AFRICAN WILD DOGS (*LYCAON PICTUS*) CAN SUBSIST ON SMALL PREY: IMPLICATIONS FOR CONSERVATION

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In mammalian predators, prey size typically increases with body size, such that most carnivores weighing >21.5 kg specialize on prey weighing ≥45% of their own mass. By hunting in packs, endangered African wild dogs (*Lycaon pictus*) are able to feed primarily on ungulates weighing >100% of their own individual mass and, in most populations, wild dogs specialize on such large prey. However, we show that wild dogs living outside protected areas in northern Kenya fed primarily on Kirk's dikdiks (*Madoqua kirkii*), small antelope weighing just 15% of wild dog body mass. We estimated that dikdiks constituted 70% of the prey biomass consumed by wild dogs. Despite feeding on small prey, pack size, home-range size, and vital rates in this population were similar to those recorded in protected areas where wild dogs specialize on much larger ungulates. The energy content of a dikdik was about one-tenth that of the 2nd most important prey, impala (*Aepyceros melampus*). However, because dikdiks occurred at high population densities, the 2 prey species had apparently comparable hunting profitabilities. Wild dog packs ate more small (<10-kg) prey when confined to a breeding den. Also, packs living on commercial ranches consumed fewer small prey than did those living on community lands where larger prey were depleted. However, demographic parameters were similar in the 2 land uses. Although livestock occupy virtually the whole area, wild prey have persisted because local Masai and Samburu pastoralists do not traditionally hunt wild ungulates. This tradition has helped wild dogs to recolonize successfully and to reach densities comparable with those recorded in protected areas. The apparent ability of wild dogs to persist on small prey, in a livestock-dominated ecosystem, suggests that other important populations might occur, or be recoverable, in Africa's unprotected rangelands.

Key words: African wild dog, carnivore conservation, dikdik, foraging, human–wildlife conflict, impala, *Lycaon*, *Madoqua*, predation, ungulate

In large mammalian carnivores, average prey size generally increases with predator body size (Carbone et al. 1999; Gittleman 1985; Radloff and du Toit 2004; Sinclair et al. 2003). Carbone et al. (1999) observed a transition in the relationship between predator mass and prey mass, such that predators weighing <21.5 kg tend to feed on prey <45% of their own body mass, whereas larger predators, particularly large canids and felids, tended to specialize on larger prey.

African wild dogs (*Lycaon pictus*) are social coursing predators, weighing approximately 25 kg on average (Wood-

roffe et al. 2004b). Radloff and du Toit (2004) showed that, in a southern African savanna, wild dogs tended to kill ungulates weighing 120% of their own body weight (the greatest prey : predator size ratio in a guild of sympatric predators), conforming with the scaling rule of Carbone et al. (1999). Wild dogs are able to take particularly large prey because cooperative hunting allows packs to kill animals that would be too large for a single wild dog to subdue (Creel and Creel 1995). The tendency of wild dogs to kill prey larger than themselves has been documented throughout their broad geographic range: in most areas they specialize on impala (*Aepyceros melampus*; average weight ~40 kg) or other medium-sized antelope (Fig. 1).

African wild dogs are endangered, having suffered major declines due to habitat loss, deliberate and accidental killing by people, and disease (Woodroffe et al. 2004b). Declines
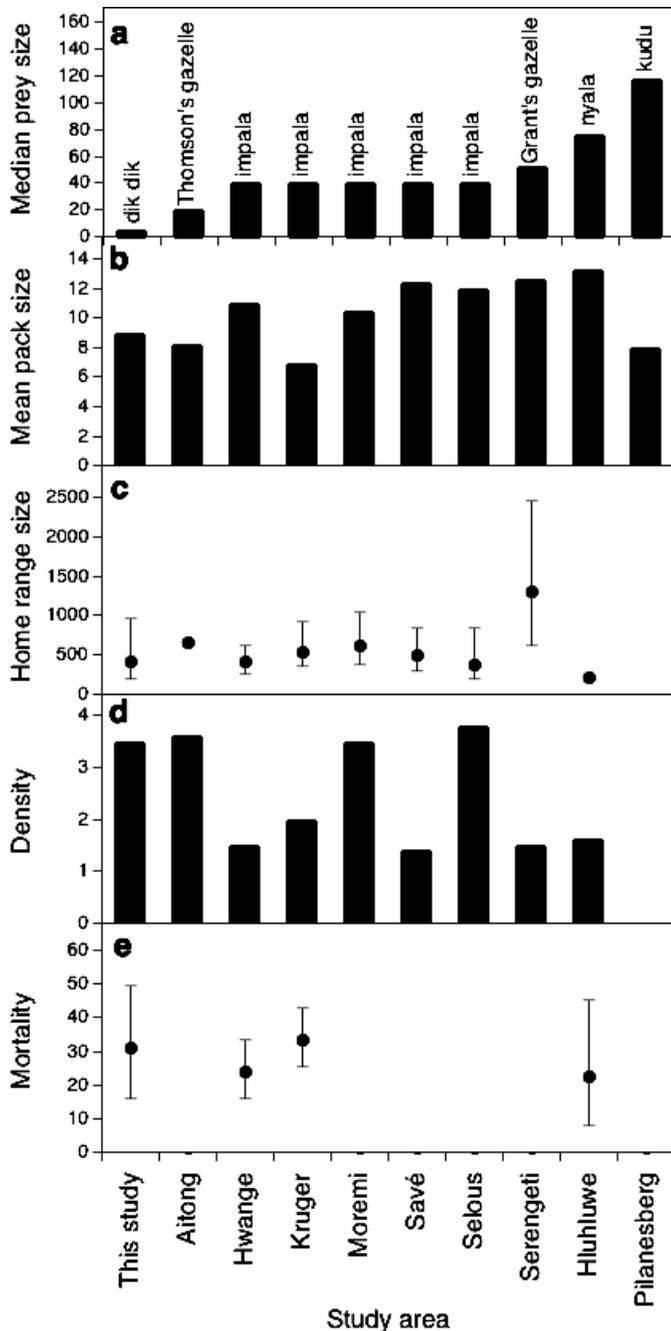
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appear to have been particularly severe outside protected areas (Fanshawe et al. 1997), not only because people kill wild dogs, but also because human activities can make such areas uninhabitable by extirpation or severe depletion of prey through clearance for agriculture (Beard 1977), commercial and subsistence hunting (Loibooki et al. 2002), and competition with livestock (Fritz et al. 1996). However, wild dogs also may fare poorly inside protected areas, where competition with larger predators limits their densities to low levels (Creel and Creel 1996; Mills and Gorman 1997). Avoidance of areas of high prey density, favored by competing species, helps to explain why packs occupy home ranges far larger than predicted from their metabolic needs (Creel and Creel 1996; Durant 1998; Gittleman and Harvey 1982; Mills and Gorman 1997). This wide ranging behavior means that, in all but the largest protected areas, most wild dog packs spend at least some of their time in human-dominated landscapes beyond reserve borders. Here they encounter people, guns, snares, poison, high-speed roads, and domestic dog diseases, all of which threaten the persistence of even nominally protected populations (Woodroffe and Ginsberg 1998, 1999). However, if conflicts between wild dogs and people could be resolved, and if sufficient prey remains, Africa's extensive semiarid rangelands could potentially support important populations of this endangered carnivore, as well as providing connectivity between protected areas that are otherwise increasingly isolated.

