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Differentiated payments for ecosystem services based on estimated prey consumption by lions within communal conservancies in northwest Namibia

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ABSTRACT

When effectively applied, differentiated payments for ecosystem services (DPES) can help offset certain costs incurred by communities living alongside destructive wildlife. In areas with human-lion conflict (HLC), strategies for addressing the costs of living with large carnivores have primarily focused on compensation payments for lost livestock, but a more complete approach would include the value of prey species consumed by lions that might otherwise have market value for local communities. We introduce an approach for translating the value of prey species consumed by lions from opportunity costs into DPES as one approach for assessing the costs of coexistence with lions. Because lions are unequally distributed across the landscape, efficient DPES require spatially explicit lion movement data. Using data from GPS-collared lions, we link the movements of five lions within six communal conservancies in northwest Namibia to predation rates to estimate the differentiated opportunity costs to each conservancy in the form of wild prey species consumed by lions. Using two population estimates, we show how movement and predation data could be scaled up and suggest applications for addressing other human-wildlife scenarios.

1. Introduction

Across Africa, lion (*Panthera leo*) populations are diminishing outside of fenced protected areas (Packer et al. 2013; Bauer et al., 2015), primarily due to land transformation and human-lion conflict (HLC) (IUCN, 2018). Climate change and increasing human population pressure will likely result in further habitat transformation, declines in prey species, and encroachment of people into wildlife areas. Among the many challenges for lion conservation outside of fenced protected areas is that the costs and benefits of living with lions often do not align. Attempts to reduce negative interactions between humans and lions should address the costs incurred by affected communities without constraining local rights (Dickman et al., 2011). In recent years, ecologists, social scientists, and conservationists have examined human-carnivore relationships and developed relevant mitigation strategies (Kellert et al., 1996; Zabel and Holm-Müller, 2008; Meena et al., 2020), including innovative mechanisms for reducing conflict (Dolrenry et al., 2016), paying compensation for losses (Mishra et al., 2003), and, in some instances, increasing tolerance by providing monetary incentives (Dickman et al., 2011). Most schemes have sought to minimize the direct costs of living with carnivores via improved awareness and herding practices (Dolrenry et al., 2016; Weise et al., 2019) or financial assistance when livestock are killed (e.g. Mishra et al., 2003; Hazzah et al., 2014; Jhala et al., 2019).

The ecosystem services framework was originally developed to link natural processes to their positive effects on humans (Daily, 1997) and to foster activities for which there is little pre-existing motivation (Prokofieva, 2016), but there has been little scholarship quantifying the costs of living alongside large carnivores within this framework. Since the Millennium Ecosystem Assessment, ecosystem service programs have increasingly relied upon prices as the "common metric" (MA Framework 2003, p. 128) for measuring and integrating ecosystem services into conservation policy (MA Synthesis, 2005; Sustaining Environmental Capital, 2011). Economic approaches have subsequently become the dominant paradigm for assessing the status and value of ecosystem services, though debate continues over the efficacy of this approach (Heydinger, 2016; Costanza, 2020; Victor, 2020). Where payments for ecosystem services (PES) have been explicitly linked to

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lion conservation, this has been based on livestock loss compensation and the associated program was found lacking (Anyango-van zwieten et al., 2014). Some of the challenges of large carnivore conservation are that the costs and benefits of carnivores' continued existence are unevenly distributed (Kellert et al., 1996; Macdonald, 2001), and the effects of conflict interventions are largely unquantified (de la Torre et al., 2021). Applying the ecosystem service framework, Dickman et al. (2011) reviewed financial instruments to pay local people for living alongside carnivores. Their concept of 'payments to encourage coexistence' (PEC), a form of PES, differentiates among compensation and insurance schemes, revenue-sharing initiatives, and conservation payments. They provide guidelines for 'