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Research article

Conservation with hard borders: Ethiopian wolves are threatened by fragmentation and isolation

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Unlike most canids, versatile and capable of navigating vast landscapes, endangered Ethiopian wolves (*Canis simensis*) are endemic to an archipelago of Afroalpine islands. As a habitat specialist, the Ethiopian wolf is ill-equipped to move across a highly transformed and densely populated agriculture matrix. Hard borders imposed by expanding subsistence agriculture lock Ethiopian wolves into further isolation, with few opportunities for dispersal and recolonisation. We report and evaluate empirical information from long-term monitoring across the species' range to understand processes of habitat loss, recolonisation and extinction in recent and historical times, and to assess what conservation measures and strategies would ensure their persistence. Ethiopian wolves occurred in six isolated populations, totalling 454 wolves (population sizes ranged between 281 and 24) occupying 2700 km^2 of Afroalpine habitat. We describe three population extinctions and three local extinctions within fragmented populations, and present evidence of factors accelerating the extinction process, such as disease (rabies and canine distemper virus), persecution, road kills and poisoning. Of all the suitable habitat available to wolves, 86% was included within nine protected areas, including three new Community Conservation Areas and two national park extensions in the past 10 years. As all Ethiopian wolf populations are small and vulnerable to stochastic events and environmental perturbation, conservation efforts to ensure the long-term survival of the species need to integrate: 1) support for protected areas to halt agriculture encroachment and to regulate sustainable uses of natural resources; 2) efforts to minimise all causes of mortality, including but not limited to disease; and 3) conservation translocations to overcome fundamental barriers to dispersal in the highlands of Ethiopia.

Keywords: Afroalpine, *Canis simensis*, extinction, recolonisation, small population size, translocations

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Introduction

There is wonderful variation across canids, a family present across the globe, except Antarctica. Most canids, notably middle-sized ones such as coyotes (*Canis latrans*) and golden jackals (*C. aureus*), but also grey wolves (*C. lupus*), are versatile and often more than capable of navigating vast landscapes (Macdonald and Sillero-Zubiri 2004). In the last century, dramatic canid range expansions, such as the golden jackal in Europe or the red fox (*Vulpes vulpes*) in the circumpolar Arctic, have been reported, sparking debates, wildlife management decisions and more ecological research (Trouwborst et al. 2015, Elmhagen et al. 2017, Krofel et al. 2017, Gallant et al. 2020). In the last decades, a large predator, the grey wolf, has been rapidly recolonising many regions of its former distribution range in Europe from where it had been extirpated, including France, Switzerland, Germany and Scandinavia (Hindrikson et al. 2017, Bijl and Csányi 2022). While we are largely concerned with grey wolves straddling political borders and land uses, their close relatives – Ethiopian wolves (*C. simensis*) – due to their recent biogeography and high specialisation to the Afroalpine ecosystem, are facing hard borders imposed by the encroaching subsistence agriculture frontier.

The Ethiopian wolf presents a unique and concerning conservation challenge. Endemic to Ethiopia, and red listed as 'Endangered' (EN), only a few hundred adult wolves remain across an archipelago of isolated Afroalpine islands (Marino 2003, Marino and Sillero-Zubiri 2011). The Ethiopian wolf is a highly specialised predator of diurnal rodents, the dominant herbivores of the Afroalpine ecosystem (Sillero-Zubiri and Gottelli 1995a, Sillero-Zubiri et al. 1995, Marino et al. 2010), and while their slight bodies and specialist dentition make them supreme rodent hunters and the top predator in the ecosystem, this specialisation came at a cost. Ethiopia, currently the second most populated country in sub-Saharan Africa, has a fast growing population that is expected to increase by 27% over the next decade (United Nations Development Programme 2023). Human expansion into the Afroalpine habitats continues to erode the wolves' shrinking ranges, locking them into further isolation (Marino 2003). When habitats are fragmented due to human activities like deforestation or urbanisation, carnivores often find themselves confined to smaller and increasingly isolated patches of suitable habitat (Crooks 2002, Crooks et al. 2011). As populations become smaller and more isolated, stochastic events and environmental perturbations make it more challenging to maintain viable breeding populations (Benson et al. 2016, Nordstrom et al. 2023).

With Ethiopian wolves existing only in small populations, any additional threat may lead to tipping points and into the extinction vortex. The most immediate threat is posed by viral diseases transmitted by domestic dogs, with large packs and the social nature of wolves increasing the risk of epizootics resulting in large demographic fluctuations (Haydon et al. 2002, Haydon et al. 2006, Marino et al. 2013). In the Bale Mountains, the largest population, outbreaks of rabies and canine distemper virus (CDV) have reduced local populations by up to 75% (Sillero-Zubiri et al. 1996a, Randall et al. 2004, Gordon et al. 2015) and their recovery has been delayed when disease extirpated whole breeding units or packs (Marino et al. 2013). This is because their expansionist strategy relies on packs attaining certain size before a splitting can create new breeding units (Marino et al. 2013). The disease risk is higher for smaller populations, as demonstrated by back-to-back outbreaks in the smallest Ethiopian wolf population which decimated numbers to just a surviving pair (Marino et al. 2017).