Here, we describe the feeding ecology of African wild dogs in a rangeland area of northern Kenya with no formal protection. We compare our findings with observations of wild dog feeding ecology inside protected areas and discuss implications both for predator–prey dynamics and for wild dog conservation.

MATERIALS AND METHODS

Study area.—This study was carried out from 2001 to 2005 in northern Kenya, in Laikipia District (0°6′N, 37°2′E), and parts of neighboring Samburu, Isiolo, and Baringo districts, covering approximately 5,700 km^2 (Woodroffe et al. 2005). The area is mainly semiarid bush land and savanna, used for subsistence pastoralism and commercial ranching, as well as for tourism and small-scale cultivation. Within the study area, most of the larger land parcels are owned or occupied either by private individuals (commercial ranches), or by local Samburu, Masai, or Pokot communities (community lands). None of the area is formally protected; however, wildlife is abundant in some areas (Khaemba et al. 2001; Mizutani 1999) and carnivores are present on most properties (Frank et al. 2005). Nevertheless, livestock outnumber wild ungulates throughout the region, with livestock densities higher on community lands than on commercial ranches (Georgiadis et al. 2003; Khaemba et al. 2001).

FIG. 1.—Comparison of wild dog diet and population parameters in northern Kenyan rangelands with those recorded in other studies. a) Median prey size (kills only; the Pilanesberg population is able to kill large prey by chasing them into game fences [Van Dyk and Slotow 2003]); b) mean pack size (adults and yearlings); c) average annual home-range size (mean and range); d) average population density (adults and yearlings per 100 km^2); and e) annual mortality of radiocollared adults and yearlings (mean and 95% confidence interval). Diet data are derived from Fuller and Kat (1990; Aitong), Woodroffe and Ginsberg (1997; Hwange and Moremi), Mills and Gorman (1997; Kruger), Pole et al. (2004; Savé), Creel and Creel (2002; Selous), Schaller (1972; Serengeti), Krüger et al. (1999; Hluhluwe), and Van Dyk and Slotow (2003; Pilanesberg). Pack sizes are from the same sources except for Hwange, Kruger, and Serengeti (Fuller et al. 1992); Moremi (Creel et al. 2004); and Hluhluwe

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(Maddock 1999). Home ranges are from the same sources except Savé (Pole 2000) and Hluhluwe (Andreka et al. 1999). Densities are from the same sources. Mortality data are from Woodroffe et al. (in press).

African wild dogs disappeared from the region in the early 1980s (Fanshawe et al. 1997); however, they reappeared in Laikipia during 1999 and quickly reached densities comparable with those observed in protected areas. In 2004, the minimum estimated population size in the study area (based on the known sizes of radiocollared packs and conservative estimates of the sizes of regularly sighted uncollared packs) was approximately 200 adults and yearlings in 15 packs (Woodroffe et al. 2004a), giving an average density of 3.5 adults and yearlings per 100 km^2.

Wild dog population monitoring.—Much of the study area—especially community land—is inaccessible to vehicles, being largely roadless, hilly, rocky, and covered with dense vegetation. Hence, wild dogs were difficult to observe and impossible to follow for any distance.

Wild dogs were monitored through aerial and ground-based telemetry of 9 radiocollared packs, combined with opportunistic observations of uncollared packs ($n = 913$ sightings in 5 years) by project staff (including 12 field scouts employed to monitor wild dogs in collaboration with local nongovernmental organizations and group ranches—Woodroffe et al. 2005). Details of wild dog radiocollaring and telemetry are given by Woodroffe et al. (2004a); wild dogs were handled with permission from the Kenya Wildlife Service and the Kenyan Ministry of Education, Science and Technology, according to guidelines of the IUCN/SSC Canid Specialist Group and the American Society of Mammalogists (Animal Care and Use Committee 1998), and following a protocol approved by the Animal Care and Use Committee of the University of California, Davis.

Population parameters were derived from data collected between July 2001 and December 2005. Pack size was estimated as the number of adults and yearlings in each radiocollared pack, immediately preceding breeding each year. Annual home-range size was estimated from aerial telemetry data, using minimum convex polygons and excluding packs monitored for less than 1 calendar year (mean 51.9 fixes per pack per year $\pm$ 8.3 SD). Annual home-range size estimates were available for 2 packs inhabiting community land (monitored for 1 and 5 calendar years, respectively), and for 5 packs inhabiting commercial ranches (monitored for 1, 1, 1, 2, and 4 calendar years). Annual mortality of radiocollared animals was estimated using an extension of the Kaplan–Meier procedure to permit staggered entry of animals (Pollock et al. 1989). These analyses were restricted to radiocollared animals (cf. Creel et al. 2004) because, although photoidentification (Maddock and Mills 1994) could be used to recognize and monitor individual uncollared animals on commercial ranches, this was not possible on community lands.

Diet analysis.—Diet of wild dogs was investigated through a combination of scat analysis and opportunistic observations of kills. Wild dog scats were collected opportunistically in the course of routine monitoring and were distinguished from those produced by other species on the basis of their appearance and distinctive smell. Observers recorded the location where each scat was found and whether it was found close to a known den. Wild dogs occupy dens only when caring for young pups;

accumulated scats were collected from recently abandoned dens. A small number of scats produced by young pups were excluded from analyses. Between January 2001 and December 2004, 4,670 analyzable wild dog scats were collected. Most of these were collected in the course of monitoring 7 radiocollared packs, four living primarily on community land (Churo, Lendile, Losaen, and Mugur packs; total 2,952 scats) and 3 living primarily on commercial ranches (Lolldaiga, Sosian, and Tenai's packs; total 681 scats). A further 423 scats were collected from an uncollared pack (Lerata pack) that was observed regularly on community land. The remaining 614 scats could not be confidently assigned to any of the study packs.

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, without use of a microscope. Most prey were identified from hair, but, of 4,670 scats, 1,067 (23%) contained hooves, teeth, horn, or bones that confirmed prey identity.

Wild dog kills were observed opportunistically, often in the course of monitoring radiocollared packs. We distinguished between kills that were directly observed (i.e., wild dogs were seen in the act of killing or feeding), and those for which prey remains were found, with wild dogs identified as the predator on the basis of tracks and other feeding signs.

Prey abundance.—Data on the absolute densities of prey of wild dogs, estimated using ground-based distance sampling (Buckland et al. 2001), were taken from the work of Augustine (2002). The same source provided information on prey-detection distances by human observers. These data apply only to part of one of the commercial ranches in the study area. Aerial census data were available for much of the study area, including community lands (Georgiadis et al. 2003); however, one of the principal prey species of wild dogs, Kirk's dikdik (*Madoqua kirkii*), is too small (average 3.5 kg; Table 3) and cryptic to be counted from the air. Dung transects were therefore used to estimate relative prey densities on commercial ranches and community lands. Dung transects were conducted in the home-range cores (≤ 5 km from previously occupied den sites) of 7 packs, 5 on community land and 2 on commercial ranches. Within each home range, dung piles were counted 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-long pole with one end on the transect line; hence each transect was 4.74 m wide. A 3rd person recorded the number of dung piles from prey species of wild dogs. Dung was identified to species on the basis of size and shape, where necessary using a reference collection held at Mpala Research Centre.

Prey body size and energy content.—Prey species were classified based on body masses given in Kingdon (1997). Following Carbone et al. (1999), prey species were considered

small if they weighed <10 kg, because this approximates to 45% of the mean body weight of wild dogs in the area (23 kg). Species weighing ≥10 kg were considered large. We further classified prey as very small if they weighed ≤3 kg.

