



# Time allocation to balance group living trade-offs in Ethiopian wolves

Elisa Sandoval-Serés<sup>1</sup> · James Foley<sup>1</sup> · Elizabeth Preston<sup>1</sup> · Edris Ebu<sup>2</sup> · Jorgelina Marino<sup>1,2,3</sup>

Received: 16 August 2023 / Revised: 20 October 2023 / Accepted: 30 October 2023 / Published online: 15 November 2023  
© The Author(s) 2023

## Abstract

Living in groups requires individuals to make trade-offs to maintain group cohesion and enhance individual and inclusive fitness. One way animals can do this is by adjusting the way they allocate time to different behaviours. Ethiopian wolves (*Canis simensis*) are highly social, cooperative breeders (only the dominant pair breeds and all members help to raise the litter), but solitary foragers. To investigate how Ethiopian wolves allocate their time to balance the costs and benefits of group living, we analysed the time budgets of 47 wolves across six behaviours. We hypothesized that group size and territory density would affect wolves' time allocation between solitary (foraging) and communal activities (patrolling and socialising) differently in relation to their age, dominance status or sex, and whether the pack was breeding or not. Our results showed that the time spent foraging alone increased at higher territorial densities, as expected from interference competition, particularly among subadults, subordinates and individuals in breeding packs. On the other hand, as pack size increased, adult wolves spent a lower proportion of time patrolling, while the time spent socialising did not change. Living in groups reduces the costs of communal activities, but crowded territories come at the cost of interference competition for solitary foragers, particularly the animals further down the hierarchy ranks, subadults, and individuals investing in breeding. Such trade-offs could impose an upper limit to group size and population growth within a limited space. Furthermore, anthropogenic disturbance could alter the balance of social and solitary activities of Ethiopian wolves.

## Significance statement

How does a species balance the costs and benefits of living in a group through time allocation? We studied a social carnivore that hunts alone: the Ethiopian wolf. Living in large packs is beneficial because wolves could spend less time on communal activities, but living in a crowded territory required more time spent hunting, especially for subadult or subordinate individuals, as well as for breeding packs. Wolves needed to adjust their behaviour to balance their solitary and communal activities effectively, and the demands of both of these contrasting activities could impose limits to group size. This can have conservation implications, as disturbances by humans or other species could negatively affect the balance between the social and solitary aspects of the life of the endangered Ethiopian wolf.

**Keywords** Time budgets · Behavioural trade-offs · Endangered canid · Sociality

## Introduction

Group living comes with costs and benefits to individual fitness (Elbroch et al. 2017; Gall and Manser 2018; Williamson 2019). Among carnivores, sociality facilitates access to mates, learning, communal breeding and cooperative hunting (Gittleman 1989), sometimes at the cost of intragroup competition for resources (Sheppard et al. 2018). Group living is not only influenced by access to food and habitat resources (Gittleman 1989), but also by the time available to different activities (Pollard and Blumstein 2008; Dunbar et al. 2009). Available time can constrain group size (Pollard

---

Communicated by C. Soulsbury.

✉ Elisa Sandoval-Serés  
elisa.sandoval@biology.ox.ac.uk

<sup>1</sup> Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, The Recanati-Kaplan Centre, Tubney House, Tubney OX13 5QL, UK

<sup>2</sup> Ethiopian Wolf Conservation Programme, PO Box 215, Robe, Bale, Ethiopia

<sup>3</sup> IUCN Canid Specialist Group, Oxford, UK

and Blumstein 2008); for example, if increasing amounts of time must be spent for individuals to meet a basic need, such as foraging, this may come at the cost of time spent in social interactions. Weak social bonds can also lead to group instability and impose a limit to group size (Pollard and Blumstein 2008; Dunbar et al. 2009).

When social carnivores depend on small-sized prey, the costs of intragroup competition are exacerbated, as the presence of another member of the group may interfere with hunting. More time is then needed for foraging to compensate for this conspecific interference (Gittleman 1989; Sandell 1989; Sillero-Zubiri and Gottelli 1995a). In such cases, meeting nutrient requirements might be limited by time more than by prey availability (Dunbar et al. 2009). Time constraints influence social behaviours and the size of social groups, and should therefore be considered when investigating the trade-offs of group living.

The behaviour of animals depends on their biological, ecological and social circumstances (Ausband et al. 2016; Methion and Díaz-López 2020). Whether an animal performs solitary or social activities at a given time, will depend on the benefits attained in those circumstances (Dorning and Harris 2017; Elbroch et al. 2017). For instance, in social species of otters (e.g. giant otter) group living is more common when intraspecific competition for resources is reduced (even though they often continue foraging alone) (Lodé et al. 2021). Specific characteristics of individuals can also affect the time allocation of particular behaviours. For example, the social rank of an animal affects the time allocated to foraging, where dominant individuals consistently spend less time feeding than subordinates among yellow baboons (Altmann and Muruthi 1988), bighorn sheep (Pelletier et al. 2004) and mountain goats (Hamel and Côté 2008). However, sex or age differences in time allocation to foraging are more varied and less consistent (Marshall et al. 2012). Conflicts over the timing and location of activities will be higher when the differences between group individuals are greater (Conradt and Roper 2000, 2005; Sueur et al. 2011; Marshall et al. 2012) and this could lead to group fission.

The Ethiopian wolf (*Canis simensis*) presents an interesting study system for understanding individual-group time allocation trade-offs, as they are both highly social but perform key behaviours alone. This endemic canid is a highly specialized hunter of diurnal rodents in Afroalpine highlands (Sillero-Zubiri and Gottelli 1994, 1995a; Marino and Sillero-Zubiri 2013). Due to the small size of their prey, they spend the majority of their day foraging to meet their energy requirements (Sillero-Zubiri 1994; Ashenafi et al. 2005; Marino et al. 2010). When Ethiopian wolves live at high densities (1 wolf/km<sup>2</sup>) they compete for access to the best foraging patches, as close proximity to other wolves interferes with hunting success (Sandell 1989;

Sillero-Zubiri and Gottelli 1995a, b; Marino et al. 2006). In contrast to this solitary behaviour, Ethiopian wolves engage in many social activities including: (a) territorial defence, which they do as a group, patrolling and marking the boundaries of the territory, (b) cooperative breeding, by guarding the den and providing food to the pups, and (c) maintaining strong social bonds and hierarchies through frequent and diverse social behaviours such as playing and allogrooming (Sillero-Zubiri 1994; van Kesteren et al. 2013). Typically, an Ethiopian wolf pack is composed by 6 to 8 individuals that are closely related (Sillero-Zubiri et al. 1996), sharing a communal territory (Sillero-Zubiri and Gottelli 1995a) and helping raise the pups of the dominant pair (Sillero-Zubiri 1994). For this solitary forager the advantages of group living are evident in that larger packs maintain larger territories (Sillero-Zubiri and Macdonald 1998), with larger per capita area of good-quality foraging habitat (Marino et al. 2012; Tallents et al. 2012). When a large pack divides, the break-away group inherits part of the natal territory (Marino et al. 2012).

It is not yet clearly understood how species that are both highly social, but require solitary time for key activities, such as Ethiopian wolves, balance their time, and whether strategies are specific to conditions of individuals or packs or both. Even though it is known that there can be behavioural differences between individuals and demographic categories of wolves (e.g. age, status, sex, breeding/non-breeding) (Sillero-Zubiri 1994; Sillero-Zubiri and Macdonald 1998), it is still not known how group living affects these specific categories. Thus, our aim was to determine and describe how Ethiopian wolves allocate their time to balance the costs and benefits of living in a group depending on individual and pack characteristics. In Ethiopian wolves, we hypothesized that the trade-offs in time budgets to balance the needs for solitary foraging with social living, as well as the interference magnitude on intragroup competition, will vary depending on the individuals' age, sex, position in the social hierarchy, pack breeding status, and the number of conspecifics in the social group. To test this hypothesis, we assessed time allocation patterns among Ethiopian wolves accounting for individual and pack-level characteristics. We compared time budgets of individuals across multiple packs to test two main predictions: (1) Increased interference competition at larger wolf densities will lead to more time spent foraging for subadults and subordinates (which could be excluded by older or more dominant individuals) and individuals from breeding packs (which would have higher energy requirements associated with pup care). Furthermore, in breeding packs, females will spend more time foraging than males due to the costs of lactation and pup feeding. (2) Individuals in larger groups will spend less time patrolling, as the cost will be shared among more pack

members, and this effect will be higher for adults, dominant individuals, and males (which normally patrol more frequently, Sillero-Zubiri and Macdonald 1998). However, time socialising will increase to help maintain social bonds especially for breeding packs, when group cohesion for pup care is especially important.

