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Livestock predation by endangered African wild dogs (*Lycaon pictus*) in northern Kenya

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Abstract

Most large mammalian carnivores are in global decline, principally due to conflict with livestock farmers. Because endangered African wild dogs (*Lycaon pictus*) range widely, often beyond the boundaries of protected areas, they may be particularly exposed to lethal control by farmers, even where nominally protected by reserves. Hence, effectively conserving wild dogs demands resolution of their conflicts with farmers. We investigated livestock depredation by African wild dogs living outside protected areas in northern Kenya. Scat analysis confirmed the distribution of depredation events reported by local farmers, indicating that farmer reports – collated by local Community Liaison Officers – gave a reasonably good index of the true pattern of depredation. Although livestock were abundant throughout the study area, depredation was exceedingly uncommon (approximately one attack per 1000 km^2 per year) and the costs of tolerating wild dogs were very low (US $3.40/wilddog/year) where wild prey remained, even at low densities. However, where wild prey were seriously depleted, wild dogs killed livestock repeatedly, and the cost of sustaining them rose to US $389/wilddog/year. Hence, although wild dogs had a negligible economic impact in the region, their impact was locally severe. Conservation activities for wild dogs are most likely to be successful if targeted at areas where wild prey remain, and where traditional herding practices have been retained.

Keywords: African wild dog; *Lycaon pictus*; Human wildlife conflict; Livestock depredation; Carnivore conservation; Wolf; *Canis lupus*

1. Introduction

Virtually all of the world's large carnivore species have experienced major declines and range contractions in the last hundred years (Linnell et al., 2001; Woodroffe, 2001), such that many are now considered globally or regionally endangered (IUCN, 2002). Conflict with farmers over livestock depredation has been a major cause of these declines (Treves and Karanth, 2003). Indeed, killing of animals considered predators of livestock has driven the extinction of several species, including the Falkland Island wolf (*Dusicyon australis*, in 1876; Macdonald and Sillero-Zubiri, 2004), the Guadelupe caracara (*Polyborus lutosus*, in 1900; Fuller, 2000) and the thylacine (*Thylacinus cynocephalus*, in 1930; Paddle, 2000).

The population consequences of predator control can extend deep into protected areas. Livestock predation usually occurs outside reserves, in human dominated landscapes; however, because most large carnivore species range widely, animals killed outside reserves may in fact have spent most of their time inside reserves

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(Stander, 1990; Forbes and Theberge, 1996). This results in a powerful edge effect, strong enough to cause the extinction of wide-ranging carnivores in all but the largest protected areas (Woodroffe and Ginsberg, 1998, 2000). Hence, effective protection of large carnivores is likely to demand resolution of conflicts with farmers, even when reserves are the mainstay of local conservation efforts.

African wild dogs (*Lycaon pictus*) are one of the world's most endangered large carnivore species, extirpated from 25 of the 39 countries where they formerly occurred (Fanshawe et al., 1997). The world population is estimated at fewer than 6000, and is still declining (Woodroffe et al., 2004). Conflict with people has been a major cause of this decline (Woodroffe and Ginsberg, 1999), and is an ongoing problem: shooting and poisoning together accounted for the deaths of 26% of 196 adult wild dogs that died while under study in protected areas (Woodroffe et al., 2004). Deliberate killing of animals that range beyond reserve borders may help to explain why wild dogs have disappeared from all but the largest unfenced reserves – wild dog populations require reserves in excess of 3500 km^2 to have even a 50% chance of persistence, an area far larger than that required by other African carnivores (Woodroffe and Ginsberg, 1998). Hence, effective conservation of wild dogs, both inside and outside protected areas, demands resolution of conflicts with farmers.

Wild dogs' true impact on local people's livelihoods has only rarely been assessed. Ranchers interviewed in South Africa and Zimbabwe ranked wild dogs as the least popular predator species, disliked even more than spotted hyaenas (*Crocuta crocuta*), jackals (*Canis mesomelas*), lions (*Panthera leo*) and leopards (*Panthera pardus*; Lindsey, 2003). Livestock farmers' principal complaint was that wild dogs affected their income by killing livestock (Lindsey, 2003). However, some field studies have suggested that such negative attitudes might not reflect wild dogs' true impact. An investigation of wild dog predation on livestock in Zimbabwe suggested that farm workers' claims were exaggerated, with wild dogs truly responsible for fewer than half of reported attacks (Rasmussen, 1999). Both in Zimbabwe and southern Kenya, wild dogs appeared to ignore livestock where wild prey were available (Rasmussen, 1999; Fuller and Kat, 1990). Based on these observations, Woodroffe and Ginsberg (1997) speculated that wild dogs might prey on livestock only where wild prey were depleted.

Resolving conflicts between farmers and wild dogs is likely to involve a combination of wildlife management, livestock husbandry, and education (Woodroffe et al., 1997; Rasmussen, 1999; Ogada et al., 2003). To provide the information needed to underpin such conservation activities, the World Conservation Union's Canid Specialist Group called for research on conflicts between people and wild dogs to be carried out "*as a matter of urgency*" (Ginsberg and Woodroffe, 1997). Here, we present preliminary findings of a study established to meet this need. We evaluate the true extent of wild dog depredation on livestock, and compare patterns of depredation with the availability of wild prey.

