Ethiopian wolves. In light of the rapid and extensive destruction of native fauna and flora in the Ethiopian highlands (Williams et al. 2005), our study documents a set of vanishing behaviors (Caro and Sherman 2012) that merit further study and urgent conservation attention.

SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmmal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

SUPPORTING INFORMATION S1.—Short video clip of Ethiopian wolves (*Canis simensis*) in association with the gelada herd (*Theropithecus gelada*) at Guassa, Ethiopia. These clips show representative gelada response to Ethiopian wolf presence. Compilation of footage from 2007, 2008, and 2011.

SUPPORTING INFORMATION S2.—A cryptic African Wolf (*Canis aureus lupaster*) foraging for rodents among geladas in a manner similar to that of Ethiopian wolves (photograph reproduced with permission from Taylor Turner).

SUPPORTING INFORMATION S3.—Short video clip of aggressive response by monkey herd toward Ethiopian wolf (*Canis simensis*) after failed predation attempt (not captured by video)

by the wolf on a juvenile gelada monkey (*Theropithecus gelada*). This represents the only observed instance of an Ethiopian wolf predation attempt on a gelada monkey during the period of observation.

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