
African wolf diet, predation on livestock and conflict in the Guassa mountains of Ethiopia

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Abstract

The African wolf (*Canis lupus lupaster*) was first identified in 2011 in the Ethiopian highlands, with its status as a new species confirmed in 2015. We studied the diet of a confirmed African wolf population in the Menz-Guassa Community Conservation Area of central Ethiopia from scat samples collected by den sites from August to November 2010. Rodents were found to be the principal food items occurring in 88.1% of scats (n = 101), followed by plant material (34.7%) and insects (21.8%). Information on reported livestock predation and ensuing conflict with the agro-pastoral community was obtained through a questionnaire survey. Interview respondents listed the African wolf as the most serious predator of livestock, accounting for 74.6% of the reported kills (n = 492) and 78.9% of the economic loss. Over 70% of reported livestock predation occurred during the dry season (January–April). Better livestock management during this period may significantly reduce conflict. As sympatric Ethiopian wolves primarily feed on rodents, further studies on the foraging ecology, niche overlap and interspecific interactions between the two species should be studied to determine the extent of competition between the two species.

Key words: African wolf, diet, exploitative competition, golden jackal, human–carnivore conflict

Résumé

Le loup africain (*Canis lupus lupaster*) a été identifié pour la première fois en 2011 sur les hauts-plateaux éthiopiens et

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son statut de nouvelle espèce a été confirmé en 2015. Nous avons étudié le régime alimentaire d'une population reconnue comme étant de loups africains dans l'Aire de Conservation communautaire de Menz-Guassa, au centre de l'Éthiopie, à partir d'échantillons de crottes récoltés près des tanières entre août et novembre 2010. Nous avons découvert que les rongeurs constituaient l'aliment principal, présents dans 88,1% des crottes (n = 101), suivis par des matières végétales (34,7%) et des insectes (21,8%). Nous avons recueilli des informations sur la prédation de bétail et sur les conflits qu'elle cause avec la communauté agro-pastorale au moyen d'une enquête par questionnaire. Les participants classaient le loup africain comme le plus sérieux prédateur du bétail, comptant pour 74,6% des rapports d'animaux morts (n = 492) et pour 78,9% des pertes économiques. Plus de 70% de la prédation de bétail rapportée se passait durant la saison sèche (janvier-avril). Une meilleure gestion du bétail pendant cette saison pourrait réduire significativement les conflits. Étant donné que les loups d'Abyssinie, sympatriques, se nourrissent principalement de rongeurs, il faudrait faire de nouvelles études sur l'écologie alimentaire, le recouvrement des niches et les interactions interspécifiques pour déterminer l'étendue de la compétition entre ces deux espèces.

Introduction

The African wolf (*Canis lupus lupaster*) was first reported in the Ethiopian highlands from evidence of mitochondrial haplotypes in 2010 (Rueness *et al.*, 2011). A recent genomewide sequencing confirmed its unique species

status (Koepli *et al.*, 2015; Rueness *et al.*, 2015). The African wolf was formerly confused with golden jackal (*Canis aureus*), which was once considered as a monophyletic species widely distributed throughout the Middle East, south-eastern Europe and Asia (Wayne *et al.*, 1997; Jhala & Moehlman, 2008; Rueness *et al.*, 2011). Koepli *et al.* (2015) proposed that the entire African golden jackal group belonged to the same African wolf species, while Gaubert *et al.* (2012) suggested the possibility of both African wolf and African golden jackal co-occurring in Africa. So far, the African wolf has been confirmed in several African countries including Ethiopia and Egypt (Rueness *et al.*, 2011), Algeria, Mali and Senegal (Gaubert *et al.*, 2012), Kenya (Koepli *et al.*, 2015) and Morocco (Waters *et al.*, 2015). Nevertheless, reliable population estimates are largely absent and little information is available on its conservation status (it is not yet listed under the IUCN Red List of Threatened Species).

Large carnivores are experiencing massive declines in their populations and geographic ranges around the world due persecution by humans, mainly as a result of conflict over perceived and actual livestock predation (Ripple *et al.*, 2014). The extermination of the Mexican wolf (*Canis lupus baileyi*) from its entire natural range by the 1970s (Brown, 1983), decimation of grey wolves in most areas of the United States by the mid-1930s (Mech, 1995) and the extinction of the Falkland wolf (*Dusicyon australis*) in 1876 (Sillero-Zubiri, 2015) as a result of livestock predation are some examples. During the last two decades, efforts have been made to reintroduce grey wolves in the United States, both to conserve the species but also to restore and maintain healthy wildlife communities (Bangs *et al.*, 1998; Nilsen *et al.*, 2007). Yet, the degree of the human–carnivore conflict is escalating as humans further convert land for their activities and displace or exploit herbivores and so reduce the availability of wild prey to carnivores (Thirgood *et al.*, 2000; Treves & Karanth, 2003; Graham, Beckerman & Thirgood, 2005; Lyamuya *et al.*, 2014). Understanding patterns of diet selection and the levels of perceived and actual livestock predation is thus important to developing effective conservation management plans and designing appropriate measures to reduce livestock loss (Sekhar, 1998; Ogada *et al.*, 2003; Wang & Macdonald, 2006; Constant, Bell & Hill, 2015). This is particularly important for species where little other information exists on their status and conservation.