2. Study area and methods

This study was carried out in northern Kenya, in Laikipia District (37°2′ E, 0°6′ N), and parts of neighbouring Samburu, Isiolo and Baringo Districts, covering $\approx$5700 km^2 (Fig. 1). The area is mainly semi-arid bush land and savanna, used for subsistence pastoralism and commercial ranching, as well as for tourism and small-scale agriculture. Within the study area, some properties are owned by private individuals, while others (group ranches) are communally owned. None of the area is formally protected, and livestock occur throughout the region. However, wildlife is abundant in some areas (Mizutani, 1999a; Khaemba et al., 2001) and carnivores are tolerated on most properties (Frank, 1998; Ogada et al., 2003).

African wild dogs disappeared from the region in the early 1980s (Fanshawe et al., 1997); however, they reappeared in Laikipia during 2000 and quickly reached densities comparable with those observed in protected areas (Woodroffe, 2002). In 2003, the minimum estimated population size was $\approx$150 wild dogs in 11 packs (Woodroffe, 2003). Local residents attribute wild dogs' historic disappearance to the combined effects of persecution and disease; reasons for their return are unknown but probably include improved local awareness of the importance of wildlife conservation. In addition to wild dogs, the area supports populations of lions, leopards, cheetahs (*Acinonyx jubatus*), spotted hyaenas and striped hyaenas (*Hyaena hyaena*). These last five predator species may be legally killed in defence of human life or livestock, but wild dogs receive full protection from the Kenya Wildlife Service.

Details of wild dog attacks on livestock were gathered by ten Community Liaison Officers employed in partnership with local non-governmental conservation organisations and paid, in whole or in part, by the project. These staff were educated people chosen from, and resident within, local communities, well placed to gather often-sensitive information about depredation. Following initial training, we met with the officers at least monthly, usually as a group to ascertain that data were being gathered consistently across the region. We were also in frequent radio contact with the officers between meetings, and regularly spent time in the field with them to ensure that data collection protocols were being followed. Five officers equipped with motorbikes each covered an area of $\approx$1200 km^2 (not all wild dog habitat); officers without motorbikes covered smaller areas (up to 400 km^2). Each

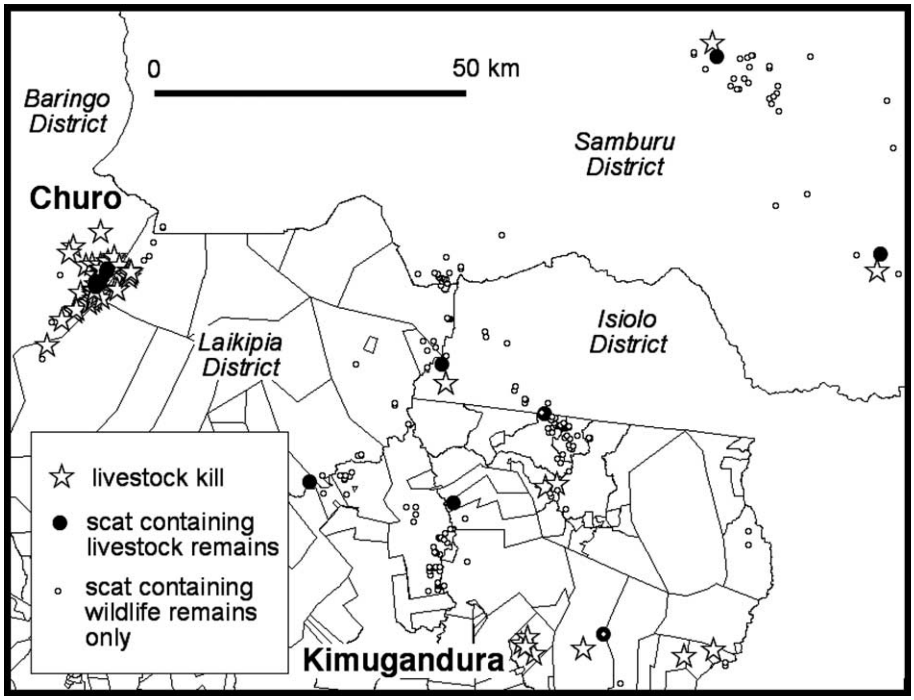

Fig. 1. Distribution of reported livestock kills (confirmed and unconfirmed), and wild dog scats containing livestock remains. Data are from 2001–2003. Note the cluster of reported attacks on the Laikipia–Baringo border in the north–east (Churo), and the much smaller cluster in the south-centre of the study area (Kimugandura).

officer travelled widely within their designated area; they solicited and followed up all reports of predator attacks on livestock (not just wild dog attacks), visiting the sites of reported attacks to confirm the veracity of each report and to gather additional data on location, timing, and the number and age of livestock killed or injured. A minority of attacks were reported some time after they had occurred, and could not be confirmed; these are referred to as ''unconfirmed attacks''. No compensation is available for livestock losses in Kenya, so farmers had no financial incentive to misrepresent their losses. In contrast with the pattern described by Rasmussen (1999), in no case did officers conclude that wild dogs were not responsible for recent reports that they investigated. As the number of depredation events per property was highly skewed, these data were analysed using non-parametric statistics.