In addition, the ability of Ethiopian wolves to recolonise empty areas or to rescue a declining population via dispersal, is limited. Their dispersal capacity is not only restricted by the hard borders generated by the encroachment of agricultural fields and human settlements, but also by their evolutionary backdrop. The species' life history, which evolved under the selective pressures imposed by limited breeding and foraging space, is characterised by longevity, philopatry and short-distance dispersal (mainly by female wolves) (Marino et al. 2012) – a 'stay at home' strategy. This is reflected in high levels of genetic differentiation between most populations, which indicated limited gene flow among populations and increasing risk of genetic drift (Gottelli et al. 2013).

Ethiopian wolf populations and their threats are being studied and monitored by the Ethiopian Wolf Conservation Programme (EWCP, www.ethiopianwolf.org) since the late 1980s. The vast knowledge acquired has informed an ongoing integrated disease management programme, which includes vaccinating domestic dogs in villages near wolf habitat, as well as preventive and reactive vaccination of the wolves themselves (Randall et al. 2006, Sillero-Zubiri et al. 2016). Still, disease risks, human-mediated mortality and habitat loss and degradation continue to pose significant threats and, with few opportunities for wolf dispersal and recolonisation, the long-term survival of these rare canids is compromised. In this paper, we compiled and evaluated empirical information from across the species range to define the latest global population estimate and to understand processes of habitat loss, recolonisation and extinction in historical and recent times. Previous global population estimates were derived from habitat extrapolations (Marino 2003, Marino and Sillero-Zubiri 2011), making this new population estimate the first obtained from intensive monitoring efforts spanning the entire range of the species. We then discussed conservation measures and strategies that would soften the borders and ensure the long-term persistence of Ethiopian wolves in their island homes.

Material and methods

Population estimation

Ethiopian wolf packs have been monitored by the EWCP since 1988 in the southern highlands (Bale Mountains, Arsi Mountains) and since 1998 in the central and northern highlands of Ethiopia (Simien Mountains, Mt Guna, North

Wollo, South Wollo and Menz-Guassa). We defined a wolf population as a group of wolves occupying an Afroalpine unit, composed by one or more habitat patches, separated from other populations by a straight-line distance of at least 20 km (Marino 2003). A local population occupies a habitat patch within a fragmented Afroalpine unit. The global Ethiopian wolf population was estimated from data collected in the 2020–2021 breeding season, when EWCP had the most intensive field presence across the species range (subsequently, the Covid-19 pandemic and a period of armed conflict has precluded regular monitoring work in most populations outside Bale). The monitoring effort over the said period involved 16 wolf monitors (with high expertise on wolf monitoring) and 17 wolf ambassadors (members of the local community), who combined collected a total of 4960 wolf sightings.

Ethiopian wolves are highly social, territorial and diurnal, which allows close monitoring techniques based on direct observations, as described in Marino et al. (2012). Focal areas are visited typically 10–20 days per month, depending on the study area. The number of individuals and pack composition in focal areas are determined each year through repeated sightings of groups throughout the breeding season, covering parturition to weaning of pups (October to March). Sex, age class (juveniles: <1 year old; subadults: 1–2 years old; and adults: >2 years old), and dominance status were determined from behavioural cues and changes in coat patterns (Sillero-Zubiri and Gottelli 1995b). Some individuals trapped during the course of vaccination interventions and vaccine trials can be identified by plastic ear-tags with colour combinations (Rototag, Dalton, Newark, UK). Monitoring outside focal areas occurs at lower intensity, over repeated field visits (up to 5 days per month). The number of wolves in these areas was estimated by multiplying the numbers of packs known to live there by average pack size. The longest monitoring time series that is available for the Web Valley, Bale Mountains National Park, was used to show population fluctuations through the years (1988–2023).

Remaining Afroalpine habitat

Optimal wolf habitat is characterized by Afroalpine meadows with short grass and herbs and a rodent biomass of 3500–4000 kg km^{-1}; good wolf habitat is characterized by *Helichrysum* shrub and montane grasslands with a rodent biomass of one third of optimal habitat; marginal wolf habitats include dense ericaceous and charanfe (*Euryops pinifolius*) heathlands, steep slopes and escarpments, rocky barren peaks and overgrazed grasslands near settlements, with a rodent biomass one fifth to one tenth of optimal habitat (Gottelli and Sillero-Zubiri 1992, Marino 2003). Building on the detailed mapping of Afroalpine habitats from the 1999–2000 field surveys (Marino 2003), the remaining Afroalpine areas were manually delimited using satellite imagery in Google Earth based on field expert knowledge and ground-truthing by EWCP. Afroalpine vegetation, characterised by short grasslands, meadows, low-growing *Helichrysum* shrubs and *Erica* bushes (Sillero-Zubiri et al. 1995), is notably different from the surrounding landcover, which includes montane forest remnants and encroaching crop fields. Habitat polygons and maps were built using QGIS3 ver. 3.12.3 (QGIS 2024).

Extinctions, recolonisation and dispersal

We defined a population extinction when wolves died out from an isolated Afroalpine unit. We defined a local extinction (sometimes also called a range contraction) when wolves ceased to exist in a particular habitat patch but continued to exist elsewhere within the Afroalpine unit. Two population extinctions, in Mt Choke and Gosh Meda, had been reported previously (Marino 2003, Marino and Sillero-Zubiri 2011). Extinctions were confirmed on evidence gathered by EWCP through field trips and interviews with the local communities and authorities, and from historical records. Additional information relayed to EWCP around the time of extinctions was assessed for reliability and their evidence value weighed accordingly. Detailed information and sources are presented in the Supporting information. 'Year of last confirmed sighting' was the last year with a reliable sighting from a resident wolf pack. 'Year of extinction' was evidenced by subsequent field visits and/or reports. Level of evidence for factors contributing to the extinctions (from EWCP staff or from partners and local communities directly reporting to EWCP), depending on the reliability of the information, was classified as: 'Yes'/'No'= firm evidence of a given factor having/not having contributed to wolf mortality or to other drivers of extinction; 'Likely'= a potential factor was present and expected to have contributed to the extinction; 'Possibly'= a potential factor is present but its contribution towards the extinction is unknown/unclear.

Information on recolonisation was collected from direct observation of wolves, including monitoring immigrant wolves that reached Delanta two years after a local extinction. The maximum dispersal distances of Ethiopian wolves within continuous habitat were also assessed from tagged individuals that moved from the pack they belonged to when they were captured in another known pack (straight-line distance from capture location to the first sighting within their new pack), and from a rehabilitated male wolf that was released back in his initial pack in Simien Mountains National Park and tracked using a GPS collar (Litetrack Iridium 250, Lotek Wireless Inc., Newmarket, ON, Canada) during approximately 8 months in 2020–2021, including during a dispersal phase (Lai et al. unpubl.).

Protected areas

We collated information about all existing protected areas in Afroalpine ranges from official sources (e.g. protected area proclamations) and own investigations (e.g. about governing bodies), and assessed them against the International Union for Conservation of Nature (IUCN) protected area categories (IUCN 2008). To calculate the amount of wolf suitable habitat protected, we overlaid the protected area boundaries over our current habitat polygons.

Results

Ethiopian wolf populations

Intensive monitoring across the species range confirmed the existence of six surviving wolf populations, isolated from each other, with a combined total of 454 adult wolves in 99 packs (Table 1, Fig. 1). The Bale Mountains had by far the largest population, with over 60% of all remnant wolves. Simien Mountains had the second largest and all others were relatively small, with fewer than 35 individuals each. Populations with larger Afroalpine ranges tended to have more wolves (Pearson's correlation coefficient: 0.74) but wolf densities varied across populations, reflecting the relative proportions of habitat quality types in each range, as shown in previous studies (Gottelli and Sillero-Zubiri 1992, Marino 2003). Menz-Guassa, a small range dominated by high quality, predominantly grassland habitat, sustained an overall density 10 times larger than that in the Arsi Mountains, composed of vast expanses of lower quality *Erica* moorland (respectively, 0.41 wolves km^{-2} versus 0.04 wolves km^{-2}). While the Bale Mountains supported an intermediate overall density (0.21 wolves km^{-2}), local populations in optimal areas reached up to 1.4–1.7 wolves km^{-2} when at carrying capacity (Fig. 2).

Habitat loss, fragmentation and extinctions

The suitable habitat for Ethiopian wolves was distributed in 19 patches across nine isolated Afroalpine units. Of these, 10 were not occupied by wolves, comprising 10% of the total area (303 km^2), leaving 2683 km^2 occupied by wolf populations (Fig. 3). Habitat patches without wolves were on average smaller (30 km^2; SE = 52 km^2) than those with wolf populations (289 km^2; SE = 382 km^2). Guassa-Menz was the smallest range sustaining a wolf population (69 km^2) and Aboi Gara in North Wollo was the smallest patch (22 km^2) sustaining a local population.

The Afroalpine habitat available to wolves in Ethiopia was 2986 km^2, which represented just 21% of the area predicted as suitable wolf habitat, before considering agriculture encroachment (Thompson 2022) (shown in red in Fig. 1). This substantial loss across the Ethiopian highlands led to the fragmentation of previously continuous Afroalpine patches and to increasing isolation between them (Fig. 1). The upper limit of subsistence agriculture (at around 3700 m above sea level, but ranging between 3400 and 4000 m) imposed a hard border between suitable and unsuitable habitat. The territories of wolf packs were contained within Afroalpine patches, with no records of wolves using or dispersing through the agriculture matrix since monitoring began in 1988.

In the past two decades, we documented the extinction of two wolf populations, in Mt Guna and Gosh Meda (a third had disappeared from Mt Choke several decades earlier), and three local extinctions. Table 2 summarises information on the timing of extinctions and evidence of contributing factors (detailed information in Supporting information). Potential extinction drivers not included in the summary were: 1) intra-guild competition with domestic dogs and African wolves (*Canis lupaster*), due to the absence of studies or direct evidence, and 2) inbreeding depression, on the basis that no phenotypical signs of inbreeding had been detected in any population.