Competition between members of the different carnivore species may lead to declines or extinction of species of

conservation concern. For example, the decline in grey wolf numbers in Italy is thought to be partially due to competition with stray dogs (Boitani, 1992). Similarly, the dingo (*Canis lupus dingo*) may have displaced by exploitative competition both the thylacine (*Thylacinus cynocephalus*) and the Tasmanian devil (*Sarcophilus harrisi*; Lever, 1994). African wild dog (*Lycan pictus*) populations may be limited by the presence of larger carnivores (Creel & Creel, 1996).

The presence of the African wolf has been confirmed throughout the Ethiopian highlands where it overlaps the much more restricted range of the Ethiopian wolf (*Canis simensis*) (Atickem *et al.*, unpublished; Marino, 2003; Marino & Sillero-Zubiri, 2011). Hence, understanding the behavioural ecology of the African wolf is important not only to develop a conservation management plan for the species itself, but also because of its potential effects on the survival of the IUCN Endangered Ethiopian wolf. Depending on the degree of overlap on diet and habitat selection, African wolves could potentially affect the survival of Ethiopian wolves through exploitation and/or interference competition (Rosenzweig, 2000). As the Ethiopian wolf has a small population of <500 individuals restricted to the Afroalpine ecosystem of the Ethiopian highlands (Marino & Sillero-Zubiri, 2011), such impacts could be very significant.

We studied the diet of African wolves to provide baseline natural history information, investigate the importance of livestock in their diet and examine potential for competition with Ethiopian wolves. We also studied the level of livestock predation by both species and other carnivores in the Guassa Mountains of Ethiopia to assist with the development of conservation management plans for the region.

Methods

Study area

The study was carried out in the Menz-Guassa Community Conservation Area of northwest Shewa, Ethiopia, an area of 111 km² ranging in altitude from 3200 to 3700 m asl (Ashenafi *et al.*, 2005; Fig. 1). Mean annual rainfall was 1650 (±243) mm per year, with more than half falling during the wet season (July and August: Fashing *et al.*, 2014). The dry season was November to February. The vegetation cover in particular grassland is totally degraded during late dry season (January and February). Guassa is a

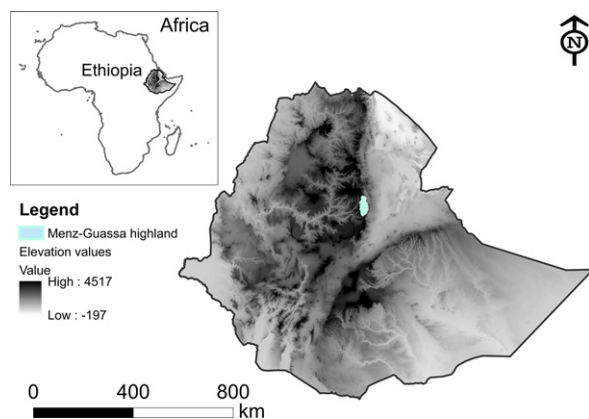


Fig 1 Study area in the central highlands of Ethiopia, Menz-Guassa Community Conservation Area

centre of endemism for Ethiopian mammals including Ethiopian wolf and gelada *Theropithecus gelada* (Venkataraman *et al.*, 2015). The Ethiopian wolf population in Menz-Guassa was estimated at 21 individuals in 2000 (Ashenafi *et al.*, 2005) and 23 individuals in 2010 (Marino *et al.*, 2011). During this study, five groups of African wolf were identified in the Guassa area with a total population size estimated at seventeen individuals.

Diet

The diet of the African wolf was studied from scat samples collected between October and December 2010. To avoid confusion with scats of other canids, samples were collected from den sites of the African wolf in areas where Ethiopian wolf and domestic dogs were not observed throughout the study period. Five den sites were identified by following African wolf individuals during the first 6 weeks of the study period with information from shepherders used to identify initial African wolf locations. All den sites were in the periphery of the park and were dominated by bushland. The Ethiopian wolf inhabits the central grasslands and was not recorded near those den sites. Unlike the Bale Mountains, where domestic dogs sometimes follow shepherds (Atickem *et al.*, 2010), we did not see any dogs out of the villages either with humans or alone.