Creel and Creel (2002) estimated the energy content of impala killed by wild dogs, using data on body composition from 2 shot impala given in Blumenschine and Caro (1986). We estimated the energy content of smaller prey using 3 dikdiks and 4 scrub hares (*Lepus saxatilis*) that had been freshly killed in road accidents. Each animal was weighed intact to within 5 g (dikdiks) or 1 g (hares) and then dissected; weights of body components were obtained to within 1 g for skin, viscera, and gut contents. Skeletons were then cleaned by stripping off as much muscle as possible, immersing them in water, and allowing them to rot for several weeks. Cleaned skeletons were weighed; the weight of muscle was then calculated by subtracting the weights of skin, viscera, gut contents, and bone from the intact weight. The resulting body composition data were averaged across individuals, and used to calculate edible mass, as well as whole-body energy content using the estimates of Creel and Creel (2002) of the energy content of muscle, viscera, and skin.

Statistical analyses.—First approximations of diet of wild dogs were estimated as the proportions of kills involving particular species and as the proportions of scats containing remains of those species. Because most scats (94.2%) contained the remains of only 1 prey species (compared with 5.7% and 0.1% containing, respectively, remains from 2 and 3 species), no attempt was made to evaluate the proportion of each scat consisting of remains of different prey species. Small prey tend to be underrepresented in diet studies based on direct observation of kills, in part because small carcasses are difficult to see and may be almost completely consumed (Mills 1996). However, such small prey may be overrepresented in diet studies based on scat analysis because their high surface area : volume ratio and small bones mean that more scats (often containing large amounts of fur and bone) are produced for each kilogram consumed (Mech 1970). However, the results of scat analyses can be adjusted by using data from feeding trials on captive animals to relate prey size to the number of scats produced. There are no published data on this relationship for wild dogs; however, Weaver (1993) derived the relationship for an ecologically similar species, the gray wolf (*Canis lupus*), feeding on a similar range of prey sizes (snowshoe hare [*Lepus americanus*, 1.2 kg] to moose [*Alces alces*, 327 kg]), as

$$\text{prey mass per scat} = 0.439 + (0.008 \times \text{prey body size})$$

Wolves are larger than wild dogs, so their scats also are likely to be larger; this means that using the equation above could overestimate prey mass per scat, particularly for small prey for which estimates would be dominated by the intercept parameter. However, in the absence of any data indicating how Weaver's (1993) equation might be adjusted, we used it (in combination with prey body size data from Kingdon [1997]) as the best currently available means of estimating the prey biomass consumed to produce each scat. The contribution of each prey species to the diet was then expressed as

a proportion of the total prey biomass consumed. Exploratory analyses suggested that using a much lower intercept value (0.2) did not alter overall conclusions. Estimates of the proportions of biomass consumed were used in descriptive analyses of diet; however, they were not appropriate for some statistical comparisons because they reduced multiple observations to a single number. Where necessary, formal comparisons were therefore conducted using the simple proportions of scats containing remains from particular prey species.

The 4,670 scats analyzed do not represent an equal number of independent data points, for 2 reasons. First, because multiple wild dogs may feed on the same kill, scats collected from a single pack on the same day may not be independent of one another. Second, because feeding trials have shown that hair from a single kill may take up to 5 days to pass through a wild dog's gut (H. Davies Mostert, pers. comm.), scats collected from the same animal less than 5 days apart may likewise be nonindependent. This issue was addressed in 2 ways. Where possible, analyses were conducted on a restricted sample, randomly discarding all but 1 scat from each cluster found (e.g., from a single resting site or den), and also discarding any scats collected fewer than 5 days apart. This reduced the sample from 4,670 to 343 scats. However, this approach could not be adopted in comparing diet during and outside the denning period, because it required condensing all the scats collected from a den site (often several hundred scats deposited over a period of several months) to a single data point. Hence, we calculated diet composition separately for each pack during and outside the denning period, and compared these proportions using a pairwise nonparametric Wilcoxon signed ranks test. This approach was appropriate because, although nonindependence of data will lead to underestimation of the variance, it should not influence the precision of the estimate itself.

Mortality rates of radiocollared wild dogs living on commercial ranches and community lands were compared using a log-rank test, which gives a test statistic distributed as chi-square (Pollock et al. 1989). Other comparisons were made using standard statistical tests; chi-square values are adjusted for small sample sizes where appropriate.

RESULTS

Wild dog diet.—Data on both scats and kills show that dikdiks were the principal prey of wild dogs in the study area. In the total data set, 81.8% of 4,670 scats contained dikdik remains, and dikdiks were estimated to constitute 70.4% of the prey biomass consumed (Fig. 2; Table 1). Of 95 kills found, 61.1% were dikdiks, and 40% of 60 hunts witnessed involved dikdiks (Table 2). The 2nd most important prey species, impala, made a far smaller contribution, occurring in just 6.7% of all scats, estimated to constitute 10.9% of prey biomass, and comprising 5.3% of kills found and 28.3% of hunts witnessed. Other important wild prey species were scrub hares, klip-springers (*Oreotragus oreotragus*), and greater kudu (*Tragelaphus strepsiceros*). Very small prey (≤3 kg) tended to be
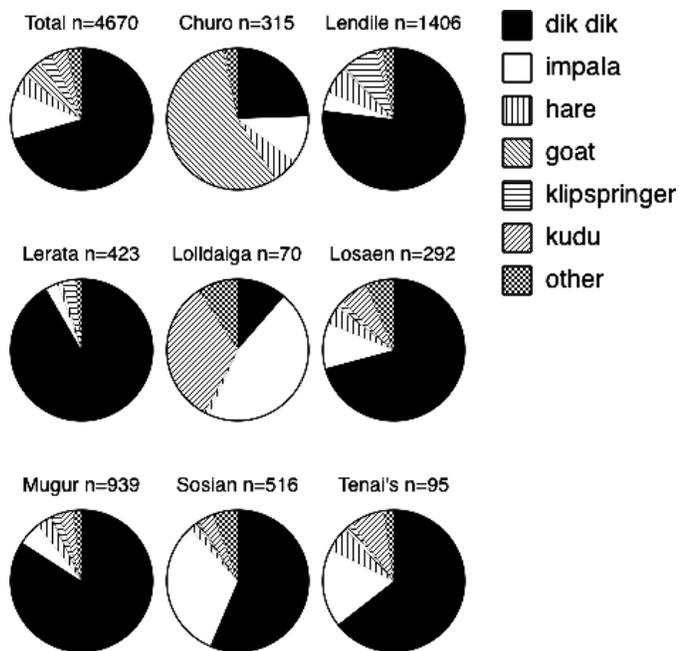
FIG. 2.—Biomass composition of wild dog diets in northern Kenyan rangelands, estimated from scat analysis. The 1st pie chart shows data from all scats; the others show data for specific packs on commercial ranches (Lolldaiga, Sosian, and Tenai's) and community land (Churo, Lendile, Lerata, Losaen, and Mugur).

taken in addition to other species (being detected in 46.8% of 28 statistically independent scats that contained multiple species, but being the sole prey species in just 4.5% of 312 statistically independent scats; $\chi^2 = 1,186$, $d.f. = 1$, $P < 0.001$; this analysis excludes 3 scats containing unidentified prey of unknown size).