With regards to population extinctions, the reasons behind the disappearance of wolves from Mt Choke were the least understood (Marino 2003). This extinction dated back to the early 1900s (Yalden et al. 1980) and could not be explained by the extent or quality of suitable habitat (Fig. 3), but the deep Blue Nile gorge encircling this plateau imposed a strong

Table 1. Extant Ethiopian wolf populations: number of wolves (1 year and older) and extent of Afroalpine habitat.

Population	Number of packs	Number of wolves	Afroalpine habitat (km^2)	Density (wolves km^{-2})
Simien Mountains	15	60	316	0.19
*Ambaras and Buahit	5	25		
Other areas	10	35		
North Wollo	6	29	94	0.31
*Abuna Yosef	3	15		
*Delanta-Gubalaftu	1	8		
Other areas	2	6		
South Wollo	8	24	145	0.15
Menz-Guassa	7	28	69	0.41
*Menz	5	21		
Anaz	2	7		
Arsi Mountains	9	32	778	0.04
Bale Mountains	54	281	1338	0.21
*Web Valley	8	47		
*Sanetti Plateau	5	32		
*Morabawa East	6	40		
Other areas	35	162		
Total	*99*	*454*	*2740*	*0.16*

Population size estimated from intensive monitoring throughout 2021.
*Focal areas with total counts; number of wolves in 'Other areas' are extrapolations based on known numbers of packs in those areas (see methods). The Afroalpine habitat was mapped from a combination of field surveys and remote sensing.

