**Hunter-Gatherers in context: Mammal community composition in a northern Tanzania
landscape used by Hadza foragers and Datoga pastoralists**

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Abstract

In many regions of sub Saharan Africa large mammals occur in human-dominated areas, yet their community composition and species-specific densities have rarely been described in areas occupied by traditional hunter-gatherers and pastoralists. Surveys of mammal populations in such areas provide important measures of biodiversity and provide ecological context for understanding hunting practices. Using a sampling grid centered on a Hadza hunter-gatherer camp and covering 36 km² of semi-arid savannah in northern Tanzania, we assessed mammals using camera traps (n = 19 stations) for c. 5 months (2,182 trap nights). In the study area (*Tli'ika* in the Hadza language), we recorded 36 wild mammal species, resembling a near complete mammal community. Rarefaction curves suggest that sampling effort was sufficient to capture mammal species richness. Species-specific densities were estimated using a random encounter model and site- and species' body mass- specific estimates of the area sampled at each camera; confidence intervals were estimated using bootstrapping. Point estimates of densities varied by c. four orders of magnitude, from 0.003 ind./km² (African wild dog) to 27.5 ind./km² (Kirk's dik dik). Densities of livestock (cattle, donkey, sheep and goat) were high, particularly when estimated using directly observed herd sizes. Cumulative biomass density of herbivorous livestock species exceeded that of all wild mammals by a factor of 3.3-38.7. We compare our study's data to camera trap rates recorded in a fully protected area of northern Tanzania with similar precipitation (Lake Manyara National Park), revealing that abundance indices of most wildlife species in *Tli'ika* were much lower. We discuss how these data inform studies of Hadza hunting and models of hunter-gatherer foraging ecology and diet.

Introduction

Across Africa, populations of many large mammal species have been declining inside and outside of protected areas [1–5] but most of our understanding of the processes generating population declines of mammal species has focused on species within protected areas [5–11]. While the causes of population declines and local extinctions vary, there is a general consensus among conservationists that ‘fortress conservation’ efforts striving towards full protection from human exploitation are not sufficient to ensure the long term survival of many mammal species [12–16]. Consequently, wildlife conservation efforts have gradually shifted towards understanding the dynamics of human-wildlife coexistence across more diverse landscapes [17–19]. To assess possibilities for sustained coexistence of people and wildlife, it is especially important to assess wildlife populations in areas that are used by subsistence hunters [20]. Unfortunately, there is a paucity of mammal monitoring programs in lands used by hunter-gatherers, which hampers our understanding of these particular coupled human-ecological systems and their conservation implications [21].

In East Africa, widely varying human impacts upon wildlife communities are reported. In human dominated areas, some communities of large mammals show signs of low species richness and density, while others exhibit species richness and densities similar to nearby protected areas [16,22–31]. Cultural and economic differences among human communities are clearly implicated in such patterns, but poorly understood. In this study, we describe the mammal communities found in the Lake Eyasi / Yaeda Valley region (Tanzania), in an area occupied year-round by Hadza hunter-gatherers and seasonally by Datoga pastoralists. Relative to wildlife research in protected areas, research outside of parks requires greater engagement, support, and guidance by the local people using the shared landscapes. Employing participatory camera-trap

monitoring [32], we describe the mammal species detected in the area centered upon a favored camping location of Hadza hunter-gatherers. This study is the first to directly assess the status of mammal populations in this area. This study builds upon previous research in which mammal communities across the wider study area were estimated using indirect (animal signs) evidence [31]. The status of wildlife populations is a vital concern to the Hadza community and is valuable for modeling the ecology of hunting and gathering in the region. Knowledge of mammal community composition is also useful for community-based land use planning and conservation in the area, efforts which currently involve collaboration between representatives of the Hadza and Datoga communities, village governments, and conservation groups funded through carbon offsets [33].

Prior studies of subsistence hunters using traditional technologies have documented patterns of local depletion of hunted species near settlements, but whether these local impacts translate into lower regional biodiversity depends on a host of factors, including the size and density of hunting communities, the technologies employed, and the scale of market-driven hunting [34,35]. Hadza hunting practices have been described as focused on “immediate returns”, and unlike norms commonly recommended by wildlife managers, do not include restrictions on killing prey based on their age, sex, or number [36]. Traditionally, local groups of Hadza are non-territorial and permit open-access to landscapes used for harvesting foods [36]. The Hadza are also known to prize the killing of large-bodied mammals [37]. Such species are particularly vulnerable to hunting pressures, because of their slow reproductive rates [38]. However, recent detailed research documents the fact that most prey items killed by Hadza are small wildlife, less than 10 kg in body mass [39]. How these variable hunting pressures directly and indirectly affect mammal communities has not been assessed yet.