This study was commenced in 2001, and the results reported here cover the period January 2001–March 2004. During this period, the study area expanded on two occasions, in each case involving the employment of additional Community Liaison Officers and, hence, potentially influencing the reporting of depredation events. First, in 2002 the original study area (≈3500 km^2) was expanded to cover the southern part of the Mathews Range in Samburu District (37°25′ E, 0°58′ N; an additional 1800 km^2). This area had been occupied by wild dogs for several years (Thouless et al., 1998) and depredation rates were very low. Second, in 2003 the study area was expanded to include an area of ≈400 km^2 on the Laikipia–Baringo border (36°29′ E, 0°48′ N) which local people (confirmed by our own sighting records and reports received by the nearest resident Community Liaison Officer) affirmed had been colonised by wild dogs only a few months earlier. All estimates of depredation rates over time or space are adjusted to take account of these changes in the size of the study areas and the distribution of observers.

Independent data on livestock depredation by wild dogs were gathered through analysis of 1576 scats collected throughout the study area (Fig. 1). These scats were collected in the course of a parallel study of wild dog ecology (Woodroffe, 2003) which involved monitoring radio-collared dogs, following up sightings, and surveying for wild dog activity; only a minority of scats were collected by Community Liaison Officers. We recorded the location where each scat was found, whether it was found close to a known den, and, where possible, which pack had produced it (Woodroffe, 2003). Scats were air dried, and then broken apart to examine the prey remains inside. Prey species were identified by comparing the gross appearance of hairs, hooves, bones and teeth found inside scats with reference material collected in the study area from animals killed by other predators or in road accidents. Reference was made where necessary to keys provided in Keogh (1983) and Mizutani (1995), but most prey remains could be identified by comparison with the reference collection. Twenty-four of 1576 scats (1.5%) contained the remains of unidentified mammalian prey.

We estimated the density of wild dogs' prey using dung transects. Although aerial census data were available (Georgiadis et al., 2003), we chose to use dung transects because one of wild dogs' principle prey species, Kirk's dik dik (*Madoqua kirkii*) is too small to be counted from the air. Data from dung transects could not be used to compare the density of different prey species within an area, because of unknown differences between species in the relative rates at which dung was deposited and decomposed. However, these data did provide an index of the abundance of particular species that could be compared across sites. Data on prey abundance were gathered at seven sites: two areas where wild dogs were reported to have repeatedly killed livestock, four areas in the home range cores of wild dog packs that seldom if ever killed livestock, and one in an area often frequented by a non-study pack that was never reported to have killed livestock. At each site, we counted dung along 20 transects, each 50 m long. For each transect, a 50 m tape was laid out, starting from a random location and running in a random direction. Two observers walked along either side of the tape, each holding a 2.37 m pole with one end on the transect line; hence each transect was 4.74 m wide. A third person recorded the number of dung piles from wild dogs' principal wild prey (dik diks, impala, *Aepyceros melampus*, and kudu, *Tragelaphus strepsiceros*), and from domestic goats, sheep and cattle, observed along each transect. As these data were highly skewed, with a preponderance of zeroes, they were analysed using non-parametric statistics.

3. Results

All attacks involved free-ranging livestock; wild dogs did not attack livestock held inside bomas (night-time corrals). The majority of the confirmed attacks on livestock (50 of 56) involved sheep or goats, with only 6 attacks on cattle. On average, wild dogs killed 3.2 (SD 2.4, range 1–13) sheep or goats per confirmed attack. The mean number of cattle killed on confirmed attacks was 1.3 (SD 0.5, range 1–2). All cases of multiple killing of cattle involved calves rather than adult animals.

Attacks on livestock sometimes involved animals being injured, in addition to those killed. Of 50 confirmed kills of sheep or goats, 18 also involved injury to an average of 1.5 (SD 0.71) animals. Likewise, three of six confirmed fatal attacks on cattle also involved an average of 2 cattle (SD 1.0) being wounded.

3.1. Reliability of reporting

To evaluate whether reports of wild dog attacks on livestock were reliable (Rasmussen, 1999), we compared the number of attacks reported for each property (group ranch or commercial ranch) with the proportion of wild dog scats found on that property that contained livestock remains. We omitted from this analysis all properties from which Community Liaison Officers had reported no attacks by any predator species, in case these properties were under-reporting depredation events; however, inclusion of these properties did not affect the conclusions. The number of reported attacks was positively correlated with the proportion of scats containing livestock remains (Spearman rank correlation; $r_s = 0.665$, $n = 20$ properties, $p = 0.004$). Excluding properties where $\leqslant 30$ scats were collected (and where the study's power to detect livestock remains in scats was therefore low) did not substantially influence this relationship ($r_s = 0.815$, $n = 9$, $p = 0.021$). These data suggest that reports of wild dog attacks are a reasonably reliable index of depredation rate in this area.