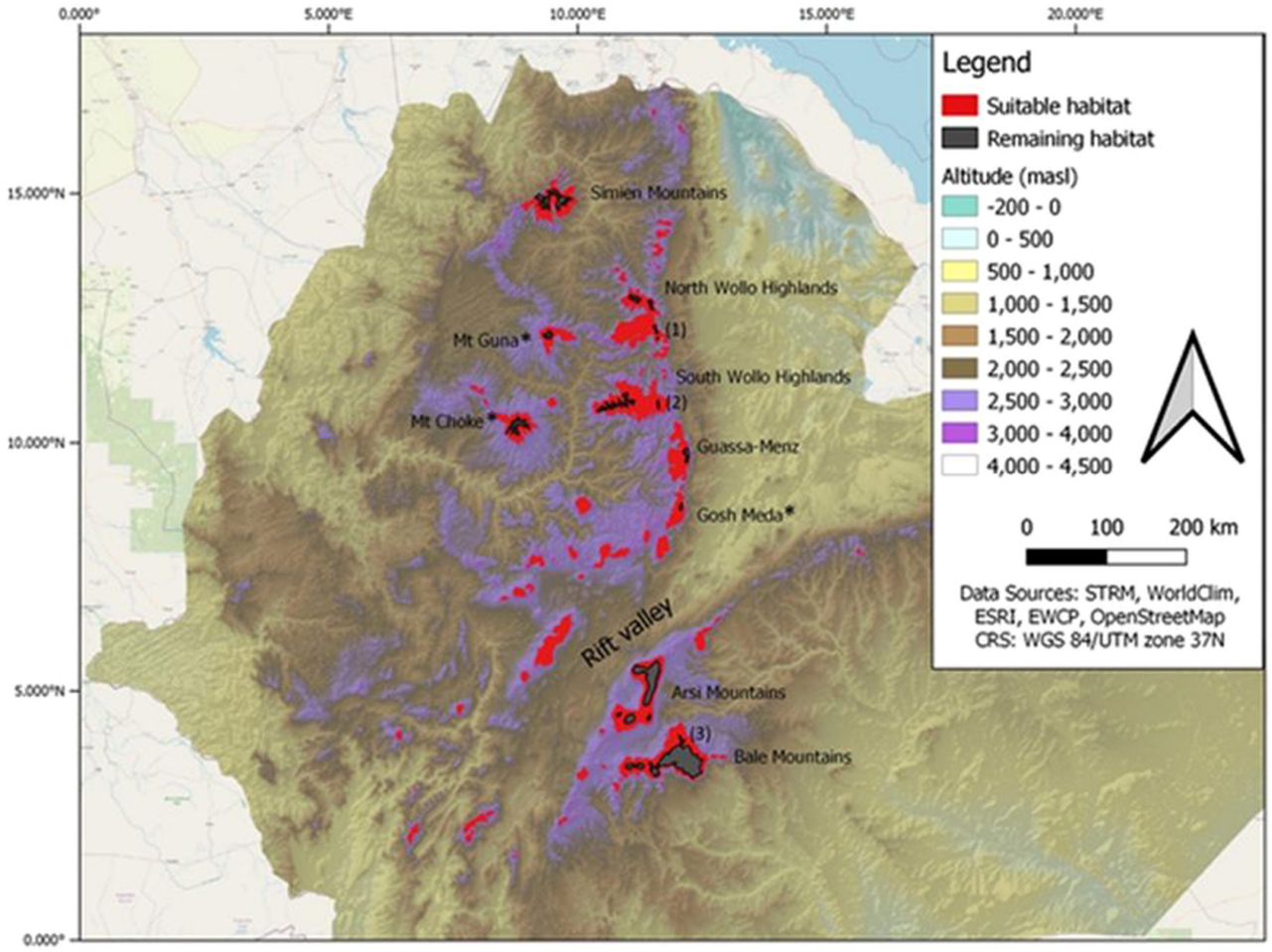

Figure 1. Distribution of Ethiopian wolf populations and Afroalpine habitats. In red, potential suitable habitat under current climatic conditions (Thompson 2022); in black, currently remaining Afroalpine habitat. Extinct populations indicated with a star symbol next to the name of the area (i.e. Mt Guna, Mt Choke, Gosh Meda), and local extinctions indicated with numbers: (1) Delanta (North Wollo); (2) Guguftu (South Wollo); (3) Gaysay (Bale Mountains).

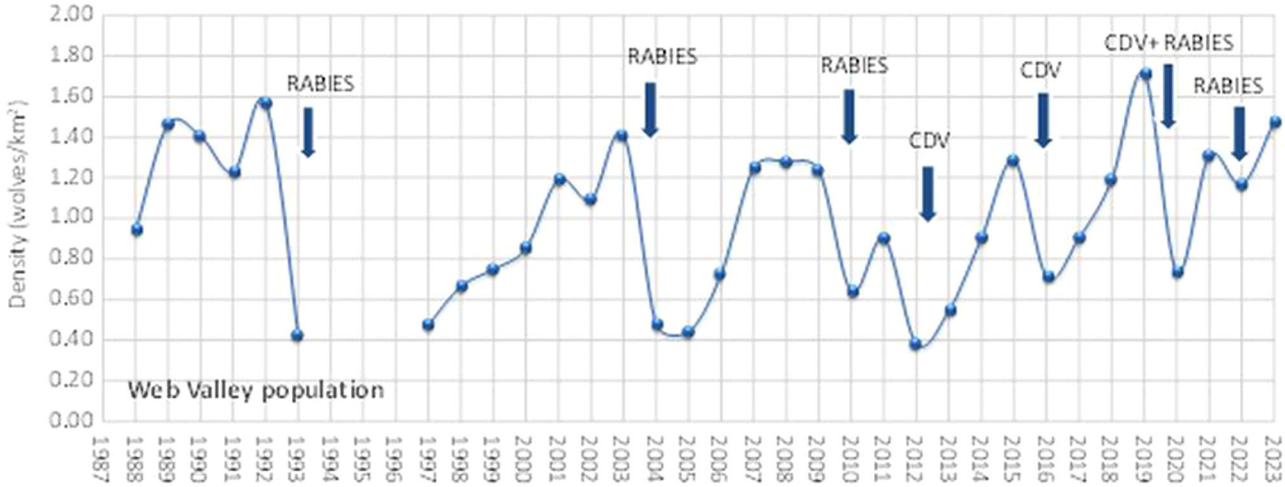

Figure 2. Time series of population density of Ethiopian wolves in the Web Valley, Bale Mountains, Ethiopia. Arrows indicate outbreaks of rabies and canine distemper virus (CDV).

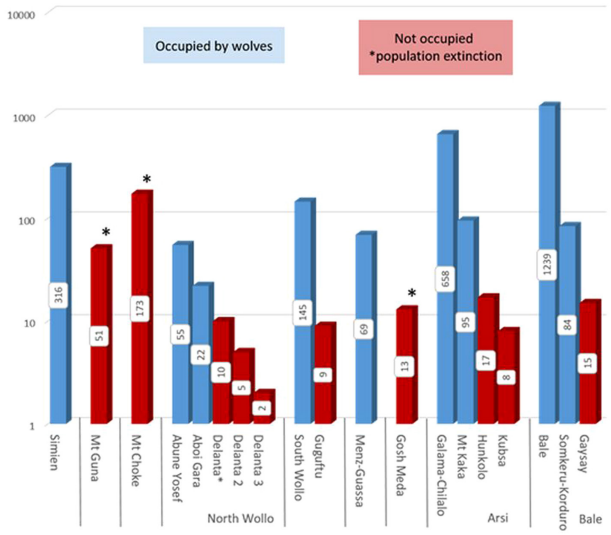

Figure 3. Size of habitat patches (km^2, logarithmic scale), indicating those occupied by Ethiopian wolves in blue, and in red where wolves went extinct or with no historical records. The spaces between bars indicate the different populations, some composed by a single habitat patch and others internally fragmented. *Delanta was subsequently recolonised (see 'Dispersal and recolonisation' section).

barrier to recolonisation. The extinctions in Mt Guna and Gosh Meda occurred in small Afroalpine areas with high levels of human activity (Table 2). While there was little information from Gosh Meda (Marino 2003), in Mt Guna the evidence indicated a set of proximate causes of wolf mortality operating over a short period of time, including rabies and persecution.