Similarly, the influence of pastoralist populations and livestock upon wildlife in Tanzania could be better elucidated. The landscape we monitored is used seasonally by Datoga pastoralists, who migrate into the hilly area of Tli'ika during the dry season (~ June-October). The hunting of large and dangerous animals, particularly lions (*Panthera leo*) and African buffalo (*Syncerus caffer*), is highly prized in Datoga culture as a way for young men to signal their bravery and receive gifts of cattle, but hunting for subsistence purposes is rare [40]. While the Datoga's direct impact upon wildlife populations through hunting is likely to be quite targeted and low overall, the effects of pastoralism on wildlife communities are debated [41–45]. The Hadza themselves adamantly claim that the Datoga's livestock degrade the land's carrying capacity for wildlife, and impedes their hunting. The abundance of livestock within the Hadza's traditional lands is a local political issue and is important for contextualizing Hadza subsistence hunting.

An earlier study proposed that wildlife densities in the study area were equivalent to those observed in national parks with similar rainfall [46]. If this was true, then the Hadza's contemporary hunting practices, including their rates of acquiring and consuming meat, could reasonably serve as a referential model for hunters living in wildlife rich environments in the past, before the neolithic incursion of agricultural and pastoral populations into the region. This issue is relevant to a wider debate in anthropology about whether ethnographically documented hunter-gatherers occupy low quality habitats [47–50]. It is important to note that the claim of high wildlife abundance in the Hadza region is based on a single aerial survey conducted in 1977. As pointed out by Blurton Jones [51; pages 30-31], later aerial surveys reveal a strong pattern of declining wildlife counts in the area: 4.45 individuals / km² in 1977, 2.09 in 1989, and 0.87 in 1992. In order to test whether wildlife densities in the core hunting territories of

contemporary Hadza are similar to that of a national park, we compare rates of wild mammal detection in this study to those recorded in a similar study done within Lake Manyara National Park, a protected area that receives a similar amount of annual rainfall (~500 mm /year).

To provide data of value to wildlife conservation efforts and longitudinal anthropological research in this area, we (1) describe mammal species richness detected in our survey, (2) report species-specific density estimates of wildlife and livestock, (3) estimate biomass densities of different functional groups of mammals, and (4) compare mammal species richness and densities in our survey to those detected using similar methods in the nearby Lake Manyara National Park.

Methods

This field research was permitted by the Tanzanian Wildlife Research Institute (TAWIRI) and the Tanzanian Commission for Science and Technology (COSTECH) (permit #: 2017-288-ER-2013-191) and subsequent explicit consent from local authorities.

Study area

Camera trapping took place on the Kideru Ridge, southeast of Lake Eyasi, in northern Tanzania. In this region east of Lake Eyasi, approximately 1000 people speak the Hadza language, and most members of this community continue to hunt and gather for wild foods using traditional technologies. Migration, population growth, and agricultural development near several villages in the region (Mangola, Mitala, Munguli, Yaeda Chini) has drastically altered the landscape that was historically occupied by Hadza [51,52]. Owing to population growth and land conversion, some areas that were important camping and hunting areas in living memory are no longer visited or used by Hadza, and the total extent of areas considered suitable for subsistence hunting has declined [52]. We carried out this research in a geographic area known to the Hadza

as Tli'ika, which corresponds to the placename 'Kideru Hills' on some maps. This area is remote from agricultural villages, and relatively unaffected by the migration, population growth, and agricultural development in other areas. This region continues to support the sustained presence of 200-400 Hadza community members who hunt mammals and birds using bows and arrows [51–53]. The surveyed area is also occupied seasonally by Datoga pastoralists, who bring their livestock into some of the hilly areas in Tli'ika during the dry season.

The area is characterized by woodland savannah habitat, with prominent stands of baobab (*Adansonia digitata*), acacia (*Vachellia* spp.), grewia (*Grewia* spp.), and Commiphora (*Commiphora* spp.) trees interspersed with open grassy areas. The area is hilly and ranges in elevation between 800-1400 meters. Annual rainfall averages ~500 mm [53] with most rainfall concentrated in the months of December – April. There are several year-round springs distributed across the Kideru Ridge, which form important water sources for people, livestock, and wildlife during the dry season. We do not share exact geographic coordinates of the study location so as to minimize the chance for misuse of these data [54].

Fig 1. Map of the study area. A) Indicates the region of Tli'ika in the Lake Eyasi area of northern Tanzania and B) shows the spatial distribution of 20 camera traps, centered upon the Hadza camp indicated in red.

Camera trap survey

One of the long-term goals of this project is to examine relationships between Hadza landscape use and patterns of wildlife distribution, and so we designed the grid to sample across different intensities of Hadza occupation and use, which arise out of their normal patterns of central-place foraging. GPS data collected between 2006 and 2018 [55] provided us with an empirical model of Hadza foraging intensities, and its variation as a function of radial distance from camp. Therefore, we designed a master grid that was composed of 16 cameras spaced 2 km apart, and a sub-grid closer to the Hadza camp, composed of 4 cameras, spaced 1 km apart, as shown in Fig. 1b. To implement this grid design, we traveled across the survey area with three