The number of sheep and goats reported to have been killed on unconfirmed attacks was significantly higher (mean 5.8 ± 5.5 SD, range 1–19) than the number reported killed on confirmed attacks (3.2 ± 2.4 SD, range 1–13; $t_{60} = 2.56$, $p = 0.013$). This suggests either that severe attacks were more likely to be remembered and reported later, or that the seriousness of attacks may sometimes have been exaggerated (Rasmussen, 1999).

3.2. Patterns of livestock depredation in time and space

During the first two years of the study, predation on livestock was minimal. In 2001, only five confirmed (and 3 unconfirmed) attacks were reported, with two attacks confirmed (and one unconfirmed) in 2002. However, this number rose to 49 confirmed (and seven unconfirmed) attacks in 2003. Across the entire study area and study period, the rate of livestock depredation was 0.48 attacks (confirmed and unconfirmed) per 100 km^2 of occupied wild dog habitat per year.

Of the 49 confirmed attacks in 2003, 44 occurred on the Laikipia/Baringo border (Fig. 1). These attacks were associated with the colonisation of this area by a new pack (the Churo Pack) which appeared (and denned) in this area for the first time in 2003. Scat analysis showed that this pack preyed far more heavily on livestock than did any of the other study packs (Fig. 2; $\chi^2 = 255.9$, d.f. = 5, $p < 0.0001$). Collection of multiple scats from the same pack on a single day risks pseudoreplication (because several animals are likely to feed from the same carcass and produce scats containing the same prey remains; Mills, 1996); however, the difference in packs' tendency to feed on livestock remained significant ($\chi^2 = 22.1$, d.f. = 5, $p = 0.0005$) even when analysis was restricted to a single (randomly selected) scat per pack per day. With the exception of attacks by the Churo Pack, which form a conspicuous cluster on the Laikipia–Baringo border, most attacks on livestock appeared to be isolated events (Fig. 1). An exception is a small cluster of four unconfirmed attacks in the southern part

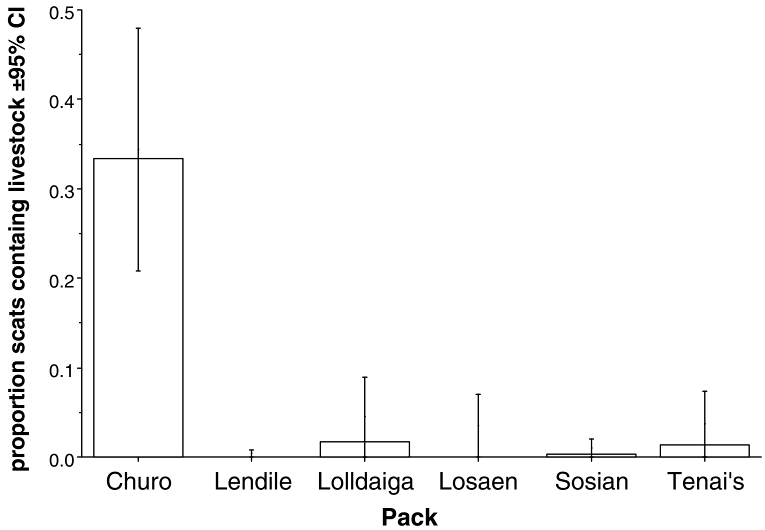

Fig. 2. Proportion of scats containing livestock remains, collected from six study packs of wild dogs. There is significant inter-pack variation in the proportion of scats containing livestock remains ($\chi^2 = 255.9$, d.f. = 5, $p < 0.0001$), even when analysis is restricted to one scat per pack per day ($\chi^2 = 22.1$, d.f. = 5, $p = 0.0005$). Error bars give exact binomial 95% confidence intervals.

of the study area (Fig. 1). If the area occupied by the Churo pack is excluded, the rate of livestock depredation across the study area falls to 0.11 attacks/100 km^2 of occupied wild dog habitat/year.

Chronic problems of livestock depredation occurred while the Churo pack was denning. During the denning period, wild dogs' movements are restricted by the need to care for small pups confined to a den (Creel and Creel, 2002). The number of reported attacks attributed to the Churo pack was higher during denning than outside this period (35 vs. 8 attacks), even though the denning period was a smaller proportion of the monitoring period for this area (92 vs. 254 days). Hence, the reported attack rate was significantly higher during denning ($\chi^2 = 52.3$, d.f. = 1, $p < 0.0001$). Moreover, attacks that occurred during denning took place within a smaller land area (45 km^2) than attacks that occurred outside denning (71 km^2). Thus, within this pack's home range, the attack rate per unit area was much higher during denning (equivalent of 310 attacks/100 km^2/year) than outside the denning period (equivalent of 16 attacks/100 km^2/year). Although the rate of reported attacks was lower outside the Churo pack's denning period, there was no significant difference between the proportion of scats collected from this pack that contained livestock remains during denning (34% of 32) and after denning (32% of 19; $\chi^2 = 0$, d.f. = 1, $p = 1$), although the sample size of scats was small. Likewise, the other study packs were no more likely to feed on livestock while denning (0.3% of 646 scats) than outside the denning period (0.3% of 334 scats; $\chi^2 = 0$, d.f. = 1, $p = 1$).