All three local extinctions (the most recent six years ago) occurred in small habitat patches (Fig. 3), and in Gaysay and Delanta, these were also associated to recent habitat fragmentation. Gaysay grasslands in the northern fringes of Bale Mountains National Park where monitoring was most intensive, suffered the combined effect of various sources of mortality including road kills, poisoning and disease, leading to the extinction of the last surviving pack in 2012; there were sporadic sightings of wolves there in 2015 and 2021, but no residential pack reestablished.

The extinction in Delanta in North Wollo exemplified the vulnerability of small populations to the risk of disease. A population consisting of 13 wolves distributed in three packs in 2016, dropped to just two animals over a year as a result of closely consecutive outbreaks of rabies and CDV (Marino et al. 2017). The two animals were last sighted in 2017 and the area remained vacated for two years (see Dispersal and colonisation section below). In contrast, the largest wolf population, in the Bale Mountains, persisted though repeated outbreaks, including co-occurrent rabies and CDV outbreaks (Marino et al. unpubl.). Figure 2 shows the fluctuations in the Web Valley population over 30 years, with densities ranging between 0.3 to 1.8 wolves km^{-2}, with abrupt decreases following rabies or CDV outbreaks.

Dispersal and colonisation

The recolonisation of the Delanta range was the first confirmation of successful dispersal across Afroalpine patches. The closest patches to Delanta were Abuna Yosef and Aboi Gara, the latter located approximately 20 km to the north of Delanta. Following two years without any wolf presence, two adult wolves were sighted in 2019, when this pair successfully raised a litter of six pups. With good survival and breeding every following year, in 2023, the pack split into two groups, indicating a healthy population and resulting in some range expansion.

The range of this dispersal event coincided with the maximum dispersal distance reported for a single wolf within the Bale Mountains, of up to 20 km (Sillero-Zubiri and Gottelli 1995b). We inferred maximum dispersal range within a continuous Afroalpine habitat patch from two ear-tagged animals in Bale Mountains that underwent dispersal. In 2015, one male wolf travelled a straight-line distance of 20.5 km and in 2017, one adult female dispersed over 36 km. Both

Table 2. Summary Ethiopian wolf extinctions and potential drivers.

	Population extinctions			Local extinctions		
	Mt Choke	Gosh Meda	Mt Guna	Guguftu	Gaysay	Delanta*
Timing of extinctions						
Year of last confirmed sighting	1924	1989	2004		2011	2017
Year of extinction		~1999	~2005	~1990	2012	2017
Contributing factors						
Small area of habitat	no	yes	yes	yes	yes	yes
Internal fragmentation	no	no	no	no	yes	yes
Isolation/barriers to dispersal	yes	likely	likely	likely	likely	likely
Viral diseases			likely		yes	yes
Road kills	no	no	no	possibly	yes	possibly
Persecution (wolf killings)			likely	likely		
Poisoning					yes	
Prey/habitat degradation	no	possibly	possibly		possibly	no

Empty cells = unknown. See methods for a description of each of the extinction characteristics and level of evidence.
*Delanta was subsequently recolonised (see 'Dispersal and recolonisation' section).

individuals were resighted in their final destination in following years, together with other wolves, indicating they had successfully settled within a pack.

Evidence of wolf movement and colonising capacities was also obtained from a rehabilitated male wolf released back in his initial pack in Simien Mountains National Park, after 51 days of treatment in captivity. A short period with his initial pack was followed by a dispersal phase, covering a distance of 623 km in 56 days (Lai et al. unpubl.). The wolf always remained within the limits of the Afroalpine habitat and eventually settled in a territory 5 km away from his previous pack, where he formed a breeding pair that subsequently raised a litter of two pups. The pack is currently composed of three individuals. More detailed information about these individuals and packs are available in Supporting information.

Protected areas

Of the current existing Afroalpine habitat in Ethiopia, 86% (2560 km^2) was included under some form of formal protection, across nine protected areas (Table 3). Of these, three Community Conservation Areas (CCAs) and two national park extensions were created over the past 10 years, and two well-established national parks were formally gazetted, many years after their creation. The Bale Mountains and Simien Mountains National Parks protected the two largest wolf populations and most of the habitat (a combined total of 1400 km^2). Two other wolf populations were within regional parks, and the remaining two were in Community Conservation Areas (CCAs). Two additional CCAs protected Afroalpine habitat where wolves went extinct.

In the context of IUCN categories of protected areas, the four National Parks were designed as category II (for ecosystem protection and protection of cultural values), with decision making and implementation by national or regional government bodies. However, some level of human activity, mainly pastoralism, and human habitation were tolerated, and zonation was included in their general management plans. Recently, when the Borena Sayint Worehimenu National Park was extended to include neighbouring communal land in 2019, a form of shared governance was adopted, with involvement of Wareda (district) and Kebele (ward) councils. Community Conservation Areas aligned to the IUCN category VI (protected area with sustainable use of natural resources) with legally recognised governance by local communities. Recently, the Amhara National Regional State increased the level of government intervention in decision making and implementation, in addition to its safeguarding role during periods of political instability and armed conflict.