Hadza research assistants and a District Government Wildlife officer, and deployed the cameras onto suitably robust, mid to large-sized trees at a height of about 60 cm. A total of 20 camera traps (Bushnell Trophy Cam, infrared flash) were deployed and they operated for a maximum of 141 days, from March to July of 2018. Most camera traps remained operational at each site for the entire study period. However, five of the cameras were stolen, and then replaced with new cameras placed in close proximity to the original locations. At one site (site 10), cameras were repeatedly stolen and we did not obtain any data from this location. Camera traps were protected by custom-made, locked metal cases and attached to trees using screws. We set the cameras so that they would record a maximum of one picture per minute. This set-up ensures relatively long battery life, and reduces data storage requirements without compromising detection probability [56]. At each camera trap site, on the day of deployment, we set distance markers at 2, 5, and 10 meters away from the camera trap to allow for distance estimation of animal detections. Photos were entered and stored in the open source software program Camelot [57]. For each picture containing an animal, we identified the species using a field guide [58], counted the number of individuals per frame, and estimated the animal's distance from the camera by comparing each picture with a reference photo that contained distance markers. Because it was impractical to identify individual animals and thus difficult to define a single contact in the camera detection zone, we removed pictures of the same species that were taken within one hour of the initial picture of the same species prior to analysis to avoid pseudo-replications at each location [59,60].

Data analyses

We estimated species richness for all mammals with a mass equal to or larger than the northern lesser galago (*Galago senegalensis*). To assess whether sampling effort was sufficient,

we plotted this metric as a function of camera trap days, using the software EstimateS 9.1 [61]. We calculated bootstrapped 95% confidence intervals using 100 resamples.

To assess the abundance of mammal species in the area, we used two metrics. First, we computed a relative abundance index (*RAI*) which scales the number of independent camera events to 100 trap nights [60,62,63]. Next, we estimated the density (*D*) of each mammal species using the following formula, which is based on the Random Encounter Model [64,65]:

$$D = N_f \frac{y}{t} \frac{\pi}{vr(2 + \theta)}$$

with N_f = mean individuals per image of each species; y = independent photo events; t = camera trap days; v = mean day range of each species; r = detection radius of each camera; and θ = camera angle. We estimated day range (v in km/day) for each species using published records [66]. When no published value could be found, we estimated this value based on allometric relationships between body mass (BM) and day range (v) for carnivores ($v = 3.877 BM^{0.22}$) and herbivores ($v = 0.875 BM^{0.22}$) [67]. Because the detection radius (r) of the camera may vary by site and by body mass of the target-animal, we estimated this variable as the maximum recorded detection radius for each site and separately for small (≤ 8.25 kg), medium (8.26-52.74 kg), and large sized species (> 52.75 kg). These size classes were determined by sorting species into three approximately equal sized ($n = 14, 13$ and 13 species for small, medium and large-bodied species, respectively) groups. If the maximum detection radius was obtained by a small or medium sized animal, we used this value as the maximum radius for larger size categories. The angle (θ) of the camera traps was 0.6180 radians [68]. It is worth noting that N_f can be considered a minimum average herd size and may substantially underestimate the density of large and highly gregarious species, because the number of individuals depicted within the frame of a single image is likely to be lower than the actual herd size. This is a particular concern for

estimating the density of livestock, which are large bodied and travel in large herds. To remove potential undercounting bias of livestock due to underestimates of herd size, we also computed an alternative density estimate for livestock. In this alternative metric, in place of N_f , we used the average size of Datoga livestock herds that were directly observed during walking transects in the wider region nearby our camera trap grid in 2018 [31].

For all species, we estimated species specific densities (D_s) per camera trap locale, averaged them across the study area and generated 95%-confidence intervals by bootstrapping (1000 resamples) the point estimates of the 19 camera sites using the *boot* package's adjusted bootstrap percentile method [69] implemented in R 3.32 [70]. We estimated the biomass density (kg/km²) at the landscape scale by multiplying mean density estimates (ind./km²) with the average body mass (kg) of each species. Body masses were obtained from [22,71,72].

We compared the relative abundance index (RAI) of mammal species in Tli'ika to RAI estimates derived from a similar camera trap study conducted in nearby Lake Manyara National Park (LMNP) [59], less than 100 km from our monitoring area, where strong restrictions on subsistence hunting and livestock are in place [73]. We consider the role of these anthropogenic influences and the environmental differences between our survey area and LMNP in the discussion.

Results

The 19 camera traps operated within a range of 68-140 camera trap nights (69 to 141 camera trap days) from March 1 to July 21, 2018 with an average of 115 nights (116 days) per site. Cumulatively, a total of 2,182 camera trap nights (2,206 trap days) were collected. We identified at least 36 wild mammal species (Table 1). Image quality did not allow for a reliable

distinction between Cape hares (*Lepus capensis*) and scrub hares (*Lepus saxatilis*) and we hence combined these events as hares. The cameras also recorded domesticated animals including dogs (*Canis familiaris*), cattle (*Bos taurus*), donkeys (*Equus asinus*), sheep (*Ovis aries*) and goats (*Capra hircus*). For estimating livestock densities, we combined sheep and goat into one category.