## Methods

### Study area

The study site was in the Bale Mountains National Park (BMNP, 7°N, 39°40'E; with an area of 2,200 km<sup>2</sup>), in southern Ethiopia (Fig. 1). Mean maximum annual rainfall is 1150 mm (mainly concentrated in the wet season: April to September) (Hillman 1986, 1988). In BMNP, two wolf populations have been monitored: Web Valley (7°N 39°42'E; 3,500 m.a.s.l.), and Sanetti Plateau (6°52'N 39°55'E; 4000 m.a.s.l.). The vegetation of these two areas mainly consist of open Afroalpine grassland, and other habitat subdivisions: sedge swamps and rocky grasslands (Sillero-Zubiri et al. 1995a). Both areas are characterized by a very high density of wolves (up to 1.2 wolves/km<sup>2</sup>), as well as, by a high biomass of rodents (25.7 kg/ha) (Sillero-Zubiri and Gottelli 1994, 1995a; Sillero-Zubiri et al. 1995b). Around BMNP, there are free-roaming domestic dogs and livestock (Sillero-Zubiri 1994; Stephens et al. 2001).

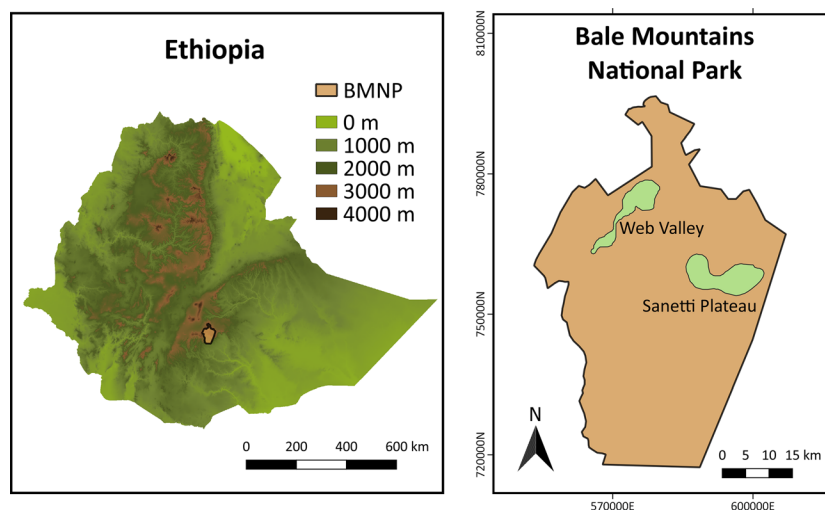
### Data collection

We used historical data collected by D. Gottelli, C. Sillero-Zubiri, and EE, who followed 85 individuals from 8 packs between 1988 and 1992. It was not possible to use blinded methods because the study involved focal wolves in the field. Packs were comprised of 3–11 individuals ( $7 \pm 2.1$

SE) that were habituated and followed from a distance of 20 to 300 m and watched through binoculars in open terrain. To recognize individuals, they used ear tags and unique coat patterns, and recognized dominant individuals each year (as dominant individuals breed once a year) by behavioural observations (e.g. mating, breeding, leading, and behaving aggressively) (Sillero-Zubiri et al. 1996). Age of wolves was calculated for individuals that were known from birth. Pack membership was defined when individuals were observed performing social activities together (e.g. socialising and patrol-marking) in the same study period of focals performed (in this period packs were temporally and spatially stable). To record behaviours (described in Table 1), they chose one individual randomly and performed a focal session (between 6:00 to 19:00 h), with a scan sampling method recording a behaviour every three minutes (Sillero-Zubiri 1994).

We combined data from wolves in the Web Valley and the Sanetti Plateau, as habitats and the structure of wolf populations are similar (Sillero-Zubiri et al. 1995a). We did not include floaters, defined as females without territory that utilize the spaces in between packs (Sillero-Zubiri et al. 1996), in the analyses. To assess the time allocation pattern of Ethiopian wolves, we classified behaviours as foraging, resting, patrol-marking, moving, socialising, and other (which includes interactions with other species) (Table 1) (Sillero-Zubiri 1994). We measured activity time proportions as the proportion of behavioural events of a certain each category within one hour, out of a possible maximum of 20 events. These proportions constituted the response variables in the models. We excluded focals conducted earlier than 7:00 or later than 18:00 h, as there were very few focals performed at those times and would have highly unbalanced the dataset. We also excluded focals shorter than 30 min, as we considered them not representative of time allocation for the whole hour (we used a minimum of 10 behavioural records

**Fig. 1** Location of Bale Mountains National Park (BMNP) in Ethiopia; and location of Web Valley and Sanetti Plateau in the BMNP. (Coordinate Reference System: EPSG: 32,637 - WGS 84 / UTM zone 37 N)



**Table 1** Description of categories of behaviours recorded during the focal observations of Ethiopian wolves between 1988 and 1992 in the Bale Mountains, Ethiopia (based on Sillero-Zubiri 1994)

General behaviours	Specific-behaviour	Description
<b>Foraging</b>	Drinking	Gulping down water
	Foraging	Searching for food (moving, digging, pouncing and checking for holes)
	Eating	Ingesting the food (killing, scavenging, regurgitating, nursing)
	Standing	Upright position with the weight on the four legs, mainly to look for food (vigilant)
<b>Resting</b>	Lying	Being in a horizontal position (with either head down, head up, or curled)
	Sitting	Rest supported by the rear part of the body
<b>Patrol-marking</b>	Walking-marking	Moving in a slow pace while urinating excreting, scratching, roll overs, sniffing
	Trotting-marking	Moving in a moderate pace while urinating excreting, scratching, roll overs, sniffing
	Standing-marking	Urinating or excreting, scratching, roll overs, sniffing in one place
<b>Moving</b>	Walking	Moving in a slow pace
	Trotting	Moving in a moderate pace
	Running	Moving in a rapid pace
<b>Socialising</b>	Socialising	Mating, playing, marking one another, behaving aggressively, greeting or grooming
<b>Other</b>	Interspecific interactions	Interactions with other species, such as dogs

per hour) (Appendix A, Table A1 summarizes excluded wolf individuals). We used 231 focals; totalling almost 441 h of observations (focals were between 30 and 60 min long, mean: 50, SE:  $\pm 0.46$ ), and including 47 individuals from 8 packs: 33 individuals (12 females, 21 males) in Web Valley, and 14 individuals (4 females, 10 males) in Sanetti Plateau. As there was a larger amount of focals between 8:00 h and 12:00 h, we used behavioural proportions to account for this difference in sampling effort. Approximately 88% of the focals were performed in 5 packs: 38% (in 10 different individuals) in Wolla pack (Web Valley population), 17% (in 8 individuals) in Nyala pack (Sanetti population), ~11% in each of the other three packs. Summary of sample size and sampling effort shown in Appendix A (Tables A2, A3, A4).

## Statistical analyses

We performed generalized linear mixed models (GLMMs) using a binomial distribution and logit link function (Bolker et al. 2009). We defined the structure of GLMMs by *a priori* specific predictions testing, instead of using model selection approaches (Field and Miles 2012; Harrison et al. 2018). We used *a priori* hypothesis approach by building models based on previous biological knowledge of the focal species and by only including in each model those covariates that have biological relevance. We analysed foraging, patrol-marking and socialising behaviours as response variables in separate models. We used the number of behavioural events in each hour (from 10 to 20) as weights for each GLMM, as when using a binomial distribution for proportional data, the number of trials (weights of a model) needs to be specified (Harrison et al. 2018). For all GLMMs, we included wolf individual or pack ID as random effect to avoid pseudo-replication (Bolker et al. 2009; Harrison et al. 2018). Pack ID was removed in one model (socialization) as it caused singularity of fit. As we measured activity proportions per hour, we included the hour of the day as a fixed covariate. We defined hour of the day as a discrete cyclical variable, because it consisted of entire hours from 7:00 to 17:00 h without including minutes. Other fixed categorical covariates were: age [adult or subadult (the subadult category included both: yearlings (1 year old), and individuals from 1 to 2 years old)]; dominance status [dominant (individuals who breed in a pack) or subordinate (helpers of the pack)]; sex (female or male); and packs breeding or non-breeding within the breeding season. The breeding season was defined as the months when pack members were providing food to the pups (October to March). We calculated density (a continuous fixed variable) as the number of adults and subadults (excluding individuals younger than 1 year old) in a pack (pack size) divided by the pack home range in km<sup>2</sup> (home range data taken from study Sillero-Zubiri and Gottelli (1995b), where they calculated pack home range using 100% minimum convex polygons calculated in the same study period when focals were conducted: 1988–1992). We defined pack size (fixed discrete variable) as the number of wolves (excluding pups) in a pack at the time of the focal observation. When analysing foraging behaviour (solitary activity), we included in the models the covariate of “wolf density” to test for the potential costs of living in a group when foraging interference occurs among wolves; when analysing social living activities (i.e. patrol-marking and socialising), we included in the models “pack size” to test for the potential benefits and costs of living in a group. To avoid cognitive biases, we compared each model with a null model using the Akaike information criterion corrected for small sample size (AICc) (Betini et al. 2017).