Scat samples were sun dried and broken to pieces to distinguish plant materials intact. The samples were then ground in a mortar and washed in a 1-mm sieve using hot water to separate prey components and other indigestible

remains (Mbizah, Marino & Groom, 2012). Finally, each component was identified assisted by magnifying instruments and reference specimens collected from Guassa Mountains and collections at Addis Ababa University. Rodent species were identified from their teeth patterns. Diet analysis was carried out based on the frequency of occurrence per scat as the percentage of scats containing a particular food item (Breuer, 2005; Klare, Kamler & Macdonald, 2011).

Human–carnivore conflict

The level of human African wolf conflict was assessed based on a questionnaire survey of 250 randomly selected households that bordered the park in the vicinity of the range of the African wolf and Ethiopian wolf during October 2010. Every second, households at the buffer zone of the protected area were sampled and no residents declined to be interviewed. From the total respondents, 180 were males and 70 were females; all were adults aged above 18 years, but they varied in their educational level (Table S1). The questionnaire focused on whether the family lost livestock due to carnivore predation during the last 3 years, and if yes, further questions were asked on which livestock species was predated, the responsible carnivore (Ethiopian wolf, African wolf, spotted hyaenas *Crocuta crocuta* and serval *Leptailurus serval*) and the time of day and season predation occurred. Community members in the Ethiopian highlands had considerable knowledge of the predators living in their vicinity and were able to reliably identify the predators responsible (Atickem *et al.*, 2010). As sheep and goats were nearly always attended by shepherds during the day, who may then kill the carnivore responsible, the diurnal predators were often confirmed from remains of the kills. African wolf and Ethiopian wolf kill sheep only during daytime. Spotted hyaenas kill at night, and so were inferred from nocturnal losses. The economic losses to African wolf and Ethiopian wolf were then estimated using average local prices of sheep and goat during 2010 (\$19.80 and \$13.80, respectively).

Households were also asked how they attempted to reduce livestock predation through a questionnaire survey (with options of guarding more attentively, moving their sheep grazing system away from the African wolf habitat, reduction in sheep number and attacking wolves to minimize their number). The attitude of the respondents towards African wolf and Ethiopian wolf (positive, negative

or neutral) was also questioned during the survey. The livestock shelter used by the local community during the night was recorded, and the number of livestock in each of the 250 households was counted during the early morning before the livestock were let out.

Killing of African wolves during their breeding season by blocking den sites was reported during the survey. To confirm these allegations, we monitored three African wolf groups using VHF collars (Telemetry Solutions, Concord, CA, U.S.A.). Den sites of the collared individuals were then monitored during March–April 2010 to record the potential activities of local community in blocking the den sites.

Results

A total of 101 African wolf scats were collected from five den sites. Rodents (*Arvicanthis abyssinicus* and *Lophuromys flavopunctatus*) were the most frequently occurring food item, present in 88.1% of scats (Table 1).

Table 1 Frequency occurrence of food items in 101 scats

Item	% Frequency of occurrence
Rodents <i>Arvicanthis</i> and <i>Lophuromys</i> spp.	88.1
Sheep	2
Bird feathers	2
Insect	21.8
Leaves of crops and grass	31.7
Vegetable	3
Plastic materials	5.9

A total of 492 domestic livestock were reportedly killed by carnivores by the 250 households in the 3 years prior to the study (Table 2). There is a significant difference on the number of livestock species kept by the local community ($X^2 = 1533.65$, d.f. = 4, $P < 0.001$). Sheep, the most abundant livestock in Guassa area comprising 60% of the livestock population, were the most common quarry, accounting for over 90% of reported events. Goats accounted for a further 7%. Large livestock species (i.e. donkeys, horses and cattle) constituted <2% of the total livestock losses reported, primarily killed by spotted hyaenas.

African wolves, generally identified by shepherds following attacks on their sheep during the day, were responsible for 75% of the losses. Of these, 79% of the predation took place between 11:00 and 15:00 hours. Ethiopian wolves were the second most reported predator, accounting for 21% of losses, with servals contributing <1%, usually taking lambs and goat kids. Spotted hyaenas accounted for 5% of reported kills, almost all during the night and on livestock found outside shelters. Overall, African wolves accounted for significantly more predation events ($X^2 = 690.28$, d.f. = 3, $P < 0.001$). A significant difference was also observed on the predation of small livestock (sheep and goat) by Ethiopian wolf and African wolf ($X^2 = 151.19$, d.f. = 1, $P < 0.001$). No hyaena kills were reported from inside livestock shelters (96% of households kept their livestock in stone-walled shelters during the night).