Mammal species richness

Among the 36 mammal species, we detected 12 ungulate species (Kirk's dik-dik, bush duiker, klipspringer, bushbuck, impala, warthog, bushpig, greater kudu, zebra, eland, giraffe, and elephant), 17 carnivore species (common and large-spotted genets, bushy-tailed mongoose, slender mongoose, white-tailed mongoose, dwarf mongoose, black-backed jackal, African civet, bat-eared fox, honey badger, caracal, aardwolf, African wild cat, spotted and striped hyenas, leopard and African wild dog), three primate species (lesser galago, vervet monkey and olive baboon) as well as bush hyraxes, hares, porcupines and armadillos (for scientific names, see Table 1). The average number of mammal species detected per camera site was 11.5, ranging from three to 20 species. The species accumulation curves of six of the 19 sites (sites # 1, 3, 5, 7, 18, 20) visually appear to have approached an asymptote by the end of the operational period, while accumulation curves of the remaining 13 sites show an increasing trend even by the end of the operational period (Fig. 2). Combining data from all cameras, it appears that species accumulation curves had plateaued by the end of the study.

254 **Table 1. Mammal species (listed in alphabetic order of the scientific name) detected during a camera trap survey conducted in**
255 **Tli'ika, Lake Eyasi region, northern Tanzania in 2018.** For each species, we report the body mass (BM), the corresponding body
256 size class, the number of independent photo events (Events), Relative abundance index (RAI: independent events/100 trap nights),
257 estimated day range v (km/day), mean number of individuals per frame (N_f), estimated density (D), estimated biomass density, IUCN
258 conservation status, and reference (Ref) for the day range. For livestock species we also report the observed herd sizes from [31] and
259 resulting estimated densities in parentheses.

Species	Scientific name	BM (kg)	Size class	Events	RAI	Day range v (km/day)	N_f (ind./pic)	D (ind./km ²)	Biomass (kg/km ²)	Conservation status	Ref
Wildlife											
Impala	<i>Aepyceros melampus</i>	52.75	Large	79	3.62	2.00	1.48	2.187	115.34	Least Concern	[66]
Bushy-tailed mongoose	<i>Bdeogale crassicauda</i>	1.65	Small	21	0.96	4.33	1.00	0.376	0.62	Least Concern	[67]
Black-backed jackal	<i>Canis mesomelas</i>	8.25	Small	45	2.06	11.78	1.00	0.208	1.72	Least Concern	[66]
Caracal	<i>Caracal caracal</i>	12.75	Medium	8	0.37	6.79	1.00	0.078	1.00	Least Concern	[67]
Vervet monkey	<i>Chlorocebus pygerythrus</i>	4.75	Small	54	2.48	1.23	1.15	3.519	16.71	Least Concern	[67]
African civet	<i>Civettictis civetta</i>	11	Medium	23	1.05	6.57	1.00	0.154	1.69	Least Concern	[67]
Spotted hyena	<i>Crocuta crocuta</i>	62.5	Large	42	1.93	40.00	1.10	0.048	2.98	Least Concern	[66]
Plains zebra	<i>Equus quagga</i>	241.25	Large	1	0.05	17.00	2.00	0.005	1.29	Near threatened	[66]

African wild cat	<i>Felis silvestris</i>	4.48	Small	4	0.18	5.39	1.00	0.042	0.19	Least Concern	[67]
Northern lesser galago	<i>Galago senegalensis</i>	0.23	Small	24	1.10	1.76	1.13	0.748	0.17	Least Concern	[66]
Common genet	<i>Genetta genetta</i>	2	Small	106	4.86	2.98	1.00	2.188	4.38	Least Concern	[66]
Large-spotted genet	<i>Genetta tigrina</i>	2.15	Small	29	1.33	4.59	1.03	0.451	0.97	Least Concern	[67]
Maasai giraffe	<i>Giraffa camelopardalis</i>	1017.5	Large	16	0.73	9.00	1.00	0.041	41.63	Vulnerable	[66]
Dwarf mongoose	<i>Helogale parvula</i>	0.32	Small	4	0.18	2.00	1.00	0.220	0.07	Least Concern	[66]
Slender mongoose	<i>Herpestes sanguineus</i>	0.48	Small	15	0.69	3.30	1.13	0.286	0.14	Least Concern	[67]
Bush hyrax	<i>Heterohyrax brucei</i>	1.85	Small	32	1.47	1.00	1.16	2.830	5.24	Least Concern	[67]
Striped hyena	<i>Hyaena hyaena</i>	30	Medium	8	0.37	8.19	1.00	0.055	1.66	Near Threatened	[67]
Crested porcupine	<i>Hystrix cristata</i>	15	Medium	15	0.69	0.59	1.00	0.885	13.27	Least Concern	[66]
White-tailed mongoose	<i>Ichneumia albicauda</i>	4	Small	16	0.73	0.25	1.00	3.847	15.39	Least Concern	[66]
Hare	<i>Lepus spp.</i>	2.15	Small	30	1.38	1.04	1.00	1.849	3.98	Least Concern	[61]
African bush elephant	<i>Loxodonta africana</i>	4125	Large	4	0.18	12.00	1.00	0.007	29.87	Vulnerable	[66]
African wild dog	<i>Lycaon pictus</i>	37.5	Medium	1	0.05	9.70	1.00	0.003	0.13	Endangered	[66]
Kirk's dik-dik	<i>Madoqua kirkii</i>	4.5	Small	478	21.91	1.22	1.05	27.451	123.53	Least Concern	[67]
Honey badger	<i>Mellivora capensis</i>	10.38	Medium	7	0.32	6.49	1.29	0.102	1.06	Least Concern	[67]
Klipspringer	<i>Oreotragus oreotragus</i>	11.78	Medium	11	0.50	1.51	1.09	0.651	7.67	Least Concern	[67]