We ran separate models per categorical variable (age, dominance status, sex, pack breeding status) to test for specific predictions regarding the variation of group living trade-offs depending on different individual and pack characteristics. In all models, we controlled for hour of the day, which was not correlated with density or pack size ( $|r| < 0.3$ ;  $p < 0.001$ ). In foraging time models, we included an interaction between density and either age, dominance status or sex, and between density and breeding status (breeding or not). We did this to test for differential responses to density according to individual or pack characteristics as set out in our predictions. In patrol-marking and socialising models, we included interactions between pack size and either age, dominance status or sex, and between pack size and breeding status for the same reason. We summarize the models in Tables 2 and 3.

We performed all GLMMs with 'lme4' package (Bates et al. 2018) and graphed the models' results in 'sjPlot' package (Lüdtke 2020) in R (Core Team 2023). All GLMMs converged and showed model adequacy (Zuur et al. 2009; Harrison et al. 2018). We assessed goodness-of-fit from marginal  $R^2$  (which encompasses the variance explained by only the fixed covariates) and conditional  $R^2$  (which encompasses the variance explained by both fixed and random covariates) (Nakagawa and Schielzeth 2013) with the 'MuMIn' package (Barton 2018) of R (R Core Team 2020). A higher  $R^2$  meant a better goodness-of-fit of a model. Marginal and conditional  $R^2$  are not directly representing explained variation in GLMMs and should be interpreted with caution (Nakagawa and Schielzeth 2013).

## Results

On average, Ethiopian wolves spent the majority of their time foraging (56%; SE:  $\pm 2.5\%$ ), followed by resting (32%; SE:  $\pm 2.3\%$ ) (Fig. 2a). Daily time allocation by Ethiopian wolves between behavioural categories are illustrated

in Figs. 2 and 3 (all standard errors  $< 0.12$ , which are found in Appendix A, Table A5); and all GLMM outputs are summarized in Tables 2 and 3. Models testing foraging behaviour and models testing patrol-marking behaviour with significant results performed better than null models. Models testing patrol-marking behaviour with non-significant results and models testing socialising behaviour were analogous to null models (AICc difference  $< 2$ ). As the null models did not outperform our predictions-based models, our models support biologically meaningful covariates.

### Time allocation to solitary foraging

The proportion of time spent foraging varied across the day for different individuals (Fig. 2). In general, wolves spent more time foraging at 13 and 14 h and less time at dawn and dusk (Fig. 2a). The peak of foraging activity for adults was at 13:00 h and for subadults at 15:00 (Fig. 2b, c), and subordinates foraged slightly more than dominants at 7 h (Fig. 2d, e). As we predicted, the higher the density of wolves, the more time they generally spent foraging, especially subadult and subordinate individuals, who invested more time foraging than adults and dominants at higher densities and this difference was bigger for subordinates (density interaction with age, log-odd difference: 0.52 [95% CI: 0.08, 0.98];  $z = 2.27$ ;  $p = 0.023$ ; density interaction with dominance status, log-odd difference: 0.69 [95% CI: 0.34, 1.05];  $z = 3.86$ ;  $p < 0.001$ ) (Fig. 4a, b). Dominant individuals, however, do reduce foraging time at higher territorial density ( $z = 3.86$ ;  $p < 0.001$ , Fig. 4b).

There was a strong evidence of a difference in the foraging activity of packs with pups (breeding) and packs without pups (non-breeding). The higher the wolf density during the breeding season, the more time breeding packs had to spend foraging (the magnitude of the increase in foraging activity was low but significant; log-odd increase: 0.25 [95% CI: 0.27, 3.35];  $z = 2.30$ ;  $p < 0.02$ ); whereas this effect was the opposite for non-breeding packs, which spent less time

**Table 2** Summary of generalized-linear-mixed models of time allocation among behaviours by Ethiopian wolves in the Bale Mountains, Ethiopia

Model	df resi-dual	Variance of random covariate		logLik	Margi-nal R <sup>2</sup>	Conditional R <sup>2</sup>
		Wolf ID	Pack			
<b>Foraging</b> ~ Hour + Age*Density	383	0.698	0.156	-1823.3	0.026	0.227
<b>Foraging</b> ~ Hour + Dominance status*Density	383	0.846	0.138	-1815.0	0.037	0.259
<b>Foraging within breeding season</b> ~ Hour + Breeding status*Density	242	-0.547	0.100	-1112.7	0.009	0.172
<b>Foraging of breeding packs</b> ~ Hour + Sex	59	1.77	NA	-248.9	0.029	0.369
<b>Patrol-marking</b> ~ Hour + Age*Pack size	64	<0.001	<0.001	-182.0	0.061	0.180
<b>Patrol-marking</b> ~ Hour + Dominance status*Pack size	64	<0.001	<0.001	-188.3	0.030	0.230
<b>Patrol-marking</b> ~ Hour + Sex*Pack size	64	<0.001	<0.001	-187.8	0.026	0.215
<b>Socialising</b> ~ Hour + Pack size	88	0.755	<0.001	-177.9	0.015	0.199
<b>Socialising within breeding season</b> ~ Hour + Breeding status*Pack size	41	<0.001	NA	-90.6	0.042	0.241

df: degrees of freedom; NA: not applicable

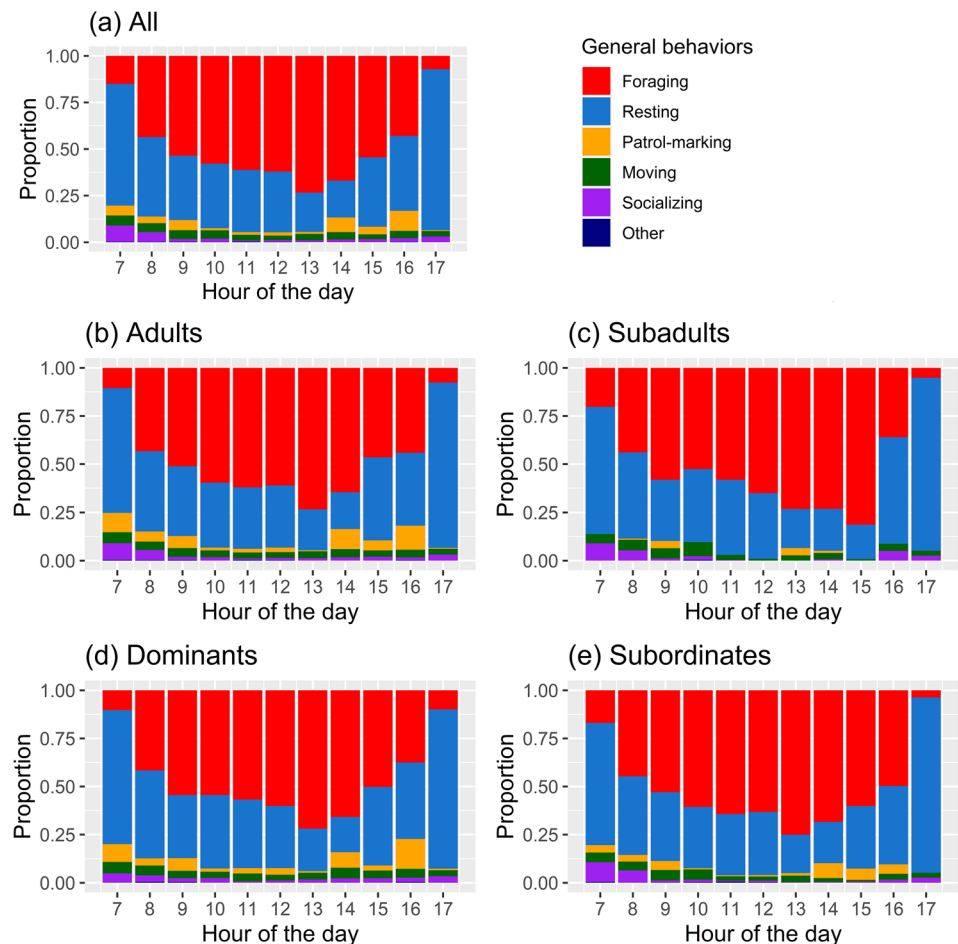
**Table 3** Summary of estimates of the generalized linear mixed models presented in Table 2 on time allocation by Ethiopian wolves among behaviours