Predation was more intense between January and April, peaking in March, with over 70% of kills occurring during this period (Fig. 2). This coincided with the birth of African wolves' pups. The three monitored groups gave birth to

Table 2 Number of livestock predated over 3-year period

Livestock	% Livestock from 2010 estimate from total 4342 livestock	Mean livestock holding/household	Carnivore predation events reported over 3-year period				
			African wolf	Ethiopian wolf	Serval cat	Hyaena	Total
Sheep	59.7	10.4 ± 2.8	351	83	0	11	445
Goat	7.8	1.4 ± 0.6	16	18	1	0	35
Cattle	18.4	3.2 ± 1.2	0	0	0	1	1
Donkey	9.4	1.6 ± 1	0	0	0	8	8
Mule	2.4	0.4 ± 0.5	0	0	0	0	0
Horse	2.4	0.4 ± 0.5	0	0	0	3	3
Total	100	–	367	101	1	23	492

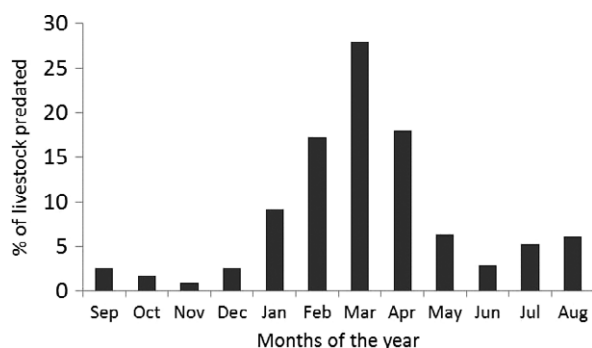


Fig 2 Livestock depredation rate across different months of the year

three to five pups between February and April, with the two collared groups changing den sites five to seven times during this period as they were blocked by the local people. From the twelve den sites used by the three African wolf groups, eight were found blocked by local people. While killing of adult African wolf is not easy, pups are more vulnerable, because they can be blocked in a den using rocks.

Over 11% of the households' total livestock holdings were reported lost to predators during the 3 years prior to the study. African wolf predation on sheep equated to approximately 0.49 sheep per household per year, while the Ethiopian wolf contributed 0.13 losses per year in each household. Collectively this equated to about \$8151 of lost revenue due to predation by African wolf and Ethiopian wolf on sheep and goat in the region, approximately \$10.9 per year per household. African wolves contributed 78.9% of the total economic loss.

While 85.2% of respondents had positive attitudes towards the Ethiopian wolf, only 19.2% of respondents had positive attitudes towards the African wolf. As a consequence, 44% of those interviewed suggested eliminating the African wolf as a solution to livestock losses, while 35.6% suggested more attentive guarding and 15.6% suggested reducing the number of sheep. Only 4.8% of respondents considered changing grazing land as a viable strategy to reduce stock losses.

Discussion

In the Guassa Mountains, Ethiopia, African wolves primarily fed on small rodent prey, plant material and insects, a diet similar to that reported for Eurasian golden jackals (Lanszki, Helati & Szabo, 2006; Jaeger *et al.*, 2007; Giannatos *et al.*, 2009). While carnivores primarily feed on meat, the high

occurrence of plants is common in many carnivores including grey wolf, coyote (*Canis latrans*) and red fox (*Vulpes vulpes*) (Lanszki, Helati & Szabo, 2006; Stahler, Smith & Guernsey, 2006; Jaeger *et al.*, 2007). As livestock and domestic animals accounted for <5% of the diet, African wolves appear to feed predominantly on natural prey.

The high occurrence of rodents in the African wolf diet suggests potential for competition with the Ethiopian wolf because the Afroalpine Murinae community are also the main prey of the Ethiopian wolf (Sillero-Zubiri & Gottelli, 1995; Ashenafi *et al.*, 2005). In the Bale Mountains, rodents accounted for 96% of the prey occurrence the Ethiopian wolf diet, with *Tachyoryctes macrocephalus*, *Arvicanthis blicki* and *Lophuromys* the main prey species (Sillero-Zubiri & Gottelli, 1995). As the range of the African wolf overlaps the much more restricted range of the endangered Ethiopian wolf, significant potential for competition exists between the two species. Competition between different carnivores has been reported to lead to declines or extinction of certain species (Boitani, 1992; Lever, 1994; Creel & Creel, 1996), and this represents a clear conservation concern. *Ad hoc* observations suggested the African wolf ate rodents from traditional rodent traps in the farmland, and so the extent to which it hunts, as opposed to scavenges rodents, is not clear. Nevertheless, further investigation into the foraging ecology of the African wolf and the nature of potential interference competition with the Ethiopian wolf is needed to better understand the potential effects on the conservation and survival of both species.