Aardvark	<i>Orycteropus afer</i>	65	Large	2	0.09	2.20	1.00	0.050	3.27	Least Concern	[66]
Bat-eared fox	<i>Otocyon megalotis</i>	4	Small	11	0.50	5.26	1.09	0.113	0.45	Least Concern	[67]
Leopard	<i>Panthera pardus</i>	41.5	Large	7	0.32	3.90	1.00	0.092	3.80	Vulnerable	[66]
Olive baboon	<i>Papio anubis</i>	15.25	Medium	15	0.69	5.00	1.20	0.213	3.24	Least Concern	[66]
Warthog	<i>Phacochoerus africanus</i>	68.75	Large	8	0.37	1.25	2.13	0.282	19.40	Least Concern	[74]
Bushpig	<i>Potamochoerus larvatus</i>	75	Large	28	1.28	3.00	1.18	0.420	31.52	Least Concern	[75]
Aardwolf	<i>Proteles cristata</i>	11	Medium	7	0.32	6.57	1.00	0.052	0.58	Least Concern	[67]
Bush duiker	<i>Sylvicapra grimmia</i>	17.5	Medium	16	0.73	1.64	1.00	0.994	17.39	Least Concern	[67]
Bushbuck	<i>Tragelaphus scriptus</i>	35.75	Medium	46	2.11	1.95	1.07	2.182	78.00	Least Concern	[66]
Greater kudu	<i>Tragelaphus strepsiceros</i>	215	Large	102	4.68	2.85	1.04	1.323	284.43	Least Concern	[67]
Eland	<i>Taurotragus oryx</i>	475	Large	1	0.05	3.40	1.00	0.013	6.32	Least Concern	[67]
Livestock											
Cattle	<i>Bos indicus</i>	253	Large	128	5.87	2.96	3.81	8.978	2271.51		[67]
							(51.22)	(120.701)	(30537.26)		
									)		
Donkey	<i>Equus africanus asinus</i>	137.5	Large	28	1.28	2.58	1.36	3.809	523.78		[67]
							(4.88)	(13.699)	(1883.60)		
Sheep and goat	<i>Capra spp.& Ovis spp.</i>	25	Medium	5	0.23	1.78	8.80	0.564	14.09		[67]
							(25.58)	(1.638)	(40.95)		
Domestic dog	<i>Canis lupus familiaris</i>	14.7	Medium	46	2.10	7.00	1.09	0.324	4.76		[67]

262

263 **Fig. 2. Camera site-specific (Site 1-9; 11-20) and landscape scale (Tli'ika) estimates of**
 264 **mammal species richness in Tli'ika, northern Tanzania.** Species richness estimates are
 265 plotted against sampling effort; dashed lines indicate 95% confidence intervals of the mean.

266

267 Mammal population densities

268 Relative abundance index (RAI) and the density estimated by the random encounter
 269 model (D) were significantly and positively correlated ($\tau = 0.545$; $p \leq 0.001$; $n = 36$) and we
 270 hence mainly focus on the absolute density (D) in this section. Wildlife species densities varied
 271 by c. four orders of magnitude, from 0.003 ind./ km² (African wild dog) to 27.5 ind./km² (Kirk's
 272 dik dik). Based on herd size estimates derived solely from numbers of livestock appearing in the

273 frame of camera images, cattle (9.0 ind./km²) and donkey (3.8 ind./km²) were estimated to be the
274 second and third most abundant species, respectively. However, if cattle and donkey densities
275 were estimated based on directly assessed herd sizes, cattle were by far the most abundant
276 species (120.7 ind./km²). Based on these density estimates, cumulative densities of livestock
277 species (136.0) were c. 2.5 times greater than the cumulative wildlife species density (54.0
278 ind./km²). Densities of domestic dogs [0.32 ind./km² (95% CI: 0.06-1.09)] were slightly greater
279 than those of similar-sized black-backed jackals [0.21 (0.08-0.45)].
280

281

282

283 **Fig 3. Population density estimates of mammal species in Tli'ika, northern Tanzania based**
 284 **on a random-encounter model.** Error bars indicate bootstrapped 95% confidence intervals of
 285 mean density estimates. Abbreviated species names: Cgenet = Common genet; LSgenet = Large-
 286 spotted genet; BTmongoose = Bushy-tailed mongoose; Smongoose = Slender mongoose;
 287 WTmongoose = White-tailed mongoose; Dmongoose = Dwarf mongoose; BBjackal = Black-
 288 backed jackal; Galago = Northern lesser galago; Livestock includes cattle, donkey, sheep and
 289 goat.