Dependent variable	Fixed covariates or intercept	Esti-mate	95% Confidence interval (CI)		Z	Pr (> z ) significance: p < 0.05*
			Lower	Upper		
<b>Foraging</b> (Fig. 4a)	Intercept (Adult)	-0.66	-1.37	0.03	-2.07	0.038*
	Hour	0.08	0.06	0.11	7.25	< 0.001*
	Subadult	-0.89	-1.67	-0.16	-2.34	0.019*
	Density	0.22	0.04	0.40	2.38	0.017*
	Subadult *Density	0.52	0.08	0.98	2.27	0.023*
<b>Foraging</b> (Fig. 4b)	Intercept (Dominant)	-0.56	-1.50	0.31	-1.26	0.201
	Hour	0.09	0.06	0.11	7.47	< 0.001*
	Subordinate	-0.66	-1.54	0.27	-1.44	0.151
	Density	-0.07	-0.34	0.20	-0.52	0.604
	Subordinate* Density	0.69	0.34	1.05	3.86	< 0.001*
<b>Foraging within breeding season</b> (Fig. 4c)	Intercept (Breeding packs)	-0.09	-0.61	0.80	0.25	0.80
	Hour	0.04	0.01	0.07	2.89	< 0.004*
	Non-breeding packs	1.77	0.04	0.47	2.28	0.02*
	Density	0.25	0.27	3.35	2.30	0.02*
	Non-breeding packs*Density	-0.98	-1.74	-0.25	-2.59	0.01*
<b>Foraging of breeding packs</b>	Intercept (Female)	0.26	-1.04	1.60	0.40	0.69
	Hour	0.10	0.030	0.16	2.88	< 0.004*
	Male	-0.73	-2.18	0.64	-1.09	0.28
<b>Patrol-marking</b> (Fig. 4d)	Intercept (Adult)	0.73	-0.78	2.33	0.94	0.348
	Hour	0.01	-0.05	0.07	0.40	0.687
	Subadult	-0.32	-0.51	-0.14	-3.36	< 0.001*
	Pack size	-5.56	-8.60	-2.65	-3.74	< 0.001*
	Subadult*Pack size	0.83	0.41	1.28	3.83	< 0.001*
<b>Patrol-marking</b>	Intercept (Dominant)	-0.42	-2.78	1.97	-0.35	0.726
	Hour	0.02	-0.043	0.09	0.67	0.503
	Subordinate	-0.12	-0.45	0.20	-0.74	0.462
	Pack size	0.51	-1.86	2.94	0.42	0.672
	Subordinate* Pack size	-0.12	-0.51	0.25	-0.64	0.522
<b>Patrol-marking</b>	Intercept (Female)	-3.52	-10.93	4.01	-0.97	0.333
	Hour	0.02	-0.04	0.08	0.66	0.509
	Male	0.38	-0.76	1.50	0.69	0.491
	Pack size	3.49	-3.84	10.94	0.97	0.331
	Male*Pack size	-0.60	-1.74	0.53	-1.10	0.278
<b>Socialising</b>	Intercept	-2.00	-3.54	-0.45	-2.59	0.009*
	Hour	-0.05	-0.12	0.01	-1.69	0.090
	Pack size	0.09	-0.10	0.27	0.98	0.324
<b>Socialising within breeding season</b> (Fig. 4e)	Intercept (Breeding packs)	-1.40	-3.59	0.74	-1.29	0.196
	h	-0.08	-0.18	0.02	-1.64	0.101
	Non-breeding packs	2.96	-0.04	5.85	1.98	0.047*
	Pack size	0.04	-0.23	0.30	0.34	0.73
	Non-breeding packs*Pack size	-0.56	-1.03	-0.07	-2.28	0.022*

foraging when density increased (density interaction with pack breeding status, log-odd difference: -0.98 [95% CI: -1.74, -0.25];  $z = -2.59$ ;  $p = 0.01$ ). Additionally, time of the day had an effect on the foraging activity of packs within the breeding season ( $z = 2.89$ ;  $p < 0.004$ ) (Figs. 3a, b and 4c). Contrary to expectations, females within breeding packs did not spend more time foraging than males within breeding

packs ( $z = -1.09$ ;  $p = 0.28$ ). However, time of the day had an effect on the foraging activity of individuals in breeding packs ( $z = 2.88$ ;  $p < 0.004$ ), females spent more time foraging from 8:00 h to 11:00 and from 13 to 16 h, whereas males spent more time foraging from 11:00 h to 14:00 h (Fig. 3c, d).

**Fig. 2** Daily time allocation by Ethiopian wolves between behavioural categories in Bale Mountains National Park, Ethiopia, represented as proportions of each behavioural category per hour. (a) All eight packs (N=47 wolves); (b) adults (N=36); (c) subadults (N=19); (d) dominants (N=16); (e) subordinates (N=33)



### Time allocation to social activities

In respect to time allocation in communal behaviours, time of the day did not have an effect on patrol-marking or social behaviours (Table 1) ( $p > 0.09$  in all models). Individual time spent patrol-marking behaviour decreased with the size of the group for adults (log-odd decrease:  $-0.32$  [95% CI:  $-0.51, -0.14$ ];  $z = -3.36$ ;  $p < 0.001$ ), but this was not the case for subadults. Interestingly, subadults patrol-marked less than adults when packs had fewer than 6 members, but above 6 members subadults patrol-marked more than adults, and subadults spent more time patrol-marking when the pack size increased (pack size interaction with age, log-odd difference:  $0.83$  [95% CI:  $0.41, 1.28$ ];  $z = 3.83$ ;  $p < 0.001$ ) (Fig. 4d). There was no evidence of a difference in time spent patrol-marking between individuals of different dominance status or sex (dominance status:  $z = 0.42$ ;  $p = 0.462$ ; sex:  $z = 0.69$ ;  $p = 0.491$ ). There was also no evidence for an interaction of dominance status or sex with pack size on time spent patrol-marking (dominance status:  $z = -0.64$ ,  $p = 0.522$ ; sex:  $z = -1.10$ ,  $p = 0.278$ ).

In contrast to our prediction, larger groups did not spend more time socialising ( $z = 0.98$ ;  $p = 0.324$ ). Wolves in

breeding packs spent less time socialising than wolves in non-breeding packs at low pack sizes; however, individuals within breeding packs of larger pack sizes (6 or more members) spent more time socialising than individuals within non-breeding packs of the same size; in other words, non-breeding packs spent less time socialising when the pack size increased (pack size interaction with pack breeding status, log-odd difference:  $-0.56$  [95% CI:  $-1.03, -0.07$ ];  $z = -2.28$ ;  $p = 0.022$ ) (Fig. 4e).

### Discussion

Ethiopian wolves spent the majority of their time foraging; with a peak around noon, which corresponds to prey activity (Sillero-Zubiri and Gottelli 1995a, b). As we predicted, the higher the wolf density inside a territory, the more time wolves spent foraging, particularly subadults, subordinates and breeding packs. There was however, an exception to this general rule: dominant individuals and non-breeding packs actually spent less time foraging as density increased. However, contrary to expectations, females in breeding packs did not spend a higher proportion of their time

foraging when compared with males in breeding packs, possibly because both sexes can babysit and take turns to leave the den to go foraging. When packs were larger, adult wolves spent less time patrol-marking but subadults spent more time on this activity. Contrary to predictions, pack size did not affect how much time individuals spent socialising. However, there were differences in the socialising activity between breeding and non-breeding packs: when packs breed in small packs, less time is allocated to socialising, whereas larger breeding packs allocate more time socialising compared to their non-breeding counterparts.

### The costs of living in a group for solitary foragers

When foraging among other individuals is counterproductive, crowded spaces increase intraspecific competition among individuals of the same group (Williamson 2019; Methion and Díaz-López 2020; Li et al. 2021) and competition within territories affect individual foraging behaviour (Makin and Kotler 2019; Williamson 2019). For example, white-faced capuchins foraged in different canopy areas to avoid interference within the same group (Williamson 2019), and bottlenose dolphins foraged alone when catching easy prey and foraging cooperation was not required (Methion and Díaz-López 2020). Our results add to the evidence that group living can increase foraging competition (Molvar and Bowyer 1994; Williamson 2019) and also showed that this cost is not shared equally across group members: Ethiopian wolves need to spend more time foraging at high densities, except for the dominant pair. Larger Ethiopian wolf packs benefit from higher per capita access to quality foraging areas (Marino et al. 2012; Tallents et al. 2012), but within crowded territories interference seems to affect subadult and subordinate individuals more, as well as, individuals in breeding packs. Behavioural studies showed that dominant Ethiopian wolves could compete more advantageously for the best foraging patches (Sillero-Zubiri and Gottelli 1995b), with subordinate animals waiting for longer until a patch is vacated and the disturbed subterranean rodents become available again, this result was similar in red foxes (Dorning and Harris 2017) and elephants (Li et al. 2021). With lower time requirements for foraging, dominant animals are able to rest more or invest more time in other activities, for example, dominant Ethiopian wolves normally scent-mark more to indicate social status (Sillero-Zubiri and Macdonald 1998), as is also the case in meerkats (Jordan 2007) and dholes (Ghaskadbi et al. 2016). Individuals from breeding packs had to spend more time foraging in crowded territories, which was not the case for individuals from non-breeding packs. As individuals from breeding packs have more energy requirements associated with pup food provisioning (e.g. regurgitating and giving a full rodent

to pups) (Sillero-Zubiri et al. 2011), it is coherent that foraging competition due to higher wolf densities affects individuals from breeding packs more than individuals from non-breeding packs. For example, in African wild dogs, there has to be an adequate number of individuals hunting in each pack to be able to satisfy the high-energy demands of pup rearing (Courchamp 2002).