Livestock—particularly goats—also were taken (Table 1). Livestock predation was never witnessed by project staff but was reported intermittently by herders. Predation on livestock varied substantially between packs (Fig. 2); estimates derived from scat analysis suggest that livestock comprised 55.9% of the prey biomass consumed by the Churo pack, compared with only 0.5% of the biomass consumed by other packs. Livestock predation is discussed in detail by Woodroffe et al. (2005).

Diet variation with land use.—Analysis of the restricted sample of 343 statistically independent scats suggested that wild dogs on community lands ate a higher proportion of dikdiks than did those on commercial ranches ($\chi^2 = 3.99$, $d.f. = 1$, $P = 0.046$; Fig. 3a), and consumed a correspondingly lower proportion of impala ($\chi^2 = 15.13$, $d.f. = 1$, $P < 0.001$; Fig. 3a). Within commercial ranch land, there was no significant variation between packs in the proportions of scats containing either dikdiks ($\chi^2 = 2.34$, $d.f. = 2$, $P = 0.31$) or impala ($\chi^2 = 3.82$, $d.f. = 2$, $P = 0.15$). Although there was variation among packs living mainly on community land (dikdiks: $\chi^2 = 39.1$, $d.f. = 4$, $P < 0.001$; impala: $\chi^2 = 11.52$, $d.f. = 4$,

TABLE 1.—Diet of wild dogs on community lands and commercial ranches in northern Kenya, estimated from scat analysis. The contribution of each prey species to diet of wild dogs, expressed as a percentage of the total biomass eaten, was estimated from their percentage occurrence in scats using Weaver's (1993) equation relating prey biomass to scat production.

| | Occurrence in scats | | | | Estimated % of biomass eaten | |
| | Community | | Commercial | | | |
Prey species	Number	%	Number	%	Community	Commercial
Ungulates						
Bushbuck (*Tragelaphus scriptus*)	26	0.7	6	0.8	1.1	1.0
Kirk's dikdik (*Madoqua kirkii*)	3,254	83.9	566	71.5	74.6	53.4
Gazelle (*Gazella*)	3	0.1	0	0	0.1	0
Impala (*Aepyceros melampus*)	150	3.9	162	20.5	6.5	29.1
Klipspringer (*Oreotragus oreotragus*)	148	3.8	3	0.4	3.8	0.3
Greater kudu (*Tragelaphus strepsiceros*)	25	0.6	20	2.5	2.6	8.5
Steenbuck (*Raphicerus campestris*)	8	0.2	6	0.8	0.2	0.6
Waterbuck (*Kobus ellipsiprymnus*)	2	0.1	5	0.6	0.2	2.2
Goat (*Capra hircus*)	186	4.8	4	0.5	5.3	0.5
Sheep (*Ovis aries*)	3	0.1	1	0.1	0.1	0.1
Other mammals						
Yellow baboon (*Papio cynocephalus*)	9	0.2	1	0.1	0.3	0.1
Scrub hare (*Lepus saxatilis*)	198	5.1	37	4.7	4.4	3.3
Rock hyrax (*Procavia capensis*)	3	0.1	4	0.5	0.1	0.4
Crested porcupine (*Hystrix cristata*)	4	0.1	0	0	0.1	0
Unidentified rodent	4	0.1	0	0	0.1	0
White-tailed mongoose (*Ichneumia albicauda*)	6	0.2	0	0	0.1	0
Unknown mammal	63	1.6	11	1.4	—	—
Miscellaneous						
Bird	18	0.5	2	0.3	0.4	0.2
Millipede	4	0.1	3	0.4	0.1	0.3
Total occurrences	4,114	831				
Total scats	3,878	792				

TABLE 2.—Numbers of wild dog kills of different species recorded in community lands and on commercial ranches in northern Kenya.

	Found carcass only				Witnessed chase, kill, or feeding			
	Community		Commercial		Community		Commercial	
Prey species	Number	%	Number	%	Number	%	Number	%
Ungulates								
Bushbuck (*Tragelaphus scriptus*)	7	8	0	0	2	6	0	0
Kirk's dikdik (*Madoqua kirkii*)	51	62	7	54	13	41	11	39
Gazelle (*Gazella*)	8	10	0	0	5	16	1	4
Gerenuk (*Litocranius walleri*)	0	0	0	0	1	3	0	0
Impala (*Aepyceros melampus*)	0	0	5	38	3	9	14	50
Klipspringer (*Oreotragus oreotragus*)	9	11	0	0	2	6	1	4
Greater kudu (*Tragelaphus strepsiceros*)	4	5	1	8	5	16	1	4
Waterbuck (*Kobus ellipsiprymnus*)	1	1	0	0	1	3	0	0
Other mammals								
Scrub hare (*Lepus saxatilis*)	1	1	0	0	0	0	0	0
Miscellaneous								
Plated lizard (*Gerrhosaurus major*)	1	1	0	0	0	0	0	0
Total	82		13		32		28	

$P = 0.021$), this was due to the unusual diet of the Churo pack (which occupied very different habitat and had a very different diet from that of the other packs; Fig. 2); there was no significant interpack variation when the Churo pack was excluded (dikdiks: $\chi^2 = 2.43$, $d.f. = 3$, $P = 0.49$; impala: $\chi^2 = 0.92$, $d.f. = 3$, $P = 0.82$). Exclusion of the Churo pack did not influence the overall conclusion that more dikdiks, and fewer impala, were consumed on community land than on commercial ranches (dikdiks: $\chi^2 = 10.47$, $d.f. = 1$, $P = 0.001$; impala: $\chi^2 = 19.87$, $d.f. = 1$, $P < 0.001$).

We detected no significant difference in the proportions of dikdik kills recorded on community lands and commercial ranches (kill carcass found: $\chi^2 = 0.07$, $d.f. = 1$, $P = 0.79$; chase, kill, or feeding observed: $\chi^2 = 0$, $d.f. = 1$, $P = 1$; Table 2), but the proportion of impala kills was higher on commercial ranches than on community land (kill carcass found: $\chi^2 = 26.1$, $d.f. = 1$, $P < 0.001$; chase, kill, or feeding observed: $\chi^2 = 10.2$, $d.f. = 1$, $P = 0.001$).

These differences reflect the relative abundance of the 2 main prey species on commercial and community lands (Fig. 3b): dung counts carried out in core wild dog home ranges showed that, although dikdik densities were comparable in the 2 land uses (Mann–Whitney $U = 2,154$, $n = 100, 40$, $P = 0.440$), impala were far less abundant on community lands ($U = 2,731$, $n = 100, 40$, $P < 0.001$).

Diet variation with breeding status.—Pairwise comparisons revealed that the diets of individual packs varied according to their breeding status. Scat analysis indicated that small prey constituted a higher proportion of prey biomass during denning than at other times of year (Wilcoxon signed rank test, $P = 0.017$; Fig. 4). This effect was due mainly to greater consumption of dikdiks during denning ($P = 0.012$), with a trend suggesting correspondingly smaller proportions of impala consumed ($P = 0.161$).

Can prey populations sustain wild dog predation?—Gorman et al. (1998) estimated that adult wild dogs in Kruger National Park, South Africa, each required a food intake of approximately 15.3 MJ/day, an estimate that accorded well with food intake rates estimated by field studies. This is likely a slight overestimate of the energy requirements of wild dogs in our study area, because the body weight of wild dogs studied in Kruger ($\bar{X} = 25.2$ kg ± 1.6 *SD*) was significantly greater than that recorded for adult wild dogs in our study area (23.0 ± 2.4 kg; $t = 2.10$, $d.f. = 25$, $P = 0.047$). However, we use their estimate to ensure that our calculations are conservative.