290

291 **Biomass densities**

292 Biomass density of all mammals was estimated at 3,653 kg/km² or 33,305 kg/km² for
293 density estimates based on camera-trap or directly assessed herd sizes, respectively (Table 1).
294 Among wildlife species, ungulates contributed 90.1%, carnivores 4.4%, primates 2.4% and other
295 species 3.1% of the total biomass (839 kg/km²). Within the domesticated species, the livestock
296 group contributed more than 99% of the biomass density and domestic dogs less than 1% (Fig.
297 4). Overall, livestock biomass density exceeded biomass of all wild mammals by a factor of c.
298 3.3 (density based on camera trap herd size estimates) or 38.7 (density based on direct herd size
299 estimates). Biomass density of wild carnivores exceeded that of domestic dogs by a factor of c.
300 7.7.

301

Fig. 4. Biomass density estimates of wild and domestic carnivores and herbivores in Tli'ika, northern Tanzania. Estimates of biomass were categorized into herbivores (wildlife: all predominantly herbivorous animals; domesticated: livestock) and carnivores (wildlife: all predominantly carnivorous animals; domesticated: domestic dogs). We estimated herbivore biomass of domestic animals based on camera trap herd size estimates (Domesticated, method 1) and based on direct herd size estimates (Domesticated, method 2).

312 **Comparison of relative abundance indices with Lake Manyara NP**

313 Relative abundance indices of ungulates, carnivores and other taxa in LMNP were c. 2.9, 1.5 and
314 5.9 times higher than in Tli'ika, respectively (Fig. 5). Notable exceptions to this general pattern
315 were substantially higher dik-dik densities in Tli'ika compared to LMNP. In addition, multiple
316 mammal species that were detected in Tli'ika were not detected in LMNP: bush duiker, eland,
317 greater kudu, aardwolf, bat-eared fox, caracal, striped hyena, African wild dog, and African wild
318 cat. Species-specific differences in RAI scores between the two areas ($RAI_{Kideru} - RAI_{LMNP}$) were
319 not significantly correlated with the body mass of the species; this was true for ungulates
320 (Kendall's tau = -0.303, $p = 0.197$, $n = 12$), carnivores (tau = -0.022, $p = 0.901$, $n = 17$) and in
321 other taxa (tau = -0.429; $p = 0.239$, $n = 7$).

Fig 5. Relative abundance indices (RAI; camera trap events / 100 trap nights) for mammal species in Tli'ika and Lake Manyara National Park (LMNP), in northern Tanzania.

Species were grouped in ungulates (top panel), carnivores (mid panel) and other mammal species (lower panel). Abbreviated species names: Cgenet = Common genet; LSgenet = Large-spotted genet; BTmongoose = Bushy-tailed mongoose; Smongoose = Slender mongoose; WTmongoose = White-tailed mongoose; Dmongoose = Dwarf mongoose; BBjackal = Black-backed jackal; Galago = Northern lesser galago

Discussion

This camera trap study documents high mammal species richness, relatively low wild mammal species' and biomass densities, and high livestock densities in an area inhabited by hunter-gatherers and pastoralists. Beyond confirming previous findings from animal sign surveys in the wider study area this study provides estimates of absolute densities for the entire mammal community as compared to relative density estimates in [31]. This study also provides important data for understanding the historical and ecological contexts of contemporary Hadza hunting practices and diet.

Wildlife persistence in a human-dominated landscape

Research on the patterns and chronology of Anthropogenic defaunation suggest that this process can be classified in three phases: 1. wildlife exploitation using simple technologies; 2. adoption of more sophisticated technologies to exploit wildlife; 3. habitat conversion to urban or agricultural space [76,77]. As these anthropogenic factors intensify, particularly large-bodied mammal species (which often require large home ranges) are often the first species to become locally extinct [10,11,25,78]. Our results corroborate that the study area supports a near complete mammal community, indicative that current human activities in the area do not reduce overall mammal species composition. Multiple factors likely help to sustain a near complete mammal community, including predominant use of traditional weapons to hunt wildlife, low human population density, a large extent of relatively intact habitat (the Kideru ridge provides c. 800 km² of habitat), and sustained connectivity to the Ngorongoro Conservation Area [31,79]. While subsistence hunting likely increases the risk of local extinctions, the survey area is notable for being quite remote from roads or agricultural villages, and currently having low human population density overall. Thus, the local anthropogenic drivers of defaunation are not as

extreme as in other areas in Tanzania. It is important to note that the Hadza community in the area has helped develop local land-use by-laws to limit agricultural development and land conversion. In addition, village game scouts carry out periodic anti-poaching patrols, limiting the pressure of hunters using snares and firearms that would otherwise be manifest by non-Hadza. These anti-poaching efforts are financed by revenue gained from REDD+ mechanisms, facilitated and organized by a Tanzanian NGO, Carbon Tanzania [33].