Regarding different sexes in breeding packs, even though females can have a higher energy demand due to allolactation and pup food provisioning [even subordinate females contribute more food to the pups than males (Sillero-Zubiri 1994)], female Ethiopian wolves irrespective of their ranking had no statistical evidence of spending a higher amount of time foraging than males within breeding packs. We might not have found differences in foraging activity between sexes from breeding packs because we did not consider individual status, and it is especially the dominant female that provides more food to the pups (Sillero-Zubiri et al. 2011). In several carnivore species, including sea otters (Garshelis et al. 1986), polecats (Lodé 1999), meerkats (Brotherton et al. 2001), and foxes (Dorning and Harris 2017), females feed the pups more often than males; and it is less common that males allocate more time to rearing pups than females, as described in raccoon dogs (Kauhala et al. 1998) and banded mongooses (Cant 2003). In Ethiopian wolves, the fact that the amount of foraging time was similar between females and males in breeding packs, and both sexes babysit and provide food to the pups, suggest that males also share the responsibility to satisfy the energy demands of breeding, this is common in cooperative breeding systems, where males also contribute to help females absorb the costs of breeding (Woodroffe and Vincent 1994).

### The benefits of living together

Under intense competition for the scarce Afroalpine habitat, one of the key advantages of sociality in Ethiopian wolves is the communal defence of a territory, with dominant and subordinate animals participating, and dominants of both sexes patrolling and marking at similar rates (Sillero-Zubiri and Macdonald 1998). Our results showed that wolves allocated similar amounts of time to patrol-marking across sexes and dominance categories, and when pack size was larger, adults spent comparatively less patrolling time than subadults. While Ethiopian wolves are expansionists and, thus, larger groups defend larger territories (Marino et al. 2012; Tallents et al. 2012), the costs of defence in terms of time investment becomes proportionally lower for adults in larger groups. This could be because larger groups were more likely to defeat smaller ones, and the number of scent-marks deposited per km is higher when more wolves are involved in the activity (Sillero-Zubiri and Macdonald



1998). Another possible explanation is division of labour, as more wolves participating means less time that each individual has to spend doing the communal activity, and is able to have more time to perform other behaviours, such as solitary foraging. This may be the case particularly for adults, who spend less time patrol-marking in larger groups. Labour division has been observed in other carnivores, such as in meerkats, where individuals take turns to perform vigilance behaviours allowing other members of the group to reduce their own vigilance and allocate more time in foraging (Ridley et al. 2013). However, subadults actually patrol-mark more at larger pack sizes. This might suggest that there are other factors at play, subadults (which are never dominant individuals) may be “paying to stay” in the group by contributing to communal activities like patrol-marking. At large pack sizes patrol-marking may also be used as a group cohesion activity, and larger territories may require more patrol-marking (Sillero-Zubiri and Macdonald 1998). Alternatively, subadults may be patrol-marking and exploring territory edges to assess breeding positions and opportunities at the margin of the territory, as at large pack sizes packs are more likely to split into two breeding packs (Marino et al. 2012). This result needs to be investigated further to assess whether these subadults are patrol-marking together or alone, and for what purpose.

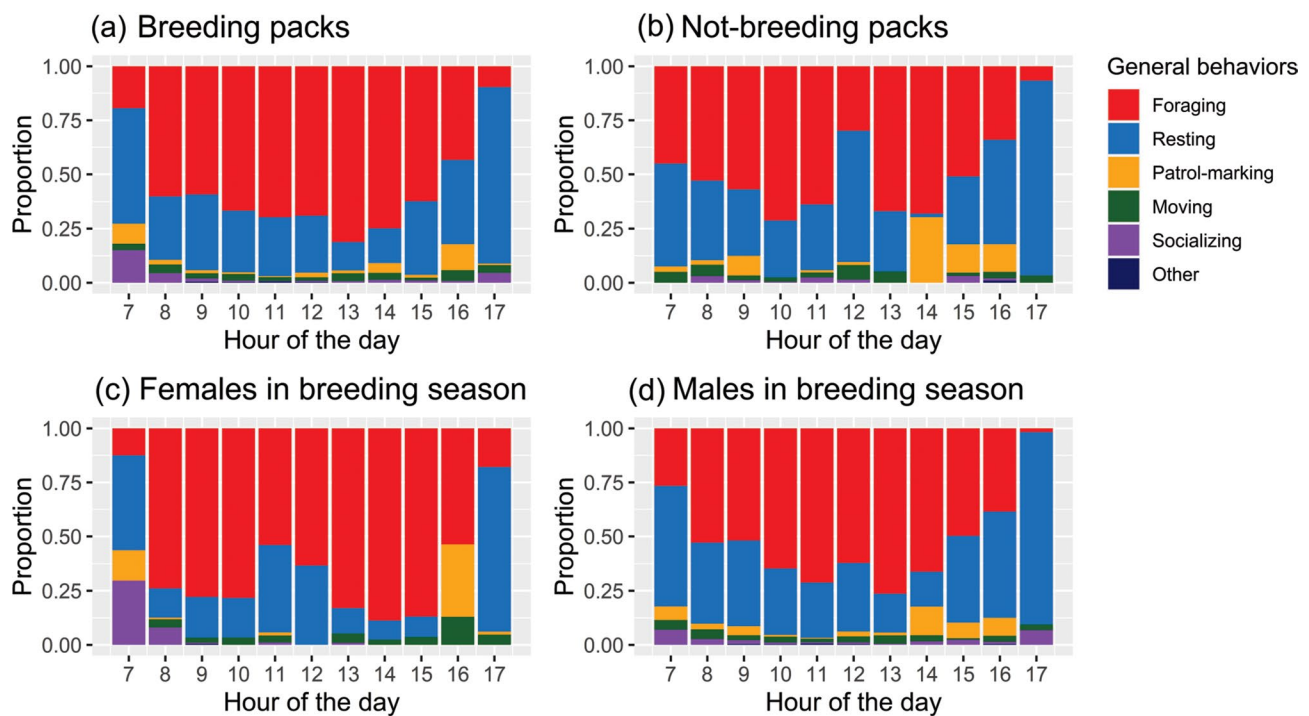
Socialising is important to maintain the cohesion of a group (Dunbar 1992; Pollard and Blumstein 2008; Dunbar et al. 2009), but in Ethiopian wolves we did not see a uniform effect of pack size on the time allocated to socialise. Animals in packs of different sizes did not change the proportion of time they allocated to socialising. However, during the breeding season, small packs (<6 members) spent less time socialising possibly due to the extra demands for foraging, feeding the pups and guarding. Similar behaviours have been observed in breeding female baboons, which had to sacrifice uncommitted resting time and social time to feed their offspring, compromising their social bonding and, in turn, group membership stability within the group (Dunbar and Dunbar 1988). The fact that Ethiopian wolves are social species which perform solitary activities (Sillero-Zubiri and Gottelli 1995a), might explain why pack size did not seem to affect the proportion of socialising time. It may be enough to maintain key bonds within a group, rather than with every pack member, and group level social time may be enough to maintain group cohesion. Maintaining pack cohesion however, may become too costly when packs become larger and they eventually split up. Studies have documented Ethiopian wolf packs of 10 or more individuals splitting up (larger than the pack sizes included in this study) after a subordinate becomes pregnant (Marino et al. 2012), indicating that in larger packs it is more difficult to

maintain reproductive suppression of subordinate females (van Kesteren et al. 2013).

### Conservation implications

Habitat loss is one of the big threats to the persistence of Ethiopian wolf populations (Stephens et al. 2001), and population growth of this species is negatively density-dependent (Marino et al. 2006). Given that Ethiopian wolves needed more time to forage in higher densities, loss of habitat or reductions in territory could mean more foraging time and perhaps a reduction in group size. Wolves spent more time foraging (67.5%) in a non-protected area with human impact (Ashenafi et al. 2005), than in the Bale Mountains National park (56%), indicating behavioural adaptations when wolves are disturbed or in degraded habitat. A similar situation is seen for gorillas, where survival in unsuitable habitats required high demands of feeding and resting time (Lehmann et al. 2008). In low-quality habitats, competition for best patches might impose time constraints to sociality. Indeed, in areas with low prey abundance in the Bale Mountains, Ethiopian wolves live as pairs or with just one offspring from the previous year (Marino et al. 2012). Any additional source of disturbance and degradation by humans, livestock and their domestic dogs, will avoid a negative impact on the herbivorous rodent prey and the Ethiopian wolves themselves (Atickem et al. 2010; Vial et al. 2010, 2011a, b; Yaba et al. 2011; Perry et al. 2018).