Creel and Creel (2002) estimated that an average-sized impala killed by wild dogs would contain 233 MJ of energy. Using a similar approach, we estimate that the average dikdik contains approximately 25 MJ, and the average hare approximately 12 MJ (Table 3). These estimates suggest that the daily energy requirement of 1 wild dog should constitute about 0.065 impala (15.3 MJ/233 MJ), 0.61 dikdiks (15.3 MJ/25 MJ), or 1.28 hares (15.3 MJ/12 MJ).

Augustine (2002) estimated ungulate densities in an 82-km^2 area in the southern part of Mpala Ranch, one of the commercial ranches in our study area. Augustine's study area was used by 3 packs of wild dogs in 2004: the Sosian pack (comprising 8 adults and yearlings), Tenai's pack (7 adults and yearlings), and the Pontoon pack (4 adults). Aerial telemetry indicated that the Sosian pack spent 62% of its time in Augustine's study area (26 of 42 radiolocations), Tenai's pack 20% (9 of 45 locations), and the Pontoon pack 14% (2 of 14 fixes). The Pontoon pack was newly formed in September 2004 and was therefore in existence for only 105 days in 2004. Hence, the average number of wild dogs using Augustine's 82-km^2 study area during 2004 was 6.5 adults and yearlings (calculated as [8 × 0.62 Sosian Pack members] + [7 × 0.2 Tenai's pack members] + [4 × 0.14 × (105/365) Pontoon pack members]). This represents a local density of 0.079 adults and yearlings per square kilometer. Examination of scat data indicates that 53.4% of the biomass consumed by wild dogs on commercial ranchland comes from dikdiks, and 29.1% from
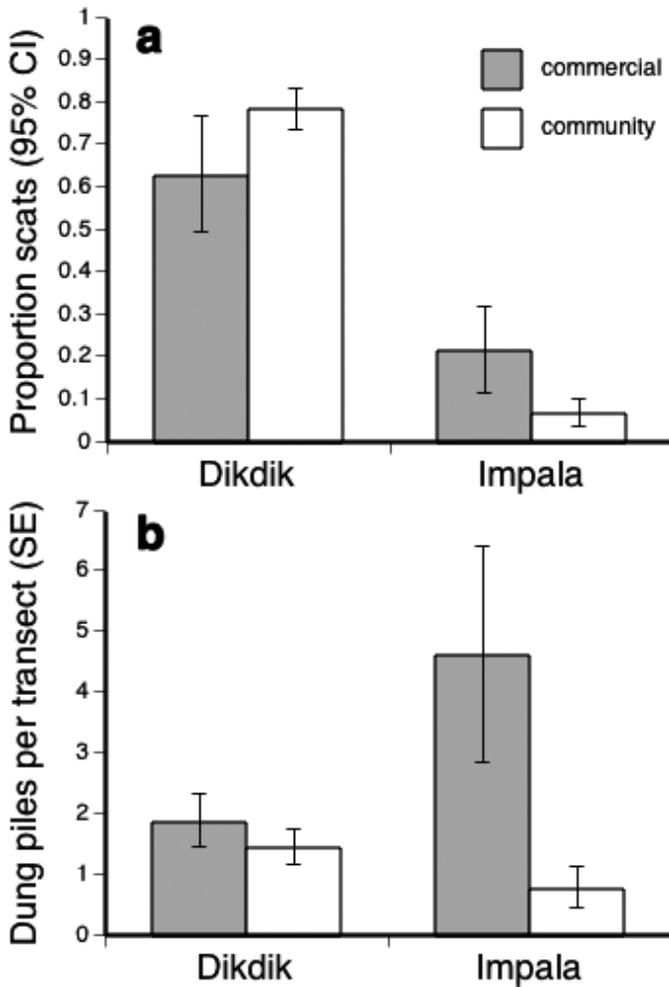
FIG. 3.—Relationships between land use in northern Kenya and a) the proportion of wild dog scats containing the 2 principal prey species (based on the restricted sample of 343 statistically independent scats), and b) the abundance of these 2 prey species (measured as density of their dung on 140 transects, 100 on community lands and 40 on commercial ranches).
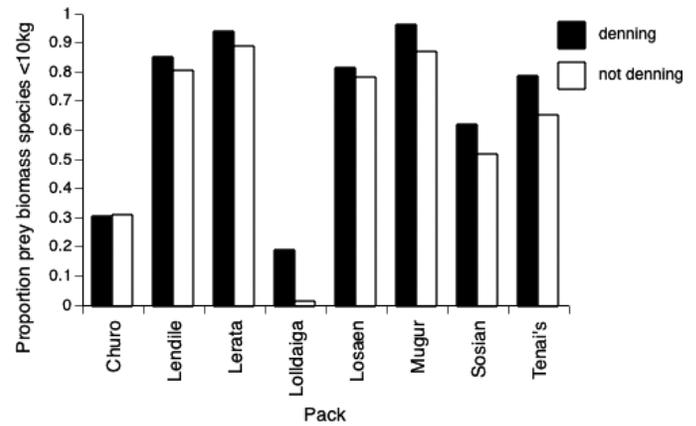

FIG. 4.—Variation in wild dog diet with breeding status in northern Kenyan rangelands. The graph depicts the proportions of prey biomass, estimated from scat analysis, contributed by prey species weighing <10 kg, during and outside the denning period. Packs tend to consume more small prey when they are denning (Wilcoxon signed rank test $P = 0.017$).

impala (Table 1). Hence, wild dogs are expected to consume, on average, 0.0258 dikdiks km^{-2} day^{-1} (calculated as (15.3 MJ dog^{-1} day^{-1}) ÷ (25 MJ/dikdik) × 0.534 × (0.079 dogs/km^2)), and 0.0015 impala km^{-2} day^{-1} (calculated as (15.3 MJ dog^{-1} day^{-1}) ÷ (233 MJ/impala) × 0.291 × (0.079 dogs/km^2)). This is equivalent to 9.42 dikdiks km^{-2} year^{-1} and 0.55 impala km^{-2} year^{-1}. If the dogs ate only dikdiks, the equivalent figure would be 17.65 dikdiks km^{-2} year^{-1}. If they ate only impala, the value would be 1.89 impala km^{-2} year^{-1}.

Augustine (2002) estimated that his study area supported, on average, 138.7 dikdiks/km^2 (95% confidence interval [95% *CI*] 123.6–155.6) and 20.3 impala/km^2 (95% *CI* 14.3–29.0). Hence, the estimated annual offtake of these ungulates by wild dog predation was 6.8% of dikdiks and 2.7% of impala (7.6% and 3.8%, respectively, if the lower 95% confidence limits are used as conservative estimates of ungulate density). If wild dogs ate only dikdiks, the equivalent annual offtake would be 12.8% (14.3% using the lower confidence limit); if they ate only impala, the offtake would be 9.3% (13.2% using the lower confidence limit). For comparison, the maximum human hunter offtake sustainable by impala populations has been estimated as 22% in the presence of predators (Fairall 1983), and 30% under random culling in the absence of predation (van Rooyen 1994). This suggests that the return of wild dogs to the predator guild in Augustine's study area is unlikely to cause local impala populations to decline. Maximum sustainable yields have not been projected for dikdiks, although Hendrichs (1975) estimated annual production as 30% of the standing crop. Our largest estimates of dikdik offtake are less than half of this annual production and, although the impact of other mortality factors remains unknown, the continued abundance of dikdiks in the