Although camera traps recorded an impressive number of mammal species, we did not capture some of the prominent species that are known to occur in the wider study area and were detected during previous walking surveys: e.g. African lions (*Panthera leo*), cheetah (*Acinonyx jubatus*), wildebeest (*Connochaetes taurinus*), Thomson's gazelle (*Eudorcas thomsonii*) and buffalo (*Syncerus caffer*) [31]. Some of these non-detections are likely due to mismatches between the camera trap grid and the habitat selection of the species in the study area (e.g. wildebeest and Thomson's gazelle which mainly occur in the grasslands of the Yaeda valley) while population densities of other species (lions, cheetah, buffalo) may be very low or absent and have thus not been captured by camera traps [59]. On a positive note, our photo capture of the endangered wild dog (*Lycaon pictus*) confirms the presence of this species in the study area [31,58]. Overall, these comparisons underline the general consensus that a combination of multiple survey methods is necessary to capture an entire mammal community in a given area [80]. An added benefit of using camera traps is the ability to identify animals to species level in almost all cases. Based on indirect signs, this may be difficult to achieve even for highly skilled trackers [81]. For example, our data allowed identification of mongoose to the species-level (not possible in [31]) and this extended the known range of the bushy-tailed mongoose (*Bdeogale crassicauda*) [58]. As recently as 2007, BW had observed ground pangolin (*Smutsia temminckii*)

in the survey area, but has not seen one since, despite yearly visits and extensive travels throughout the area. Trade in pangolins has occurred in this region, and perhaps caused this species' local extirpation. Black rhinoceros (*Diceros bicornis*) were extirpated in the 1970's [52].

In contrast to high levels of observed species richness, relative abundance of most wildlife species were markedly lower than in a fully protected national park in northern Tanzania (Fig. 5). Wildlife densities are primarily determined by bottom-up (i.e. resource availability) processes but top-down processes (e.g. predation, disease) can lower their resource-determined densities as well [82,83]. While our observational study only provides a snapshot in time and thus prevents elucidating the processes leading to the observed species densities, we discuss some underlying hypotheses.

Importantly, net primary productivity (NPP) in the reference study area (LMNP) was greater than in Tli'ika. Computed using MODIS satellite imagery¹, between the years 2001 and 2015, NPP averaged 9,909 kg carbon / m² (SD = 1126) in LMNP, while in the Tli'ika camera-trapping zone, it averaged 6,396 kg carbon / m² (SD = 704). The two locations receive similar amounts of precipitation (~500 mm /year) but the amount of runoff and groundwater available in LMNP is greater because it draws from a larger and higher elevation watershed [84]. Given the positive relationship between NPP and ungulate densities in East Africa - this difference may explain some of the observed contrasts in relative abundances between Tli'ika and LMNP [85],

¹ Terra Net Primary Production Yearly Global 1km (MODIS/055/MOD17A3).

but hunting pressures and competition with Datoga livestock in Tli'ika are likely to be stronger factors contributing to the large observed differences.

In general, Hadza hunters fear elephants (*Loxodonta africana*) and are very weary of African buffalo (*Syncerus caffer*); the former are not hunted whatsoever, the later, only occasionally [86]. In addition, Hadza hunters do not consider hyena (*Crocuta crocuta* and *Hyena hyena*), civets (*Civettictis civetta*), or jackals (*Canis mesomelas*) to be suitable for human consumption. Civets and jackals are rarely hunted, but hyenas are considered a potentially dangerous animal and are occasionally killed [40]. Interestingly, against a trend of generally lower mammal abundance in Tli'ika, the African civet and the black-backed jackal are found at higher densities in Tli'ika. Although relative abundance of leopards (*Panthera pardus*) was lower than in LMNP, their density [9.2 ind./100 km² (0.8-46.4)] is in the medium-high range of African wide densities of this species [87,88]. Likely, this is facilitated by their wide feeding niche and the relative high abundance of potential small prey species such as dik-diks [89].

Lower relative abundances of most species does not mean, however, that hunting pressures are solely responsible. It is also the case that the Hadza very actively hunt dik-dik [39], and yet the estimated density of dik-dik in the Hadza region remains greater than that of LMNP. As top down regulation of herbivore populations may differentially affect species of varying body masses [90] and its strength may be conditional on the primary productivity [91], long-term monitoring of the mammal community is imperative to elucidate Hadza hunting effects on mammal populations.

Resource competition between livestock and wildlife is a local concern and that may also contribute to low species densities and overall low wildlife biomass density. Some species which occur at relatively low densities (e.g. zebra, eland) are both preferred prey for Hadza and are also

primarily or obligate grazers [92] and thus require large quantities of grass [93] which makes reduced grass availability (as a consequence of high livestock densities) a likely alternative explanation. Though we cannot disentangle the influences of these multiple factors in this study, it is surely notable that the biomass of domesticated livestock (particularly cattle) in this area clearly exceeds that of wildlife, a finding that is corroborated by walking transects across the wider area [31]. This has implications for local land use planning, and should be a target for continued ecological monitoring. Ideally, experimental or quasi-experimental studies can shed more light on the relative contribution of each of these factors on wildlife population trajectories [94].