Discussion

The Ethiopian wolf, an Afroalpine endemic, is the most endangered African carnivore, and one of the rarest canids in the world. We report fewer than 500 Ethiopian wolves surviving in six isolated populations, with Bale Mountains being the largest with around 280 wolves. Our global estimate is the first based on field observation of wolf packs across the species' range, and is therefore more robust than previous calculations derived from habitat extrapolation (360 to 440 in 2011 (Marino and Sillero-Zubiri 2011) and 442–487 in 2000 (Marino 2003)). It is worth noting that the global

Table 3. Protected areas containing Afroalpine habitats in Ethiopia.

Afroalpine Unit	Protected area (current name)	Year of creation (proclamation year)	Afroalpine habitat protected (km^2)*	Governance	Decision making/implementing body
Bale Mountains	Bale Mountains NP	1970 (2014)	1100	Federal government	Ethiopian Wildlife Conservation Authority
Simien Mountains	Simien Mountains NP	1969 (2014)	300		
	*extension	2008			
Arsi Mountains	Arsi Mountains NP	2011	770	Regional government	Forest and Wildlife Enterprise (Oromiya National Regional State)
South Wollo	Borena Sayint Worehimenu NP	2009 (2019)	140	Regional government (shared governance)	Environment and Forest Protection Authority (Amhara National Regional State) + Wareda-Park and Kebele-Park Councils
	*extension	2019			
Mt Guna	Guna Mountain CCA	2016	40	Local communities	Community Councils. With support from Environment and Forest Protection Authority (Amhara National Regional State)
Mt Choke	Choke CCA	2019	60		
North Wollo	Abuna Yosef, Zigit and Aboi Gara CCA	2016	80		
	*extension	2020			
Guassa-Menz	Guassa CCA	2003 (2012)	70		
	*extension (Anaz)	2022			

NP: National Park; CCA: community Conservation area. Year of proclamation: when the protected area was officially recognised/gazetted.
*The size of the Afroalpine habitat protected includes the extension.

number can be significantly affected by disease-driven fluctuations in the large Bale Mountains population. Due to its relatively large size, this population shows long-term resilience to the impacts of disease outbreaks, the most immediate threat to wolf survival, while all other populations are very small and face a high risk of extinction. This study confirmed (in addition to two previously known extinctions) the disappearance of wolves from Mt Guna and of local extinctions in three small habitat patches. On the other hand, we also documented wolf populations surviving for decades in small habitat patches, such as Guassa-Menz in the central highlands, which can accommodate no more than 25 wolves.

The Ethiopian wolf is representative of species with narrow environmental niches that typically have small geographic ranges, but that compensate geographic rarity by being locally abundant (Williams et al. 2009). Wolf density across Guassa-Menz was of 0.4 wolves km^{-2}, and in the best wolf habitats of the Bale Mountains, density may be as high as up to 1.8 wolves km^{-2}. Ethiopian wolf abundance is remarkably high for a carnivore its size, even several times higher, when compared to other terrestrial carnivores such as coyotes (Gese and Bekoff 2004) or grey wolves (Nowak et al. 2024, Roffler et al. 2024). While small range size and environmental specialisation can be a successful trait as long as it is compensated for by demographic commonness (Williams et al. 2009), human modification of Ethiopia's highlands is rapidly eroding this evolutionary advantage. High-altitude subsistence farming is overtaking large portions of the species range, restricting the surviving populations to ever higher elevation. Overgrazing by livestock is only exacerbating this habitat loss (Vial et al. 2011), and habitat degradation may be contributing to the low wolf densities observed in some Afroalpine areas (e.g. in Arsi Mountains and South Wollo, four times lower than in Guassa-Menz). Wolves living at low density and in small groups may also lose their competitive ability against the African wolf (also a medium-sized canid, but smaller) (Gutema et al. 2018, Gutema et al. 2022), which can become abundant in some Afroalpine areas, and even take over the Afroalpine niche after local extinctions.

Overall, it was the continued loss of habitat that underlined the extinction of wolf populations reported here. Small populations are not only vulnerable to demographic, environmental and genetic stochasticity, but also to habitat loss that diminishes the potential for dispersal to alleviate the effect of fragmentation on extinction rates (Reed 2004). In Mt Choke, wolves have been absent for nearly one hundred years, and in Mt Guna, the last surviving pack disappeared rather swiftly from the accumulative effects of disease, persecution and possibly general human interference. In Gaysay, despite the close proximity to the core Bale population and the sporadic arrival of transient wolves, the habitat patch has remained unoccupied more than 10 years after the extinction. In the case of Delanta, the local extinction was only temporary, showing that recolonisation and recovery is possible when suitable habitat is available within dispersal distance.