TABLE 3.—Energy content of major wild dog prey species in the rangelands of northern Kenya. Data on impala are from Creel and Creel (2002). Following Creel and Creel (2002), energy contents are estimated from body composition data by assuming an energetic value of 11.64 MJ/kg of muscle and 6.19 MJ/kg of viscera and skin.

| | | Weight and energy content of body parts | | | | | | | |
| | | Muscle | | Viscera | | Skin | | | |
Species	Mean mass (kg)	Weight (kg)	Energy (MJ)	Weight (kg)	Energy (MJ)	Weight (kg)	Energy (MJ)	Total energy (MJ)	Edible mass (kg)
Kirk's dikdik	3.54	1.76	20.5	0.35	2.1	0.39	2.4	25	2.5
Impala	31.9	17.1	199.4	4.3	26.7	1.23	7.6	233	22.6
Scrub hare	1.33	0.88	10.3	0.16	1.0	0.11	0.7	12	1.2

TABLE 4.—Data used to calculate the approximate profitability, for wild dogs in northern Kenya, of hunting Kirk's dikdiks and impala, with examples of profitability. Measures of error (in parentheses) are derived from the 95% confidence intervals (95% CIs) around the density estimates shown in the 1st line. Profitabilities across a range of detection distances are shown in Figs. 5 and 6.

Parameter	Kirk's dikdik	Impala
Data for commercial ranch land		
Individuals/km^2 (95% CI)[a]	138.7 (123.6−155.6)	20.3 (14.3−29.0)
Mean number of individuals per group[b]	1.96	8.14
groups/km^2 (error estimate)	70.8 (63.1−79.4)	2.5 (1.8−3.6)
Average energy content in MJ	25	233
maximum running speed[c] in km/h	42	47
Example for 50-m detection distance		
Groups detected per km traveled (error estimate)	7.08 (6.31−7.94)	0.25 (0.18−0.36)
Kilometers traveled to detect 1 group (error estimate)	0.14 (0.13−0.16)	4.0 (2.78−5.56)
Chase distance in km	0.125	0.152
Total km traveled (error estimate)	0.265 (0.255−0.285)	4.15 (2.93−5.71)
Profitability in MJ/km (error estimate)	94.3 (87.7−98.0)	56.1 (40.8−83.8)
Distance in km at which a human observer has a 50% detection probability[b]	0.031	0.088
Profitability on commercial ranches in MJ/km (error estimate)	81.9 (75.1−89.1)	91.7 (66.7−125)
Profitability on community land[d] in MJ/km (error estimate)	67.2	17.0

[a] Augustine (2002).
[b] D. J. Augustine, in litt.

area 5 years after recolonization by wild dogs suggests no dramatic effect of wild dog predation on dikdik densities.

Profitability of hunting small and large prey.—Because impala are the principal prey of wild dogs in most ecosystems (Fig. 1), and occur at high densities on commercial ranches in our study area, it is perhaps surprising that dikdiks—a prey species with a far lower energy content (Table 3)—comprise such a high proportion of wild dog diet. We therefore developed a simple model to investigate the relative profitability of hunting dikdiks and impala. Profitability is a function of both the energy derived from a prey item, and the energy expended in finding, killing, and consuming it. Creel and Creel (2002) estimated the profitability of various wild dog prey species by estimating, for each species, energy content, encounter rate, and distance chased. We were not able to measure encounter rates or distance chased reliably, because dense cover made it impossible to follow foraging wild dogs.

We therefore used available data to estimate approximate values, drawing upon our observation that dikdiks tend to remain hidden until detected by foraging wild dogs, as predicted for cryptic prey (Broom and Ruxton 2005). This indirect approach involved several assumptions, simplifications, and inaccuracies. Nevertheless, we adopted it—acknowledging the imprecision of its predictions—because the fact that dikdiks are not found in open areas (East 1998) means that direct measurement of encounter rates and chase distances is unlikely ever to be possible. We make no attempt to predict the optimal diet of wild dogs; we simply investigate the relative profitability of hunting their 2 principal prey species.

Both encounter rate and pursuit distance are influenced by the distance at which a predator can detect a prey animal (detection distance): a predator may have to travel further to locate a prey animal when hunting cryptic prey (detectable only when nearby) than when hunting prey that can be detected at greater distances, because its search area is necessarily constrained. However, once cryptic prey are encountered, chases will be relatively short because prey are inevitably nearby. We estimated encounter rates between foraging wild dogs and groups of dikdiks and impala, across a range of hypothetical detection distances, using data presented in Table 4. For simplicity, we assumed that prey groups were randomly distributed, and equally detectable on either side of a hunting wild dog (e.g., a dog able to detect prey up to 50 m away would search a 100-m-wide transect, or 0.1 km^2 for each kilometer traveled). For the sake of simplicity, we assumed that wild dogs would immediately pursue any prey animal detected, and that the prey animal would immediately flee directly away from the dog, with both running at maximum speeds. The chase distance can therefore be simply derived from the initial distance between predator and prey (equal to the detection distance), and their respective speeds of movement. We then characterized the profitability of each prey species as its average energy content (from Table 3), divided by the distance traveled to kill it (search distance + pursuit distance).

Following this logic, Fig. 5 shows the approximate profitability of hunting dikdiks on commercial ranch land, across a range of detection distances. Profitability is predicted to peak at detection distances of approximately 50 m, because both search distances and chase distances are comparatively short at this detection distance. For wild dogs hunting impala, profitability is predicted to peak at higher detection distances (Fig. 5) because groups are encountered less frequently; however (on commercial ranch land), the peak is higher because impala are also more energy-rich.

The true distances at which foraging wild dogs can detect dikdiks and impala, in relatively dense habitat, are unknown. Human observers engaged in counting the 2 species using distance sampling detected impala at greater distances than dikdik (Table 4); this is not surprising given the larger size and more conspicuous coloration of impala. If the detection abilities of human observers approximate those of foraging wild dogs, then, on commercial ranch land, dikdiks and impala are estimated to have comparable profitability (Table 4; Fig. 5). On community land, however, dikdiks appear markedly more
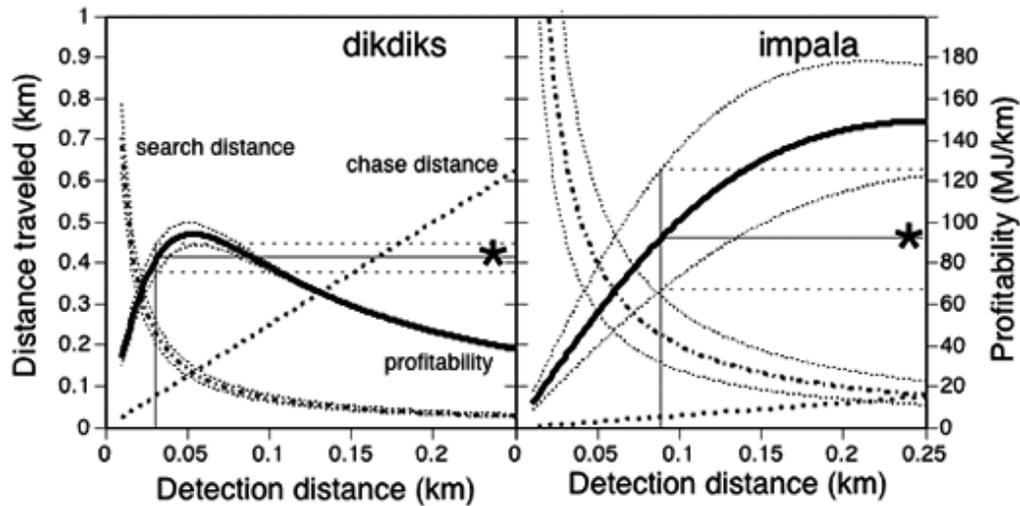
Fig. 5.—Approximate estimates of profitability, for wild dogs, of hunting dikdiks and impala on commercial ranches in northern Kenya. Curves show how search distance (heavy dashed-dotted line), chase distance (heavy dashed line), and profitability (heavy solid line; calculated as [energy content/(search + chase distance)]) vary with the distance at which a foraging wild dog detects prey animals; dotted curves denote estimates of error derived from 95% confidence intervals around density estimates (Table 4). The y axis of the impala graph is scaled such that the distances traveled range from 0 to 10 km. Thin solid straight lines ending in asterisks indicate the profitabilities that would be associated with hunting dikdiks and impala if wild dogs detected the 2 species at the same approximate distances as do human observers (Table 4; thin dashed straight lines denote error around these estimates). These estimates suggest that hunting dikdiks and impala have comparable profitabilities on commercial ranches.