Domestic dogs potentially pose an acute problem by interfering with natural Ethiopian wolf behaviour. In the Bale Mountains, wolves and dogs segregate temporally, with peaks of foraging activity at different times of the day, which reduce the degree of interference, although they still have a considerable overlap in foraging times (67%) (Sillero-Zubiri et al. 1995a; Perry et al. 2018; Foley 2019). Despite not competing directly over food - dogs are not good rodent hunters - dogs actively displace wolves from their foraging grounds (Atickem et al. 2010; Perry et al. 2018) and in the northern highlands of Ethiopia, shepherds regularly chase wolves away from their herds, so that they spend most of the day hiding until people and livestock return to their houses in the late afternoon. The sympatric African wolf, which overlaps to some degree with Ethiopian wolves in their diet (Atickem et al. 2017; Gutema et al. 2019) could also compete with Ethiopian wolves, particularly if pack sizes are small. Adaptations to such disturbances can be costly for Ethiopian wolves with long-term effects on fitness, if it forces wolves to reduce time allocated for other activities, such as patrol-marking and socialising (Sillero-Zubiri and Macdonald 1998). Further studies of time budgets in wolf populations living in different habitats and levels of anthropological impact will bring light into the degree at which

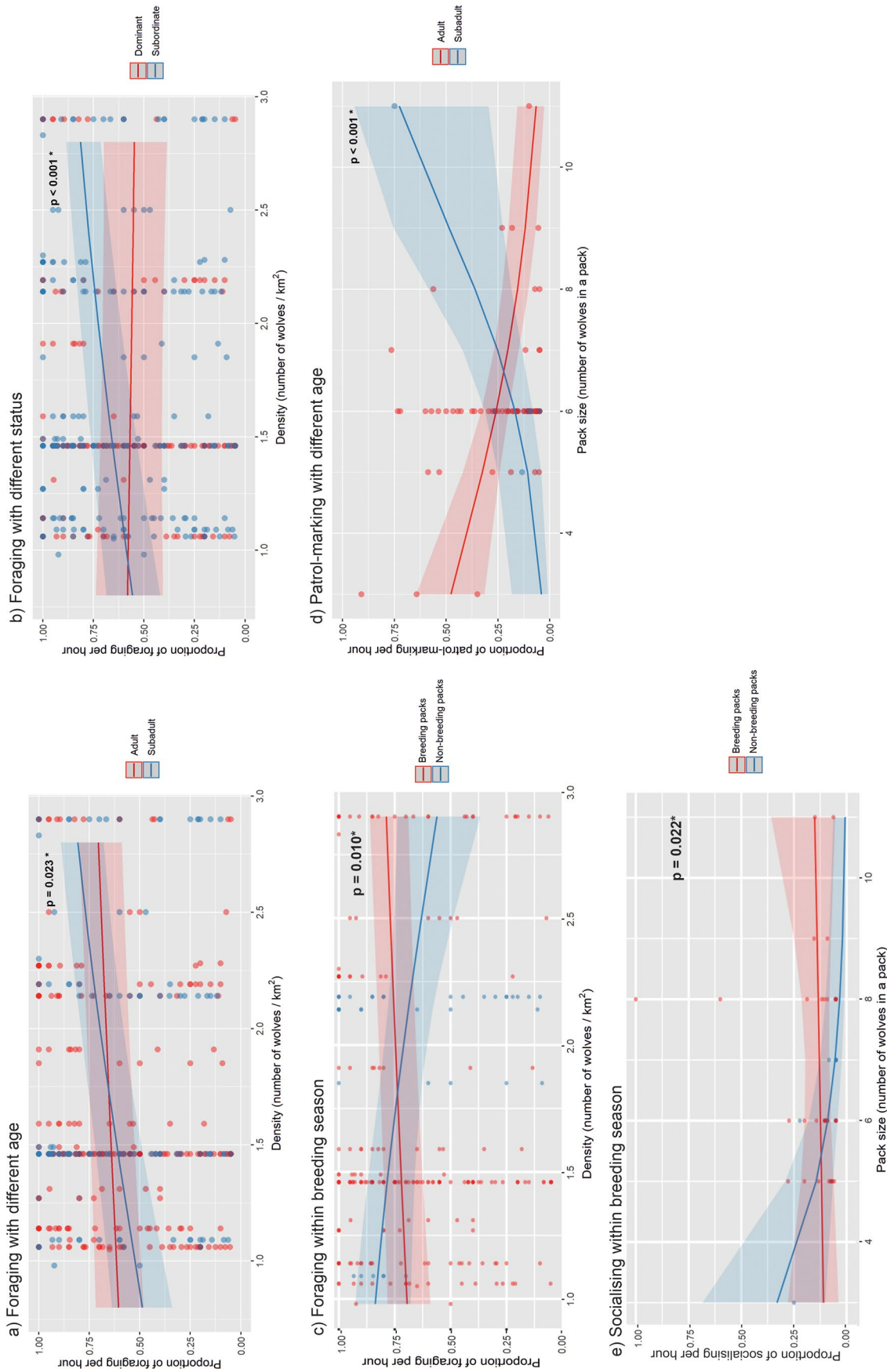


**Fig. 3** Daily time allocation within the breeding season: (a) packs breeding, and (b) packs non-breeding; (c) females in breeding packs, and (d) males in breeding packs, (seven packs during the breeding season, six months total,  $N = 12$  females and 24 males)

disturbances and prey degradation might affect the fine balance between sociality and solitary foraging in Ethiopian wolves, and the social structure of populations.

## Conclusion

There were benefits and costs of group living in Ethiopian wolves in terms of time allocation. Living in large packs was beneficial as individuals (particularly adults) could invest proportionally less time in communal activities such as territorial defence, and time socialising was not necessarily a constraint. Living in crowded territories however, required more time spent foraging, probably due to interference competition and this cost affected subadult and subordinate individuals more, as well as, individuals in breeding packs. Such a trade-off could put a cap on expansionism, driving dispersal of individuals for whom the costs of sociality are high and breeding opportunities scarce, including the fission of large groups into smaller ones. External factors like anthropogenic disturbance or interspecific competition could further alter time allocation and the fine balance between social and solitary activities.



**Fig. 4** Time allocation by Ethiopian wolves between behavioural categories with respect to packs characteristics (N=47 wolves). (a) Proportion of time foraging with different age with respect to wolf density (number of adult and subadult wolves in the pack / area of the pack's home range in km<sup>2</sup>) (N = 269 adult and 121 subadult observations); (b) proportion of time foraging with different status with respect to wolf density (N = 165 breeding and 225 subordinate observations); (c) proportion of time foraging within the breeding season depending on packs breeding or non-breeding with respect to wolf density (N = 211 breeding and 38 non-breeding pack observations); (d) proportion of time patrol-marking with different age depending on pack size (number of individuals in a pack, excluding pups) (N = 64 adult and 7 subadult observations); (e) proportion of time socialising within the breeding season depending on pack size for breeding and non-breeding packs (N = 37 breeding and 11 non-breeding packs observations). Dots represent observations, and lines the fitted line of the observations where the shadow area represents the 95% confidence interval. The “p” represents the p-value of the fixed covariate (x-axis) of the respective generalized linear mixed model described in Tables 2 and 3 (significance:  $p < 0.05^*$ )

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s00265-023-03398-4>.

**Acknowledgements** We would like to thank the Ethiopian Wildlife Conservation Authority and the Bale Mountains National Park for permission to carry out fieldwork. Thanks to Egil Drøge, Paul Johnson and Claudio Sillero for their critical reading of this manuscript. Claudio Sillero, Dada Gottelli and staff from the Ethiopian Wolf Conservation Programme collected the data and made it available. We would like to thank the reviewers for improving the quality of the manuscript. We would also like to thank our funders.

**Funding** Fieldwork was supported by the Born Free Foundation and New York Zoological Society. ES-S was supported by the Recanati-Kaplan Foundation. JM is partly funded by the Wildlife Conservation Network.

## Declarations

**Ethical approval** The field observations reported in this paper were subject to an agreement between the Ethiopian Wildlife Conservation Organisation and the New York Zoological Society. The data is from the 1990s, and then we did not have a formal requirement to have an ethical review.