Most attacks on livestock took place in the late afternoon (mode 16:00 h). The timing of livestock attacks through the day was significantly different from the pattern of attacks on wildlife that were observed opportunistically in the course of the ecological study. Livestock attacks occurred mainly in the late afternoon, but wildlife kills peaked in the early morning, with a smaller peak in late afternoon (Fig. 3; $\chi^2 = 17.5$, d.f. = 3, $p = 0.0006$). This bimodal pattern of daily hunting activity is typical for wild dogs (Kuhme, 1965; Fuller and Kat, 1990; Creel and Creel, 2002). Since wild dogs never attacked bomas, livestock would have been available as prey for wild dogs between the time they left the boma (median 09:00 h, range 08:30–10:00 h for packs that were attacked), and the time they returned (median 18:00 h, range 17:00–18:30 h).

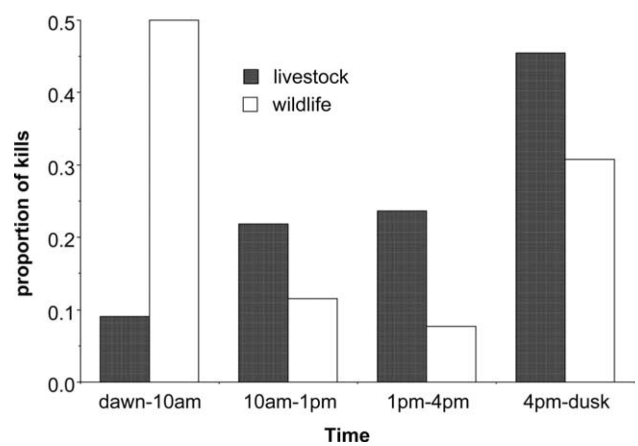

Fig. 3. Timing (in ≈3 h periods) of 55 wild dog attacks on livestock, and 26 wildlife kills observed opportunistically ($\chi^2 = 17.5$, d.f. = 3, $p = 0.0006$).

3.3. Costs of livestock depredation

The average cost of a sheep or goat in the study area is approximately KSh 2000/- (about US $25); hence the mean cost of an attack on small stock (average 3.2 sheep or goats; see above) is KSh 6400/- (US $80), with a maximum of KSh 26,000/- (US $325) for confirmed and KSh 38,000/- (US $475) for unconfirmed attacks. These estimates ignore the costs of lost production and treatment for injured livestock, which are difficult to quantify. The value of cattle varies depending upon their age and breeding experience; the cost of a wild dog attack on cattle is estimated to fall in the region KSh 8000–25,000/- (US $100–320).

These data indicate that, at the regional level, the economic impact of wild dog depredation is minimal (≈KSh 3000/- (US $38) per 100 km^2 occupied wild dog habitat per year). Given a population of about 150 wild dogs in the study area in 2003 (Woodroffe, 2003), this equates to approximately KSh 1170/- ($15) per wild dog per year. Excluding the Churo area, costs are lower still: approximately KSh 700/- (US $9) per 100 km^2 occupied wild dog habitat per year or KSh 270/- (US $3.40) per wild dog per year. However, local impacts on individuals and communities can be severe. For example, 35 confirmed kills made by the Churo Pack are estimated to have cost the local community approximately KSh 2.2 million (US $2870) during the three months that this pack spent denning in 2003. The annual cost of supporting wild dogs in the Churo area is estimated as KSh 76,000/- (US $974) per 100 km^2 occupied wild dog habitat per year, or KSh 30,400/- ($389) per wild dog per year.

3.4. Relationships with prey availability

Measurement of the relative abundance of ungulates showed that the density of dung from wild dogs' three most important prey species – dik dik, impala and kudu – varied significantly among sites (Fig. 4; dik dik $H_{20,20,20,20,20,20,20} = 20.4$, $p = 0.0024$; impala $H_{20,20,20,20,20,20,20} = 44.3$, $p < 0.0001$; kudu $H_{20,20,20,20,20,20,20} = 44.2$, $p < 0.0001$). The two sites where wild dogs had repeatedly killed livestock generally supported lower densities of wild prey than areas where little or no depredation occurred. Neither impala nor kudu were detected at these two sites; for comparison impala were detected at four, and kudu at all five, of the other sites. The mean densities of dik dik dung in the two livestock depredation areas were the lowest (Kimugandura) and third lowest (Churo) among the seven areas.

The density of livestock dung likewise varied among sites (Fig. 4; sheep and goats $H_{20,20,20,20,20,20,20} = 110.9$, $p < 0.0001$; cattle $H_{20,20,20,20,20,20,20} = 95.9$, $p < 0.0001$). The two highest mean densities of sheep and goat dung were recorded at the two sites where livestock depredation had occurred repeatedly. One of these sites (Kimugandura) had the highest mean density of cattle dung, but the other (Churo) had only the fifth highest cattle dung density.