Our survey demonstrates the possibility for co-existence of wildlife and subsistence hunters in shared landscapes, but the generally low densities of wildlife are a concern for conservation and sustainable hunting. In light of the high species richness and general low abundance of most wildlife species, additional stressors on wildlife populations caused by agricultural expansion, new forms of infrastructure or land use (e.g., road construction, mineral or petrochemical exploitation), likely entail high risks to the low-density wildlife populations currently residing in the area and which provide major ecosystem services to traditional Hadza livelihoods.

Wildlife monitoring in human dominated areas

Our camera trap survey is one of the few camera trap studies that provide density estimates (as opposed to density indices or occupancy estimates) for an entire mammal community [95]. The importance of assessing wildlife communities in human-dominated areas of sub Saharan Africa is increasingly being recognized [27,28,96,97], yet few studies have attempted to estimate actual wildlife densities in human dominated areas. The ones that do report

actual wildlife densities typically employed methods that rely on direct sightings by observers in the framework of strip or line distance sampling surveys [26,98]. While these estimates may be reliable for diurnal and abundant species under some circumstances, these methods fail to detect many species [59] and may underestimate densities of hunted species [99]. As case in point, dik-dik density based on camera trap methodology [27.45 ind./km² (16.35-45.56)] was almost six fold greater than based on direct sightings and distance sampling methodology in a stratum similar in habitat and partly overlapping with our camera trap grid [4.66 ind./km² (95%CI: 1.83-11.84)] [31]. Camera trapping may thus provide a suitable method for assessing wildlife communities in human-exploited areas and further advances in analytical methods [100] may further promote their use. Our current study indicates that methods for appropriately dealing with herd size require further development, as herd size estimation based on the picture frame may underestimate the true density of gregarious species. As livestock species in East Africa are typically herded in large herds, this may be a particular concern for estimating livestock densities. Clearly, this also applies to gregarious wildlife species (e.g. olive baboons, zebra, impala, greater kudu), and suggest that density estimates of most species are likely biased low overall. Despite these concerns, the comparison with camera trap rates in LMNP is indicative for overall low densities of most wild mammal species in the study area.

A major, largely unresolved challenge for camera trap surveys in human-dominated areas are vandalism and theft, which constitutes a major data and financial loss [101]. Nevertheless, we hope that continuous community engagement will facilitate longitudinal mammal monitoring in the area, and provide data valuable to local land use planning as well as fundamental research in anthropology and ecology.

Contemporary Hadza hunting, diet, and reconstructions of the past

As this is the first direct assessment of mammal communities in an area regularly hunted by the Hadza, it will inform future anthropological research investigating the Hadza's foraging economy, including patterns of prey choice, landscape utilization, and the sustainability of prey off-take. Our data show that the biomass of livestock in the Hadza's traditional lands today vastly exceeds that of wildlife. This raises several important issues. The presence of domestic livestock and the generally low densities of wildlife call into question the assumption that contemporary Hadza hunting practices should be considered representative of foraging economies that would have prevailed prior to the neolithic revolution [102]. High livestock densities are associated with decreases in wildlife biomass across Africa [103]. Prior claims that the Yaeda-Tli'ika region sustains densities of wildlife mammals similar to that of national parks with similar rainfall levels [46] are not consistent with our data. The question of whether contemporary hunter-gatherers occupy marginal habitats has been addressed in recent studies by examining the net primary productivity (NPP) of forager-occupied habitats [47,48]. Our study leads us to wonder if these studies have adequately assessed habitat quality, because the abundance of wildlife goes unmeasured in NPP-based studies.

Several studies of foraging populations (including the Hadza) document food preferences that favor meat consumption relative to plant foods [104–106]. Cross-cultural measures of the return rates (kcal / hr) of a wide variety of different wild foods show that hunted animals have higher average return rates than does the pursuit of key plant foods, including tubers and seeds [107]. These findings suggest that in general, when wildlife is more abundant, more meat will in turn be hunted and eaten. Given the high prevalence of livestock and low abundance of wildlife in the Hadza's contemporary habitat, it would be reasonable to assume that meat would have

comprised a larger fraction of forager diets in this region in the past, before the movement of pastoralist and agricultural populations into the area. Prey abundance and hunting productivity also seems to have declined precipitously in recent times, in the living memory of contemporary Hadza. Blurton-Jones [51] reports that buffalo seemed to “disappear” after 1986 in the region and that “Hadza in Tli’ika attributed the decline in large animals to Datoga fencing the water holes, making the area unattractive to wildlife” (ibid:31). Even so, the Hadza in Tli’ika continue to hunt and gather, and are ever-resourceful at making a living in their land. It is important to document these recent environmental changes in Hadzaland in order to contextualize the foraging patterns observed today, and adjust for contemporary biases in reconstructions of the past.

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