Despite its reliance on natural food items, the African wolf was reported to be the most serious livestock predator in the Guassa highlands. Sheep accounted for 90% of the reported livestock predated, mostly by African wolf, with the majority of predation events occurring in the dry season (November–February). The increased predation intensity at this time may be due to low natural abundance of rodents. High livestock predation rates at times of low natural prey abundance have been reported from several studies (Karani, 1994; Polisar *et al.*, 2003; Woodroffe *et al.*, 2005), and low rodent abundance in the dry season has been reported in the Bale Mountains during the dry season (Tallents, 2007). Furthermore, sheep in Guassa may get closer to bushland for grazing in the dry season as grass in the open Afroalpine meadows is scarce and dry, increasing their exposure to predators. Such seasonal effects on livestock predation due to ecological impact on grazing land are well reported (Coutinho & Campos, 1996; Van Bommel *et al.*, 2007; Sandra, Cavalcant & Gese, 2010). Given that the period of

high predation on livestock also coincides with the higher energetic demands of lactation (McNab, 1989) and increased food intake (Laurenson, 1995) due to the birth period of the African wolf, a series of factors may contribute to the higher risks to livestock during this period.

Mazzoli, Graipel & Dunstone (2002) reported that livestock predation by mammalian carnivores is the most important reason for the global decline of wild carnivores. In the Guassa Mountains, local people responded to livestock predation by killing the African wolf, particularly during their breeding season when they can be easily targeted with their puppies at den sites. With little law enforcement and protection for the African wolf, its population size in the Guassa mountains is likely to be controlled by the local community who eliminate pups whenever a den is located. Such lethal control has been widely reported as a response to depredation in a range of communities leading to severe population declines in many large carnivore species (Woodroffe & Ginsberg, 1998; Kruuk, 2002; Mitchell, Jaeger & Barrett, 2004; Woodroffe & Frank, 2005).

In subsistence livestock farming areas throughout much of Africa, improving livestock husbandry to reduce livestock depredation and helping local communities to develop positive attitudes towards large carnivores can have significant conservation outcomes (Ogada *et al.*, 2003; Romanach, Lindsey & Woodroffe, 2007). In the Guassa highlands, the development of livestock grazing practices that minimize the contact between African wolf and sheep from February to April when 70% of livestock predation occurs could greatly reduce livestock losses and associated economic losses. In turn, this could improve attitudes towards these carnivores. Over 80% of households held negative attitudes towards the African wolf with over 40% suggesting eliminating the African wolf was the most appropriate response to depredation. In contrast, over 80% of respondents had positive attitudes towards the Ethiopian wolf despite identifying it as a livestock predator. Similar predation rates by Ethiopian wolves have also been reported in the Simien Mountains (Yihunie, 2006) without the species perceived as problem by the local community and attitudes towards wolves were in general positive (Ashenafi, 2001; Marino, 2003; Yihunie, 2006). The relatively lower predation rate by Ethiopian wolf and long-standing conservation actions across Ethiopia may have influenced the more positive attitudes of the local community towards this species. This suggests that improved perceptions are possible but that much work is needed to change the attitude of local communities towards the

African wolf. Tessema *et al.* (2007) proposed several conservation activities, including education campaigns, income-generating actions via ecotourism to generate employment opportunities and improving the involvement of local community in park management as possible options for improving attitudes to African wolves.

The relatively low livestock predation by spotted hyaenas in the Guassa Mountains is in contrast to the Bale Mountains where hyaena accounted for 57% of livestock kills reported and 84% of the economic loss (Atickem *et al.*, 2010). The differences may emerge from the use of stone-walled enclosures (bomas) for livestock during the night in the Guassa Mountains. In the Bale Mountains, cattle were kept in the open near the household or in shabbily built wood enclosures with domestic dogs for protection (Atickem *et al.*, 2010). While ineffective, this also remains the most important conservation threat for the survival of Ethiopian wolf, as domestic dogs of the herders act as vectors for rabies and canine distemper virus (Haydon *et al.*, 2006; Randall *et al.*, 2006). Improving husbandry methods, therefore, could provide significant benefits to all large carnivores in Ethiopia.

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References

- ASHENAFI, Z.T. (2001) *Common Property Resource Management of an Afro-Alpine Habitat, Supporting a Population of a Critically Endangered Ethiopian wolf (Canis simensis)*. PhD. Thesis, Durrell Institute of Conservation and Ecology, University of Kent, Kent.
- ASHENAFI, Z.T., 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.
- ATICKEM, A., WILLIAMS, S.D., BEKELE, A. & THIRGOOD, S. (2010) Livestock predation in the Bale Mountains, Ethiopia. *Afr. J. Ecol.* **48**, 1076–1082.