profitable because, as shown in Fig. 4, impala densities are more substantially reduced (Table 4; Fig. 6).

Effects on population parameters.—We explored the effects of consuming small prey on wild dog population parameters, both by comparing our findings with results from other studies, and by comparing packs living on commercial and community lands within our study area.

Because large packs are able to hunt larger prey (Creel and Creel 1995), the observed preponderance of small prey in the diet of wild dogs might be expected to select for smaller packs. Figs 1a and 1b compare the average size of radiocollared wild dog packs in the study area (9.3 adults and yearlings ± 3.4 *SD*, $n = 23$ pack years) with pack sizes observed at other sites where wild dogs eat larger prey. There was no significant
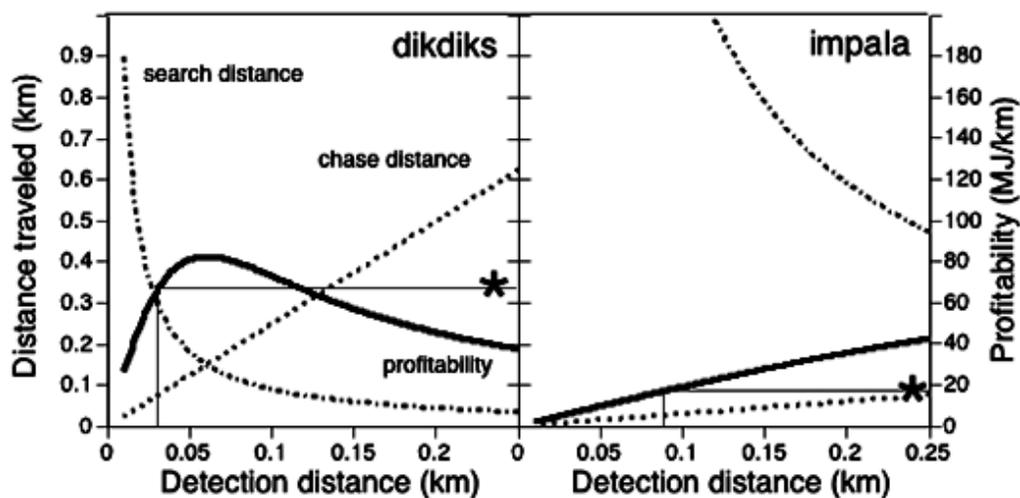

Fig. 6.—Approximate estimates of profitability, for wild dogs, of hunting dikdiks and impala on community land in northern Kenya. Curves show how search distance (heavy dashed-dotted line), chase distance (heavy dashed line), and profitability (heavy solid line; calculated as [energy content/(search + chase distance)]) vary with the distance at which a foraging wild dog detects prey animals. No estimates of error are given because densities on community land were extrapolated using relative dung densities (Table 4), and error is unknown. The y axis of the impala graph is scaled such that the distances traveled range from 0 to 10 km. Thin solid straight lines ending in asterisks indicate the profitabilities that would be associated with hunting dikdiks and impala if wild dogs detected the 2 species at the same approximate distances as do human observers (Table 4). Estimates suggest that hunting dikdiks may be more profitable than hunting impala on community land.

correlation between mean pack size and median prey size ($r = 0.05$, $n = 10$, $P = 0.90$), even when data from Pilanesberg (where a reintroduced pack is able to kill large prey by chasing them into game fences—Van Dyk and Slotow 2003) were excluded ($r = 0.636$, $n = 9$, $P = 0.066$). Observations within our study area showed no tendency for radiocollared packs living on community lands (and hence consuming fewer large prey) to be smaller, on average, than those living on commercial ranches (mean $\pm$ *SD* adults and yearlings per pack: community 10.6 ± 2.6, commercial 8.0 ± 1.9, $t = 1.88$, $d.f. = 8$, $P = 0.097$).

There was no evidence to suggest that feeding on small prey affected the ranging behavior of wild dogs. Average annual home-range size in the study area ($403 \text{ km}^2 \pm 232$ *SD*) was comparable with that recorded elsewhere (Fig. 1c). Home-range sizes of packs living on community lands (453 ± 221 km^2) were comparable with those recorded on commercial ranches ($376 \pm 246 \text{ km}^2$; $t = 0.58$, $d.f. = 12$, $P = 0.57$). Densities of wild dogs in the study area were likewise comparable with those recorded elsewhere (Fig. 1d).

The annual mortality rate of radiocollared wild dogs in the study area (25.2%, 95% *CI* $13.9–39.8\%$) was comparable with that recorded in other populations (Fig. 1e). Likewise, the annual mortality rate of wild dogs living on community lands (25.1%, 95% *CI* $8.9–49.1\%$) was very similar to that among dogs living primarily on commercial ranches (25.3%, 95% *CI* $11.1–45.2\%$; log rank test $\chi^2 = 0.002$, $d.f. = 1$, $P = 0.96$). A similar pattern was found when data were analyzed separately for adults aged ≥ 2 years (community: 23.1%, 95% *CI* $6.9–48.9\%$, $n = 6$ males and 7 females for 15.4 dog-years; commercial: 27.9%, 95% *CI* $12.3–49.1\%$, $n = 8$ males and 13 females for 21.7 dog-years; log rank test $\chi^2 = 0.19$, $d.f. = 1$, $P = 0.66$), and for yearlings (community: 38.7%, 95% *CI* $1.2–93.5\%$, $n = 3$ males and 1 female for 2.1 dog-years; commercial: 0% (95% *CI* $0–76.0\%$, $n = 1$ male and 3 females for 2.6 dog-years; log rank test $\chi^2 = 2.0$, $d.f. = 1$, $P = 0.16$), although reduced sample sizes meant that confidence intervals were very wide.

Reproductive rates in the study area cannot easily be compared with those recorded elsewhere, because of variation between sites in the age at which pups are 1st observed and recorded. Within the study area, however, the number of pups observed immediately after leaving the den (approximately 3 months of age) was similar on commercial ranches (6.4 ± 4.8 *SD*) and community lands (5.9 ± 2.9; $t = 0.29$, $d.f. = 18$, $P = 0.78$).

DISCUSSION

Examination of our data shows that wild dogs in the Samburu–Laikipia region differed profoundly from those studied elsewhere in that they subsisted primarily on small prey. Despite this, patterns of social behavior, home-range size, density, and demography appeared comparable—insofar as they could be measured—with those observed in other populations living primarily in protected areas and specializing on larger prey.