**Conflict of interest** The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

**Authorship** All authors contributed to the study. EE performed the data collection. ES-S wrote the first draft of the manuscript and performed the analyses. All authors helped on the design of the study and commented on previous versions of the manuscript. All authors read and approved the final manuscript.

**Data accessibility statement** The dataset is available as supplementary material.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

## References

- Altmann J, Muruthi P (1988) Differences in daily life between semi-provisioned and wild-feeding baboons. *Am J Primatol* 15:213–221. <https://doi.org/10.1002/ajp.1350150304>
- Ashenafi ZT, Coulson T, Sillero-Zubiri C, Leader-Williams N (2005) Behaviour and ecology of the Ethiopian wolf (*Canis simensis*) in a human-dominated landscape outside protected areas. *Anim Conserv* 8:113–121. <https://doi.org/10.1017/S1367943005001952>
- Atickem A, Bekele A, Williams SD (2010) Competition between domestic dogs and Ethiopian wolf (*Canis simensis*) in the Bale Mountains National Park, Ethiopia. *Afr J Ecol* 48:401–407. <https://doi.org/10.1111/j.1365-2028.2009.01126.x>
- Atickem A, Simeneh G, Bekele A, Mekonnen T, Sillero-zubiri C, Hill RA, Stenseth NC (2017) African wolf diet, predation on livestock and conflict in the Guassa mountains of Ethiopia. *Afr J Ecol* 55:632–639. <https://doi.org/10.1111/aje.12399>
- Ausband DE, Mitchell MS, Bassing SB, Morehouse A, Smith DW, Stahler D, Struthers J (2016) Individual, group, and environmental influences on helping behavior in a social Carnivore. *Ethology* 122:963–972. <https://doi.org/10.1111/eth.12566>
- Barton K (2018) ‘MuMIn’: Multi-Model Inference. R Package Version 1.42.1. [cran.r-project.org/web/packages/MuMIn/MuMIn.pdf](https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf)
- Bates D, Bolker B, Walker S, Singmann H, Dai B, Scheipl F, Grothendiech G, Green P (2018) lme4\*: Linear mixed-effects models using Eigen and S4Package. R Package Version 1:1–17. [lme4.r-forge.r-project.org/](https://doi.org/10.1007/978-1-4939-9723-9)
- Betini GS, Avgar T, Fryxell JM (2017) Why are we not evaluating multiple competing hypotheses in ecology and evolution? *R Soc Open Sci* 4:160756. <https://doi.org/10.1098/rsos.160756>
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* 24:127–135. <https://doi.org/10.1016/j.tree.2008.10.008>
- Brotherton PNM, Clutton-Brock TH, O’Riain MJ, Gaynor D, Sharpe L, Kansky R, McIlrath GM (2001) Offspring food allocation by parents and helpers in a cooperative mammal. *Behav Ecol* 12:590–599. <https://doi.org/10.1093/beheco/12.5.590>
- Cant MA (2003) Patterns of helping effort in co-operatively breeding banded mongooses (*Mungos mungo*). *J Zool* 259:115–121. <https://doi.org/10.1017/S0952836902003011>
- Conradt L, Roper TJ (2000) Activity synchrony and social cohesion: a fission-fusion model. *Proc R Soc Lond B* 267:2213–2218. <https://doi.org/10.1098/rspb.2000.1271>
- Conradt L, Roper TJ (2005) Consensus decision making in animals. *Trends Ecol Evol* 20:449–456. <https://doi.org/10.1016/j.tree.2005.05.008>
- Core Team R (2023) R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. [www.R-project.org/](https://www.R-project.org/)
- Courchamp F (2002) Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. *Behav Ecol* 13:20–27. <https://doi.org/10.1093/beheco/13.1.20>
- Dorning J, Harris S (2017) Dominance, gender, and season influence food patch use in a group-living, solitary foraging canid. *Behav Ecol* 28:1302–1313. <https://doi.org/10.1093/beheco/axx092>
- Dunbar RIM (1992) Time: a hidden constraint on the behavioural ecology of baboons. *Behav Ecol Sociobiol* 31:35–49
- Dunbar RIM, Dunbar P (1988) Maternal time budgets of gelada baboons. *Anim Behav* 36:970–980. [https://doi.org/10.1016/S0003-3472\(88\)80055-1](https://doi.org/10.1016/S0003-3472(88)80055-1)
- Dunbar RIM, Korstjens AH, Lehmann J (2009) Time as an ecological constraint. *Biol Rev* 84:413–429. <https://doi.org/10.1111/j.1469-185X.2009.00080.x>
- Elbroch L, Levy M, Lubell M, Quigley H, Caragiulo A (2017) Adaptive social strategies in a solitary Carnivore. *Sci Adv* 3:e1701218. <https://doi.org/10.1126/sciadv.1701218>
- Field ZA, Miles J (2012) Discovering statistics using R. SAGE Publications, London
- Foley J (2019) Integrating individual behaviour into simulations of disease management in Ethiopian wolves. PhD dissertation, University of Oxford
- Gall GEC, Manser MB (2018) Spatial structure of foraging meerkat groups is affected by both social and ecological factors. *Behav Ecol Sociobiol* 72:77. <https://doi.org/10.1007/s00265-018-2490-x>