- BANGS, E.E., FRITTS, S.H., FONTAINE, J.A., SMITH, D.W., MURPHY, K.M., MACK, C.M. & NIEMEYER, C.C. (1998) Status of gray wolf restoration in Montana, Idaho, and Wyoming. *Wildl. Soc. Bull.* **26**, 785–798.
- BOITANI, L. (1992) Wolf research and conservation in Italy. *Biol. Conserv.* **61**, 125–132.
- BREUER, T. (2005) Diet choice of large carnivores in northern Cameroon. *Afr. J. Ecol.* **43**, 97–106.
- BROWN, D.E. (1983) *The Wolf in the Southwest, the Making of an Endangered Species*. University of Arizona Press, Tucson.
- CONSTANT, N.L., BELL, S. & HILL, R.A. (2015) The impacts, characterisation and management of human-leopard conflict in a multi-use land system in South Africa. *Biodivers. Conserv.* **24**, 2967–2989.
- COUTINHO, M. & CAMPOS, Z. (1996) Effect of habitat and seasonality on the densities of caiman in southern Pantanal, Brazil. *J. Trop. Ecol.* **12**, 741–747.
- CREEL, S. & CREEL, N.M. (1996) Limitation of African wild dogs by competition with larger carnivores. *Conserv. Biol.* **10**, 526–538.
- FASHING, P.J., NGUYEN, N., VENKATARAMAN, V.V. & KERBY, J.T. (2014) Gelada feeding ecology in an intact ecosystem at Guassa, Ethiopia, variability over time and implications for theropit and hominin dietary evolution. *Am. J. Phys. Anthropol.* **155**, 1–16.
- GAUBERT, P., BLOCH, C., BENYACOU, S., ABDELHAMID, A., PAGANI, P., ADEYEMI, C., DJAGOUN, M.S., COULOUX, A. & DUFOUR, S. (2012) Reviving the African Wolf *Canis lupus lupaster* in North and West Africa, A Mitochondrial Lineage Ranging More than 6,000 km Wide. *PLoS One* **7**, e42740.
- GIANNATOS, G., KARYPIDOU, A., LEGAKIS, A. & POLYMEI, R. (2009) African wolf (*Canis aureus*) diet in southern Greece. *Mamm. Biol.* **75**, 227–232.
- GRAHAM, K., BECKERMAN, A.P. & THIRGOOD, S. (2005) Human–predator–prey conflicts, ecological correlates, prey losses and patterns of management. *Biol. Conserv.* **122**, 159–171.
- HAYDON, D.T., RANDALL, D.A., MATTHEWS, L., KNOBEL, D.L., TALLENTS, L.A., GRAVENOR, M.B., WILLIAMS, S.D., POLLINGER, J.P., CLEVELAND, S., WOOLHOUSE, M.E.J., SILLERO-ZUBIRI, C., MARINO, J., MACDONALD, D.W. & LAURENSEN, M.K. (2006) Low-coverage vaccination strategies for the conservation of endangered species. *Nature* **443**, 692–695.
- JAEGER, M.M., HAQUE, E., SULTAN, P. & BRUDESS, R.L. (2007) Day time cover, diet and space use of golden jackals (*Canis aureus*) in the agro-ecosystem of Bangladesh. *Mammalia* **71**, 1–10.
- JHALA, Y. & MOEHLMAN, P.D. (2008) *Canis aureus*. The IUCN Red List of Threatened Species. Version 2014.3. Available at: www.iucnredlist.org (Accessed on 20 July 2016).
- KARANI, I.W. (1994) An assessment of depredation by lions and other predators in the group ranches adjacent to Masai Mara National reserve. Department of Wildlife Management, Moi University.
- KLARE, U., KAMLER, J.F. & MACDONALD, D.W. (2011) A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mamm. Rev.* **41**, 294–312.