Unlike most other studies of wild dogs, our description of diet is based primarily on scat analysis, rather than on observation of kills. This approach was made necessary by the difficulties of systematically observing wild dog foraging in areas often inaccessible to vehicles. The scat data recorded a higher proportion of small prey than did our limited observations of kills. Krüger et al. (1999) likewise detected some smaller prey in wild dog scats that were not recorded from observations of kills. This is probably due to underreporting of small kills, which are often consumed almost entirely and are therefore difficult to locate. Prey remains at dikdik kill sites usually comprised just fur, bloodstains, and horns; of 3,820 scats containing dikdik remains, 864 (23%) contained 1 or more (up to 8) dikdik hooves, and a few contained dikdik horns. Although, in our study, scat analysis may have provided a more accurate picture of wild dog diet than did kill data, this methodological difference does not underlie differences observed between this and other studies: Krüger et al. (1999) reported little evidence of prey ≤ 10 kg in their analysis of wild dog scats in Hluhluwe, and no remains of small prey were found in scats from Hwange (J. R. Ginsberg, pers. comm.).

The body mass of the average dikdik (3.5 kg) was just 15% of the body mass of the average wild dog in the study area (23 kg), one-third of the minimum prey size predicted by Carbone et al. (1999). However, although this population of wild dogs may accord poorly with the quantitative predictions of Carbone et al. (1999), they conform to the qualitative pattern: dikdiks may be small ungulates, but they are ungulates nonetheless and, occurring as they do at high population densities, probably offer a higher food intake rate than the truly small prey—such as invertebrates—discussed by Carbone et al. (1999).

A key question is whether specialization by wild dogs on small prey in this area represents a choice, or a constraint due to lack of alternative prey. Evidence suggests a combination of these factors. On community lands, the lower preponderance of large prey in the diet of wild dogs appears to reflect the scarcity of such prey in these areas (Fig. 3b) and a consequently lower profitability of specializing on them (Fig. 6). On commercial ranches, however, the density of impala ($20.3/\text{km}^2$, 95% *CI* $14.3–29.0/\text{km}^2$—Augustine 2002) was comparable with that recorded in other study areas where impala were the principal prey species (e.g., Savé $11.7/\text{km}^2$, Kruger $8.8/\text{km}^2$, Selous $28.6/\text{km}^2$—Creel and Creel 2002; Mills and Biggs 1993; Pole et al. 2004). Hence, on commercial ranches at least, impala densities would probably be high enough to allow wild dogs to specialize on them, if they were the most profitable prey. Our findings suggest that, despite their lower energy content, dikdiks on commercial ranch land may have a hunting profitability comparable with that of impala because of their extremely high population densities.

While pups remain in a den, wild dogs are constrained to home ranges far smaller than those they occupy for the remainder of the year. Their tendency to kill smaller prey during this period (Fig. 4) might represent selection of more profitable prey, but could also reflect variation in prey availability brought about by differences in prey movement patterns. There are no published data on impala's movements in relation to predation

pressure, although game ranchers frequently complain that impala move away from areas occupied by wild dogs (Lindsey et al. 2005). However, impala do shift their home ranges in response to food availability (Augustine 2002; Jarman 1970), whereas dikdik territories are highly stable in the face of changing food availability (Amubode and Boshe 1990; Hendrichs 1975). Hence, it is possible that impala move away from areas of intense wild dog activity, particularly dens, forcing the dogs to kill a higher proportion of more sedentary dikdiks. However, Creel and Creel (2002) observed no change in foraging distances or prey selection of wild dogs through the course of the denning period, providing no evidence that favored prey were becoming depleted.

Despite subsisting primarily on small prey that could be killed by a single animal, wild dogs in the study area continued to live in cohesive packs that were, in all other ways, comparable with those observed elsewhere. This supports the idea that cooperative behavior is obligate in this species (Creel and Creel 1991). The density of wild dogs at our site (approximately 3.5 adults and yearlings per 100 km^2) is among the highest recorded; this may relate to the comparatively low densities of competing predators, because lion (*Panthera leo*) populations are held below carrying capacity through conflicts with livestock farmers (Woodroffe and Frank 2005).

Despite low densities of large prey, wild dogs were able to persist in community lands, with vital rates comparable with those on commercial ranches, because dikdiks were present at high densities in some areas (estimated average 107 dikdiks/km^2; Table 4). Although dikdiks do not occur at such high densities throughout their geographic range (e.g., Tsavo National Park, Kenya, 107 dikdiks/km^2 [Komers and Brotherton 1997], Arusha National Park, Tanzania, 59 dikdiks/km^2 [Amubode and Boshe 1990], and Serengeti National Park, Tanzania, 24 dikdiks/km^2 [Hendrichs 1975]), even the lowest density of dikdiks recorded, if harvested at the same rate as that recorded on commercial ranchland in this study, would provide 40.8 MJ km^{-2} year^{-1} (calculated as (24 dikdiks/km^2) × (6.8% per annum) × (25 MJ/ dikdik)), sufficient to support 0.7 wild dogs per 100 km^2 at 15.3 MJ/day. This density of wild dogs is comparable with that estimated in some potentially important wild dog populations (e.g., arid areas of Botswana—Creel et al. 2004). Dikdiks of various species are widely distributed in northeastern Africa (Kingdon 1997) and, although sensitive to overhunting, might support important populations of wild dogs in unprotected rangelands of northern Kenya and Ethiopia. Other small antelope, such as oribi (*Ourebia ourebi*), steenbok (*Raphicerus campestris*), and bush duikers (*Sylvicapra grimmia*), do not attain such high densities (East 1998) and probably could not support wild dog populations in the absence of larger ungulates.

Wild dogs were able to successfully recolonize most of our study area, without major conflict with livestock farmers (Woodroffe et al. 2005), because wild ungulate prey persisted even when greatly outnumbered by livestock (Georgiadis et al. 2003). Impala densities are lower in community lands than on commercial ranches, probably due partly to a lower density of water points (impala need to drink during the dry season— Jarman and Jarman 1979) and partly to competition with

livestock (Fritz et al. 1996), which occur at higher densities on community lands. Dikdiks appear to persist better in livestock-dominated landscapes, and also can survive in areas with no standing water (Hendrichs 1975). Perhaps unusually for Africa, offtake from prey populations due to human hunting was low across most of the study area, because Masai and Samburu pastoralists do not traditionally hunt wild ungulates, and because all forms of commercial hunting (including the bushmeat trade) are currently illegal in Kenya. This absence of a local hunting tradition has undoubtedly contributed to the persistence of wild ungulate prey in most of the study area; prey densities are greatly depleted in a part of the study area inhabited by Pokot people who have a strong culture of hunting, and this was the area where livestock predation by wild dogs by the Churo pack led to serious conflict with local farmers (Wood-roffe et al. 2005). In addition, both local pastoralists and commercial ranchers have retained an unbroken tradition of intensive livestock husbandry, which helps to reduce their conflicts with predators, including wild dogs (Ogada et al. 2003; Woodroffe et al. 2005). Although very few studies have quantified conflict between people and wild dogs in other parts of Africa (but see Rasmussen 1999), and data on wild dog distribution outside protected areas are incomplete (Woodroffe et al. 2004b), these findings provide indirect evidence that unprotected rangelands inhabited by traditional pastoralist peoples may hold great potential for wild dog conservation.

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