Reduced genetic diversity and inbreeding can also have consequences for small populations with poor connectivity, making them less adaptable to recurrent disease outbreaks and environmental changes (Frankham 2005, Willi et al. 2006, Bouzat 2010, Pflüger et al. 2019). Whole-genome sequencing confirmed reduced levels of wide heterozygosity in Ethiopian wolves, as it is in African wild dogs (*Lycaon pictus*) and dholes (*Cuon alpinus*), and consistent with their small population sizes (Gopalakrishnan et al. 2018). They also showed low diversity and enrichment of weakly deleterious variants in comparison with two North American grey wolf populations (Mooney et al. 2023). However, these and earlier studies (Gottelli et al. 2004, Gottelli et al. 2013) coincided in that these genetic patterns in Ethiopian wolves are consequences of long-term small population size, rather than recent inbreeding. From a genetic point of view, the long-term persistence of the Ethiopian wolf could be enabled through the purging of strongly deleterious recessive alleles in small population and avoidance of inbreeding under specific social and mating structures (Sillero-Zubiri et al. 1996b, Randall et al. 2007, Randall et al. 2010). Despite that the Ethiopian wolf has a small effective population size, no phenotypic manifestation of inbreeding has been observed. The estimated effective population size was approximately 100 individuals using genomics from a sample of Bale Mountains wolves (Mooney et al. 2023), and at around 245 from our global estimate and demographic data (37% of all adult wolves and 17% of all adult females, Marino and Sillero-Zubiri 2011).

Conservation implications

The future of Africa's most threatened carnivore is conservation dependent, requiring a softening of the hard borders imposed on them through better habitat protection, active management of disease, fostering of coexistence, and eventually, conservation translocations to manage several small, isolated populations as a metapopulation. Ultimately, the future not just of these wolves, but of the Afroalpine ecosystem they depend on, is linked to good governance models within Afroalpine areas and sustainable land uses, including habitat restoration of degraded land bordering Afroalpine remnants, where soils and climatic conditions make high altitude agriculture unsustainable. Elsewhere in the agriculture matrix, repurposing the use of land suitable for food production is an unrealistic option in a country with 123 million people (United Nations Development Programme 2023), consisting mainly of rural populations relying of small scale agriculture and additional support from government. A vision of improved habitat conservation and restoration is most likely to be achieved in community conservation areas, with surviving traditional resource management systems (Ashenafi and Leader-Williams 2005) and growing support for alternative livelihoods that are sustainable such as grassland restoration in degraded agricultural land and highland honey production (www.ethiopianwolf.org). Best practices

are emerging from these initiatives that can be replicated in land surrounding traditional protected areas. Over the past 20 years, the amount of habitat suitable for wolves under protection in Ethiopia has increased, but human and financial resources required to effectively implement that protection has been limited. Like in other developing countries with growing human populations and food insecurity, the challenges of habitat conservation are immense. In the longer term, a shift towards more sustainable natural resource uses will lead to healthy Afroalpine habitats and wolf populations and increased potential for nature-based tourism to contribute to local economies. In the shorter term, it is critical to avoid further Ethiopian wolf population extinctions and to sustain small population viability, through conservation translocations.

Because all Ethiopian wolf populations are very small, effective conservation would also require all sources of mortality to be mitigated. Consecutive disease outbreaks (Marino et al. 2017) and co-occurring outbreaks (Marino et al. unpubl.) are a major risk. In addition to reactive vaccination of wolves, oral vaccination is a more efficient way to provide protection against rabies proactively (Sillero-Zubiri et al. 2016).

Designing specific conservation interventions to facilitate coexistence, including behavioural change approaches, is essential to reduce other mortality factors. For instance, preventing road kills following the construction of roads across most Afroalpine ranges over the past decade and emerging conflict with pastoralists in areas where unregulated livestock grazing is leading to habitat degradation and wolves turning to livestock (Marino et al. 2010, Eshete et al. 2018).

Conservation translocations present a viable future strategy for overcoming fundamental barriers to dispersal and recolonisation in the highlands of Ethiopia. Such translocations hold the potential to rescue declining populations or reintroduce wolves to areas like Mt Choke and Mt Guna, where habitat is still available. The case study of Delanta lends support to this potential, showing that one wolf pair can kickstart a new population, while the successful release and settlement in an unoccupied territory of a rehabilitated wolf in the Simien Mountains demonstrates that holding animals in captivity before release is possible. A better understanding of the extinction process, as elucidated in this paper, is crucial for identifying suitable recipient and donor populations, as well as delineating the necessary measures for mitigating mortality in both declining and reintroduced populations.

Furthermore, genomic studies has thus far only been conducted using samples from the Bale population (Mooney et al. 2023). A larger study is imperative to assess genetic diversity and structure across populations, which will help choosing and pairing the founder individuals for translocations. In other endangered carnivores, such as African wild dogs, a metapopulation management strategy involving conservation translocations was proven effective for their recovery (Davies-Mostert et al. 2015, Nicholson et al. 2020). Strategically implementing conservation translocations and a metapopulation management strategy could be crucial for safeguarding Ethiopian wolves in the highlands.

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Data availability statement

Wolf pack composition data used to derive population estimates are available on Figshare: https://doi.org/10.6084/m9.figshare.26520658.v1.

Supporting information

The Supporting information associated with this article is available with the online version.

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