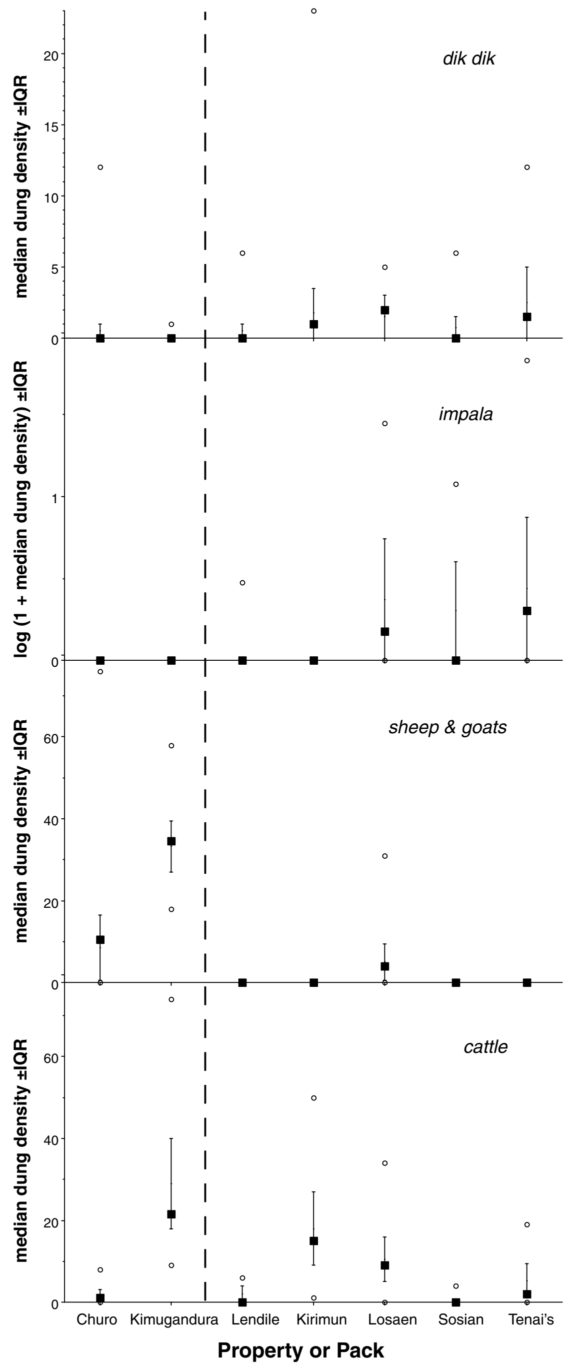

Fig. 4. Abundance of wild and domestic prey in the home ranges of seven wild dog packs, measured as dung density on 20 transects in each area. Wild dogs have repeatedly killed livestock in the two areas to the left of the dotted line, but rarely if ever in the other five areas. All transects were placed in the home range cores of study packs, with the exception of (1) Kimugandura, an area visited infrequently by the Lolldaiga pack, where several attacks were recorded, and (2) Kirimun, an area frequently used by wild dogs but outside the home ranges of the radio-collared study packs, where no attacks on livestock were reported. Solid squares indicate median dung density (±inter-quartile range); open circles give the maximum and minimum density in each area. Prey dung density varied significantly between areas (dik dik $H = 20.4$, $p = 0.0024$; impala $H = 44.3$, $p < 0.0001$; sheep and goats $H = 110.9$, $p < 0.0001$; cattle $H = 95.9$, $p < 0.0001$). Results for impala are plotted on a log scale.

4. Discussion

Our results show that, across most of the study area, wild dog predation was extremely uncommon, with approximately one attack reported per 1000 km^2 of occupied wild dog habitat per year. Given this very low level of depredation, it is important to stress that none of the area is formally protected, and livestock were available to wild dogs throughout the region. Aerial censuses show that the area supports ≈15 cattle and 45 sheep or goats per km^2, with livestock greatly outnumbering wild ungulates (Georgiadis et al., 2003). These densities suggest that ≈0.007% of the region's small livestock might be consumed by wild dogs annually. Given the abundance of livestock, the low level of depredation appears to represent a preference for wild prey. Perhaps the most dramatic demonstration of this preference is the observation that, across four successful breeding attempts on commercial sheep farms (two packs in two successive years), only one fatal (and one non-fatal) attack on livestock was reported. On another occasion, a pack denned on community land less than 1 km from an active boma, yet the herders living at the boma confirmed that they experienced no livestock losses. Such findings highlight the possibilities for coexistence of wildlife and domestic livestock under the right circumstances (Mizutani, 1999a), and confirm previous observations suggesting that wild dogs prefer wild prey over livestock (Fuller and Kat, 1990; Rasmussen, 1999).