- Garshelis DL, Garshelis JA, Kimker AT (1986) Sea otter time budgets and prey relationships in Alaska. *J Wildl Manage* 50:637–647
- Ghaskadbi P, Habib B, Qureshi Q (2016) A whistle in the woods: an ethogram and activity budget for the dhole in central India. *J Mammal* 97:1745–1752. <https://doi.org/10.1093/jmammal/gyw141>. <https://doi.org/10.1093/jmammal/gyw141>
- Gittleman JL (1989) Carnivore group living: comparative trends. In: Gittleman JL (ed) *Carnivore Behavior, Ecology, and evolution*. Springer, Boston, pp 183–207. [https://doi.org/10.1007/978-1-4613-0855-3\\_8](https://doi.org/10.1007/978-1-4613-0855-3_8)
- Gutema TM, Atickem A, Tsegaye D, Bekele A, Sillero-Zubiri C, Marino J, Kasso M, Venkataraman VV, Fashing PJ, Stenseth NC (2019) Foraging ecology of African wolves (*Canis lupaster*) and its implications for the conservation of Ethiopian wolves (*Canis simensis*). *R Soc Open Sci* 6:190772. <https://doi.org/10.1098/rsos.190772>
- Hamel S, Côté SD (2008) Trade-offs in activity budget in an alpine ungulate: contrasting lactating and nonlactating females. *Anim Behav* 75:217–227. <https://doi.org/10.1016/j.anbehav.2007.04.028>
- Harrison XA, Donaldson L, Correa-Cano ME, Evans J, Fisher DN, Goodwin CED, Robinson BS, Hodgson DJ, Inger R (2018) A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ* 6:e4794. <https://doi.org/10.7717/peerj.4794>
- Hillman JC (1986) Conservation in Bale Mountains National Park, Ethiopia. *Oryx* 20:89–94. <https://doi.org/10.1017/S0030605300026314>
- Hillman JC (1988) The Bale Mountains National Park area, Southeast Ethiopia, and its management. *Mt Res Dev* 8:253–258
- Jordan NR (2007) Scent-marking investment is determined by sex and breeding status in meerkats. *Anim Behav* 74:531–540. <https://doi.org/10.1016/j.anbehav.2006.12.015>
- Kauhala K, Helle E, Pietilä H (1998) Time allocation of male and female raccoon dogs to pup rearing at the den. *Acta Theriol* 43:301–310
- Lehmann J, Korstjens AH, Dunbar RIM (2008) Time management in great apes: implications for gorilla biogeography. *Evol Ecol Res* 10:517–536
- Li L-L, Plotnik JM, Xia S-W, Meaux E, Quan R-C (2021) Cooperating elephants mitigate competition until the stakes get too high. *PLoS Biol* 19:e3001391. <https://doi.org/10.1371/journal.pbio.3001391>
- Lodé T (1999) Time budget as related to feeding tactics of European polecat *Mustela putorius*. *Behav Process* 47:11–18. [https://doi.org/10.1016/S0376-6357\(99\)00043-1](https://doi.org/10.1016/S0376-6357(99)00043-1)
- Lodé T, Lélis M, Lemasson A, Blois-heulin C (2021) Solitary versus group living lifestyles, social group composition and cooperation in otters. *Mammal Res* 66:13–31
- Lüdecke D (2020) ‘sjPlot’: Data Visualization for Statistics in Social Science. R Package Version 2.8.5, [cran.r-project.org/web/packages/sjPlot/index.html](https://cran.r-project.org/web/packages/sjPlot/index.html)
- Makin DF, Kotler BP (2019) Does intraspecific competition among Allenby’s gerbils lead to an Ideal Free distribution across foraging patches? *Behav Process* 167:103922. <https://doi.org/10.1016/j.beproc.2019.103922>
- Marino J, Sillero-Zubiri C (2013) *Canis simensis*. The IUCN Red List of Threatened Species 2013 e:T3748A10051312. <https://doi.org/10.2305/IUCN.UK.2011-1.RLTS.T3748A10051312.en>
- Marino J, Sillero-Zubiri C, Macdonald DW (2006) Trends, dynamics and resilience of an Ethiopian wolf population. *Anim Conserv* 9:49–58. <https://doi.org/10.1111/j.1469-1795.2005.00011.x>
- Marino J, Mitchell R, Johnson PJ (2010) Dietary specialization and climatic-linked variations in extant populations of Ethiopian wolves. *Afr J Ecol* 48:517–525. <https://doi.org/10.1111/j.1365-2028.2009.01140.x>
- Marino J, Sillero-Zubiri C, Johnson PJ, Macdonald DW (2012) Ecological bases of philopatry and cooperation in Ethiopian wolves. *Behav Ecol Sociobiol* 66:1005–1015. <https://doi.org/10.1007/s00265-012-1348-x>
- Marshall HH, Carter AJ, Rowcliffe JM, Cowlshaw G (2012) Linking social foraging behaviour with individual time budgets and emergent group-level phenomena. *Anim Behav* 84:1295–1305. <https://doi.org/10.1016/j.anbehav.2012.09.030>
- Methion S, Díaz-López B (2020) Individual foraging variation drives social organization in bottlenose dolphins. *Behav Ecol* 31:97–106. <https://doi.org/10.1093/beheco/arcz160>
- Molvar EM, Bowyer RT (1994) Costs and benefits of group living in a recently social ungulate: the alaskan moose. *J Mammal* 75:621–630
- Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining  $R^2$  from generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>
- Pelletier F, Hogg JT, Festa-Bianchet M (2004) Effect of chemical immobilization on social status of bighorn rams. *Anim Behav* 67:1163–1165. <https://doi.org/10.1016/j.anbehav.2003.07.009>
- Perry LR, Marino J, Sillero Zubiri C (2018) Going to the dogs: free-ranging domestic dogs threaten an endangered wild canid through competitive interactions. *J Biodivers Endanger Species* 6:1000211. <https://doi.org/10.4172/2332-2543.1000211>
- Pollard KA, Blumstein DT (2008) Time allocation and the evolution of group size. *Anim Behav* 76:1683–1699. <https://doi.org/10.1016/j.anbehav.2008.08.006>
- Ridley AR, Nelson-Flower MJ, Thompson AM (2013) Is sentinel behaviour safe? An experimental investigation. *Anim Behav* 85:137–142. <https://doi.org/10.1016/j.anbehav.2012.10.017>
- Sandell M (1989) The mating tactics and spacing patterns of solitary carnivores. In: Gittleman JL (ed) *Carnivore Behavior, Ecology, and evolution*. Springer US, Boston, MA, pp 164–182. [https://doi.org/10.1007/978-1-4613-0855-3\\_7](https://doi.org/10.1007/978-1-4613-0855-3_7)
- Sheppard CE, Inger R, McDonald RA, Barker S, Jackson AL, Thompson FJ, Vitikainen EIK, Cant MA, Marshall HH (2018) Intra-group competition predicts individual foraging specialisation in a group-living mammal. *Ecol Lett* 21:665–673. <https://doi.org/10.1111/ele.12933>
- Sillero-Zubiri C (1994) Behavioural Ecology of the Ethiopian Wolf, *Canis simensis*. PhD dissertation, University of Oxford
- Sillero-Zubiri C, Gottelli D (1994) *Canis simensis*. *Mamm Species* 485:1–6. <https://doi.org/10.2307/3504136>
- Sillero-Zubiri C, Gottelli D (1995a) Diet and feeding behavior of Ethiopian wolves (*Canis simensis*). *J Mammal* 76:531–541
- Sillero-Zubiri C, Gottelli D (1995b) Spatial organization in the Ethiopian wolf *Canis simensis*: large packs and small stable home ranges. *J Zool* 237:65–81. <https://doi.org/10.1111/j.1469-7998.1995.tb02747.x>
- Sillero-Zubiri C, Macdonald DW (1998) Scent-marking and territorial behaviour of Ethiopian wolves *Canis simensis*. *J Zool* 245:351–361. <https://doi.org/10.1017/S0952836998007134>
- Sillero-Zubiri C, Tattersall FH, Macdonald DW (1995a) Habitat selection and daily activity of giant molerats *Tachyoryctes macrocephalus*: significance to the Ethiopian wolf *Canis simensis* in the Afroalpine ecosystem. *Biol Conserv* 72:77–84. [https://doi.org/10.1016/0006-3207\(94\)00067-Z](https://doi.org/10.1016/0006-3207(94)00067-Z)
- Sillero-Zubiri C, Tattersall FH, Macdonald DW (1995b) Bale Mountains rodent communities and their relevance to the Ethiopian wolf (*Canis simensis*). *Afr J Ecol* 33:301–320. <https://doi.org/10.1111/j.1365-2028.1995.tb01041.x>
- Sillero-Zubiri C, Gottelli D, Macdonald DW (1996) Male philopatry, extra-pack copulations and inbreeding avoidance in Ethiopian wolves (*Canis simensis*). *Behav Ecol Sociobiol* 38:331–340. <https://doi.org/10.1007/s002650050249>
- Sillero-Zubiri C, Gottelli D, Marino J, Randall D, Tallents L, Macdonald DW (2011) Ecology and reproductive strategy of an

- afroalpine specialist: Ethiopian wolves in the Bale Mountains. *Walia* 2011:61–79
- Stephens PA, D'Sa CA, Sillero-Zubiri C, Leader-Williams N (2001) Impact of livestock and settlement on the large mammalian wildlife of Bale Mountains National Park, southern Ethiopia. *Biol Conserv* 100:307–322. [https://doi.org/10.1016/S0006-3207\(01\)00035-0](https://doi.org/10.1016/S0006-3207(01)00035-0)
- Sueur C, King AJ, Conradt L, Kerth G, Lusseau D, Mettke-Hofmann C, Schaffner CM, Williams L, Zinner D, Aureli F (2011) Collective decision-making and fission-fusion dynamics: a conceptual framework. *Oikos* 120:1608–1617. <https://doi.org/10.1111/j.1600-0706.2011.19685.x>
- Tallents LA, Randall DA, Williams SD, MacDonald DW (2012) Territory quality determines social group composition in Ethiopian wolves *Canis simensis*. *J Anim Ecol* 81:24–35. <https://doi.org/10.1111/j.1365-2656.2011.01911.x>
- van Kesteren F, Paris M, Macdonald DW, Millar R, Argaw K, Johnson PJ, Farstad W, Sillero-Zubiri C (2013) The physiology of cooperative breeding in a rare social canid; sex, suppression and pseudopregnancy in female Ethiopian wolves. *Physiol Behav* 122:39–45. <https://doi.org/10.1016/j.physbeh.2013.08.016>
- Vial F, Sillero-Zubiri C, Marino J, Haydon DT, Macdonald DW (2010) An analysis of long-term trends in the abundance of domestic livestock and free-roaming dogs in the Bale Mountains National Park, Ethiopia. *Afr J Ecol* 49:91–102. <https://doi.org/10.1111/j.1365-2028.2010.01233.x>
- Vial F, Macdonald DW, Haydon DT (2011a) Limits to exploitation: dynamic food web models predict the impact of livestock grazing on Ethiopian wolves *Canis simensis* and their prey. *J Appl Ecol* 48:340–347. <https://doi.org/10.1111/j.1365-2664.2010.01943.x>
- Vial F, Macdonald DW, Haydon DT (2011b) Response of endemic afroalpine rodents to the removal of livestock grazing pressure. *Curr Zool* 57:741–750. <https://doi.org/10.1093/czoolo/57.6.741>
- Williamson RE (2019) Intraspecific niche divergence in foraging and habitat use in wild Costa Rican capuchin monkeys. MSc thesis, University of Calgary
- Woodroffe R, Vincent A (1994) Mother's little helpers: patterns of male care in mammals. *Trends Ecol Evol* 9:294–297. [https://doi.org/10.1016/0169-5347\(94\)90033-7](https://doi.org/10.1016/0169-5347(94)90033-7)
- Yaba M, Mekonnen T, Bekele A, Malcolm J (2011) Food selection and feeding behavior of giant mole rat (*Tachyoryctes macrocephalus*, Ruppell, 1842) from the Santti Plateau of Bale Mountains National Park, Ethiopia. *Asian J Appl Sci* 4:735–740. <https://doi.org/10.3923/ajaps.2011.735.740>
- Zuur A, Ieno E, Walker N, Saveliev A, Smith G (2009) Mixed effects models and extensions in Ecology with R. Springer, New York

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.