- KOEPFLI, K.P., POLLINGER, J., GODINHO, R., ROBINSON, J., LEA, A., HENDRICKS, S., SCHWEIZER, R.M., THALMANN, O., SILVA, P., FAN, Z., YURCHENKO, A.A., DOBRYNIN, P., MAKUNIN, A., CAHILL, J.A., SHAPIRO, B., ÁLVARES, F., BRITO, J.C., GEFFEN, E., LEONARD, J.A., HELGEN, K.M., JOHNSON, W.E., O'BRIEN, S.J., VAN VALKENBURGH, B. & WAYNE, R.K. (2015) Genome-wide Evidence Reveals that African and Eurasian Golden Jackals Are Distinct Species. *Curr. Biol.* **25**, 2158–2165.
- KRUUK, H. (2002) *Hunter and Hunted, Relationships between Carnivores and People*. Cambridge University Press, Cambridge, U.K.
- LANSZKI, J., HELATI, M. & SZABO, L. (2006) Feeding habits and trophic niche overlap between sympatric golden jackal (*Canis aureus*) and red fox (*Vulpes vulpes*) in the pannonian ecoregion, Hungary. *Can. J. Zool.* **84**, 1647–1656.
- LAURENSEN, M.K. (1995) Behavioral costs and constraints of lactation in free-living cheetahs. *Anim. Behav.* **50**, 815–826.
- LEVER, C. (1994) *Naturalized Animals, the Ecology of Successfully Introduced Species*. T. and A. D. Poyser Ltd, London.
- LYAMUYA, R., MASENGA, E., FYUMAGWA, R. & RØSKAFT, E. (2014) Human-carnivore conflict over livestock in the eastern part of the Serengeti ecosystem, with special emphasis on African wild dogs. *Oryx* **48**, 378–384.
- MARINO, J. (2003) Threatened Ethiopian wolves persist in small isolated Afroalpine enclaves. *Oryx* **37**, 62–71.
- MARINO, J. & SILLERO-ZUBIRI, C. (2011) *Canis simensis*. The IUCN Red List of Threatened Species 2011, e.T3748A10051312. Available at: <http://dx.doi.org/10.2305/IUCN.UK.2011-1.RLTS.T3748A10051312.en> (Accessed on 27 January 2016).
- MARINO, J., STEWART, A.E., GORDON, C.H., GOTTELLI, D., TEFERA, Z., LAURENSEN, M.K. & SILLERO-ZUBIRI, C. (2011) Ethiopian wolf status review. In: *Strategic Planning for Ethiopian Wolf Conservation* (Eds IUCN/SSC Canid Specialist Group). Oxford, United Kingdom.
- MAZZOLI, M., GRAIPEL, M.E. & DUNSTONE, N. (2002) Mountain lion depredation in southern Brazil. *Biol. Conserv.* **105**, 43–51.
- MBIZAH, M.M., MARINO, J. & GROOM, R.J. (2012) Diet of four sympatric carnivores in Savé Valley Conservancy, Zimbabwe, implications for conservation of the African wild dog (*Lycaon pictus*). *S. Afr. J. Wildl. Res.* **42**, 94–103.
- McNAB, B.K. (1989) Basal rate of metabolism, body size, and food habits in the order Carnivora. In: *Carnivore Behavior, Ecology, and Evolution*, Vol. 1 (Ed. J. L. GITTLEMAN). Cornell University Press, Ithaca, NY.
- MECH, L.D. (1995) The challenge and opportunity of recovering Wolf populations. *Conserv. Biol.* **9**, 270–278.
- MITCHELL, B.R., JAEGER, M.M. & BARRETT, R.H. (2004) Coyote depredation management, current methods and research needs. *Wildl. Soc. Bull.* **32**, 1209–1218.
- NILSEN, E.B., MILNER-GULLAND, E.J., SCHOFIELD, L., MYSTERAUD, A., STENSETH, N.C. & COULSON, T. (2007) Wolf reintroduction to Scotland: public attitudes and consequences for red deer management. *Proc. Biol. Sci.* **274**, 995–1003.