While the majority of the study area experienced very low rates of depredation, livestock farmers in the Churo area suffered disproportionately high losses. Patchy distributions of depredation events have been described before, both for wild dogs (Rasmussen, 1999) and for related species (e.g., Stahl et al., 2002; Moberly et al., 2003; Treves et al., 2004), although the extent of geographical clustering observed in this study is unusually striking. A similar cluster of wild dog depredations was reported from an adjoining area during 1996, when, on a single farm, a group of four female wild dogs killed an estimated 274 merino sheep over the course of about 14 months (Kock et al., 1999).

The average cost of maintaining an individual wild dog in the study area (US $15/dog/year including Churo, $3.40/dog/year excluding Churo) was markedly lower than the estimated annual cost of supporting individual lions ($360), leopards ($211), cheetahs ($110) or spotted hyaenas ($35) on commercial ranch land in the same region (Frank et al., in press). While the estimated cost of supporting each wild dog at Churo (US $389/dog/year) exceeded the cost of supporting the average lion, it is worth noting that lion depredation, like wild dog depredation, varies in severity from property to property, with the average cost of supporting a lion ranging from US $0 to US $2076 (Frank, 1998). It appears that the most severe wild dog depredation may still have a smaller economic impact than the most severe depredation by other carnivores. Local people's attitudes appear to reflect this: interviews carried out in Laikipia during 2001 revealed that people were less negative towards wild dogs (and striped hyaenas) than to other carnivores, which were perceived to be more serious predators of livestock (Frank et al., in press).

The impacts of wild dog depredation were negligible at the regional level (estimated $38/100 km^2/year including Churo, $9/100 km^2/year excluding Churo). Nevertheless, wild dogs' tendency to kill multiple animals on a single attack means that depredation events can seriously affect the livelihoods of the people whose livestock are involved. The cost of an average attack is ≈$80,with a maximum of $325 for confirmed attacks. For comparison, the average *per capita* annual income in Kenya is approximately US $360 (World Bank, 2003); this is also the approximate annual wage for herdsmen in the region. Hence an average wild dog attack costs the equivalent of 2–3 months' income for the average Kenyan, with the most severe confirmed attacks representing almost an entire year's income. Within the home range of the Churo Pack, wild dog impacts were serious not just for particular individuals, but for a whole community, with depredation over the three month denning period estimated to have cost US $2870 – the total annual income of eight average people – to the community living within a 45 km^2 area. We caution, however, that these cost estimates necessarily ignore the context of livestock production which is largely non-commercial; given the fairly high reproductive rate of sheep and goats, lost stock are readily replaceable, even if their financial value was high (Mizutani, 1999b).

Given that the cost of experiencing a wild dog attack is apparently high, even if the true risk of such an attack is low, negative attitudes to wild dogs are perhaps not surprising (Joffe, 2003). Indeed, other studies of human-wildlife conflicts have shown that local people's attitudes tend to reflect the extremes of damage, rather than the average (Naughton-Treves, 1997).

Our data suggest that livestock predation occurred where wild prey were seriously depleted and where sheep and goats were abundant (Fig. 4). Two pieces of anecdotal evidence provide further support for this observed pattern. First, the cluster of livestock attacks that occurred in an adjoining area in 1996 (Kock et al., 1999) likewise involved an area where wild ungulates were greatly depleted: a commercial sheep and wheat farm from which the majority of wildlife were excluded by game fencing. Second: the Churo pack killed an impala shortly after moving away from their den in November 2003, but local people drove the pack from the kill and took the meat. A few hours later, the same pack killed 10 goats nearby.

Predation on livestock has also been linked to low densities of wild prey in wolves (*Canis lupus*) in southern

Europe (Meriggi and Lovari, 1996) and North America (Mech et al., 1988), and in lions within our study area (Frank et al., in press). However, wolf predation on livestock may also be high where wild prey are abundant (Treves et al., 2004), and predation of hen harriers on managed game birds likewise increases when alternative prey are more abundant (Thirgood et al., 2000). Clearly, the relationship between wild prey abundance and unwelcome predation on domestic or otherwise managed animals is a complex one which merits further study.

Although the densities of wild prey were very low in the areas where wild dogs killed livestock repeatedly, the areas where they killed few or no livestock were by no means pristine habitat. Many of the community lands inhabited by wild dogs are heavily grazed and support much lower densities of wild ungulates than do the more lightly stocked commercial ranches (Khaemba et al., 2001). It appears that, in this part of Africa at least, the abundance of wild ungulates required to sustain wild dogs without serious livestock depredation is surprisingly low. A potentially important characteristic of the Churo area (which suffered serious depredation) may be that, while the rest of the study area is inhabited mainly by Masai and Samburu pastoralists, who rely on their livestock for sustenance and rarely if ever hunt wild ungulates, the Churo area is inhabited by Pokot people, many of whom are keen hunters. Alternatively, the difference may reflect higher primary production in the Churo area, allowing it to support higher livestock densities which may, in turn, out-compete wild prey. The emergence of eco-tourism as a new land use throughout the district may provide an incentive to restore populations of wild prey and, hence, mitigate conflicts between people and wild dogs.

While the difference in depredation rate experienced in the Churo area, in comparison with the rest of the study area, might be due to differences in environmental conditions, it might alternatively reflect differences in the behavioural tendencies of different wild dog packs to kill livestock. Evidence for the existence of "problem animals" or packs is patchy (Linnell et al., 1999), but there is good evidence to suggest that they occur in some carnivore species (Stander, 1990; Woodroffe and Frank, in press). The data presented in Fig. 2 clearly show that the Churo Pack preyed far more heavily on livestock than did any of the other packs. It is impossible to determine whether the Churo Pack are a "problem pack" with an innate or learned tendency to kill livestock, because their origin is unknown (the pack was not formed by dispersal from any of the radio-collared packs, so it is not known whether their stock-killing behaviour pre-dates their colonisation of the Churo area), and because they have not yet ranged into an area with a density of wild prey comparable with that in the rest of the study area. However, anecdotal evidence from another study pack suggests that stock killing behaviour may be mutable depending on the availability of wild prey. The Lolldaiga Pack moved regularly between commercial ranches supporting high densities of wild ungulates, and settlement areas where habitat has been heavily modified by livestock grazing and small-scale cultivation, and where wild prey are seriously depleted. Although this pack was reported to have killed livestock repeatedly in settlement areas (e.g., in the Kimugandura area where prey densities were measured), its diet on commercial ranches consisted almost entirely of wildlife (Fig. 2, Woodroffe, 2002).

The data presented here suggest that conservation of wild ungulate prey is crucial for coexistence of wild dogs with people and livestock in pastoralist areas of East Africa. However, it is important to note that the people who inhabit these areas – whether in community areas or on commercial ranches – almost all practice traditional livestock husbandry which involves careful herding of livestock by day and enclosure in a boma at night (Ogada et al., 2003). Such careful husbandry is probably as important as wild prey conservation in avoiding wild dog depredation of livestock. This factor must be taken into account in applying our findings to wild dogs in other parts of Africa, and to other carnivore species in other parts of the world, where herding traditions have often been lost.

Most attacks on livestock occurred in the late afternoon, in contrast with the temporal pattern of wildlife attacks which – as in other wild dog populations (Kuhme, 1965; Fuller and Kat, 1990; Creel and Creel, 2002) – occurred in both early morning and late afternoon (Fig. 3). This pattern may reflect the relative likelihood of wild dogs encountering livestock during their two daily hunting periods. Most herds that were attacked spent at least part of wild dogs' morning hunting period out of the boma (median time leaving the boma 09:00 h), but they would probably still be fairly close to areas of human habitation by the time wild dogs became inactive during the middle of the day. By contrast, such herds would still be in the bush when wild dogs start hunting again in the late afternoon (median time returning to the boma 18:00 h). It is possible that an earlier return to the boma might reduce the risks of wild dog attack; ongoing studies of livestock husbandry are investigating this possibility.

Our data indicate that wild dog predation on livestock can be minimised through conservation of wild prey and appropriate livestock husbandry. This is important, because, in our study area, the number of lions, hyaenas and leopards killed by farmers correlates with the number of livestock killed by these predators (Ogada et al., 2003). Preliminary data suggest that fewer wild dogs might likewise be killed by people where livestock predation occurs only rarely: one of two radio-collared wild dogs in the Churo Pack was killed by people, compared with one of 18 wild dogs radio-collared in other packs.

In contrast with a previous study (Rasmussen, 1999), we found that farmers' reports provided a fairly reliable index of the true depredation rate. This may be because the intensive herding practiced by subsistence pastoralists in our study area means that either farmers themselves, or their family members, are almost always present when attacks occur. Hence, farmers in our study area may have a more realistic picture of wild dogs' impact than do commercial ranchers in Zimbabwe who rarely keep their livestock under such close observation. An additional difference is that all of our depredation events were reported to project staff who were themselves members of the communities from which they gathered data. Such local involvement is likely to be crucial for collection of these kinds of sensitive data.

Our study shows that coexistence of people and wild dogs is entirely possible in some areas. However, where wild prey have been depleted – and probably where herding traditions have been lost – coexistence may not be achievable and wild dog conservation may sometimes be unsustainable for local communities. As our study population continues to grow (Woodroffe, 2003), it is possible that new packs will, like the Churo Pack, colonise unsuitable areas, and livestock depredation may increase in the region. If this occurs, the challenge will be to either restore wild prey populations, or to discourage wild dogs from occupying such areas. The dilemma of whether to encourage recovery in increasingly human-dominated landscapes, or to focus conservation efforts in reserves, has been experienced by managers of other large carnivore species (Mech, 1998). Practices of livestock husbandry and land use in southern Africa are profoundly different from those in East African rangelands, possibly requiring different solutions to the problem of conflict between people and wild dogs; further research is needed in these areas. However, as a first approximation, current data suggest that dryland pastoralist areas (where livestock densities are necessarily low and traditional husbandry practices may have been retained) are likely to hold the best potential for wild dog persistence outside protected areas. This should be taken into account in conservation planning.

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