- OGADA, M.O., WOODROFFE, R., OGUGE, N.O. & FRANK, L.G. (2003) Limiting depredation by African carnivores, the role of livestock husbandry. *Conserv. Biol.* **17**, 1521–1530.
- POLISAR, J., MAXIT, I., SCOGNAMILLO, D., FARRELL, L., SUNQUIST, M.E. & EISENBERG, J.F. (2003) Jaguars, pumas, their prey base, and cattle ranching, ecological interpretations of a management problem. *Biol. Conserv.* **109**, 297–310.
- RANDALL, D.A., MARINO, J., HAYDON, D.T., SILLERO-ZUBIRI, C., KNOBEL, D.L., TALLENTS, L.A., MACDONALD, D.W. & LAURENSEN, M.K. (2006) An integrated disease management strategy for the control of rabies in Ethiopian wolves. *Biol. Conserv.* **131**, 151–162.
- RIPPLE, W.J., ESTES, J.A., BESCHTA, R.L., WILMERS, C.C., RITCHIE, E.G., HEBBLEWHITE, M., BERGER, J., ELMHAGEN, B., LETNIC, M., NELSON, M.P., SCHMITZ, O.J., SMITH, D.W., WALLACH, A.D. & WIRSING, A.J. (2014) Status and ecological effects of the world's largest carnivores. *Science* **343**, 6167. doi: 10.1126/science.1241484.
- ROMANACH, S.S., LINDSEY, P.A. & WOODROFFE, R. (2007) Determinants of attitudes towards predators in central Kenya and suggestions for increasing tolerance in livestock dominated landscapes. *Oryx* **14**, 185–195.
- ROSENZWEIG, M.L. (2000) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- RUENESS, E.K., GULBRANDSEN, A.M., SILLERO-ZUBIRI, C., MACDONALD, D.W., AFEWORK, B., ATICKEM, A. & STENSETH, N.C. (2011) The cryptic African wolf, *Canis aureus lupaster* is not a golden jackal and is not endemic to Egypt. *PLoS One* **6**, e16385.
- RUENESS, E.K., TROSVIK, P., ATICKEM, A., SILLERO-ZUBIRI, C. & TRUCCHI, E. (2015) The African wolf is a missing link in the wolf-like canid phylogeny. BioRxiv, 017996. Available at: <http://biorxiv.org/content/early/2015/04/23/017996> (Accessed on 19 October 2016).
- SANDRA, M.C., CAVALCANT, I. & GESE, E.M. (2010) Kill rates and predation patterns of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. *J. Mamm.* **91**, 722–736.
- SEKHAR, N.U. (1998) Crop and livestock depredation caused by wild animals in protected areas, the case of Sariska Tiger Reserve, Rajasthan, India. *Environ. Conserv.* **25**, 160–171.
- SILLERO-ZUBIRI, C. (2015) *Dusicyon australis*. The IUCN Red List of Threatened Species 2015: e.T6923A82310440. Available at: <http://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T6923A82310440.en> (Accessed on 20 September 2016).
- SILLERO-ZUBIRI, C. & GOTTELLI, D. (1995) Diet and feeding behaviour of Ethiopian wolves (*Canis simensis*). *J. Mammal.* **76**, 533–535.
- STAHLER, D.R., SMITH, D.W. & GUERNSEY, D.S. (2006) Foraging and feeding ecology of the gray wolf (*Canis lupus*), lessons from Yellowstone National Park, Wyoming, USA. *J. Nutr.* **136**, 1923–1926.
- TALLENTS, L.A. (2007) *Determinants of reproductive success in Ethiopian Wolves*. PhD thesis, University of Oxford.
- TESSEMA, M.E., TEFERA, A., LILIEHOLM, R.J. & LEADER-WILLIAMS, N. (2007) Community attitudes toward wildlife and protected areas in Ethiopia. *Soc. Nat. Resour.* **23**, 489–506.
- THIRGOOD, S.J., REDPALN, S.M., NEWTON, I. & HUDSON, P. (2000) Raptor and red grouse, conservation conflicts and management solutions. *Conserv. Biol.* **14**, 95–104.
- TREVES, A. & KARANTH, K.U. (2003) Human–carnivore conflict and perspectives on carnivore management worldwide. *Conserv. Biol.* **17**, 1491–1499.
- VAN BOMMEL, L., BIJ DE VAATE, M.D., DE BOER, W.F. & DE IONGH, H.H. (2007) Factors affecting livestock predation by lions in Cameroon. *Afr. J. Ecol.* **45**, 490–498.
- VENKATARAMAN, V.V., KERBY, J.T., NGUYEN, N., ASHENAFI, Z.T. & FASHING, P.J. (2015) Solitary Ethiopian wolves increase predation success on rodents when among grazing gelada monkey herds. *J. Mammal.* **96**, 129–137.
- WANG, S.W. & MACDONALD, D.W. (2006) Livestock predation by carnivores in Jigme Singye Wangchuck National Park, Bhutan. *Biol. Conserv.* **129**, 558–565.
- WATERS, S., EL HARRAD, A., AMHAOUCH, Z., TAIQUI, L. & SENN, H. (2015) DNA analysis confirms African wolf in Morocco. *Can. Biol. Conserv.* **18**, 15–17.
- WAYNE, R.K., GEFFEN, E., GIRMAN, D.J., KOEPFLI, K.P., LAU, L.M. & MARSHALL, C.R. (1997) Molecular systematics of the Canidae. *Syst. Biol.* **46**, 622–653.
- WOODROFFE, R. & FRANK, L.G. (2005) Lethal control of African lions (*Panthera leo*), local and regional population impacts. *Anim. Conserv.* **8**, 91–98.
- WOODROFFE, R. & GINSBERG, J.R. (1998) Edge effects and the extinction of populations inside protected areas. *Science* **280**, 2126–2128.
- WOODROFFE, R., LINDSEY, P., ROMANACH, S., STEIN, A. & OLE RANAH, S.M.K. (2005) Livestock predation by endangered African wild dogs (*Lycaon pictus*) in northern Kenya. *Biol. Conserv.* **124**, 225–234.
- YIHUNIE, M. (2006) *Human - wildlife (Ethiopian wolf and Gelada baboon) conflict in and around Simien Mountains National Park*. MSc. Thesis, Addis Ababa University, Ethiopia.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1 Education level of respondents.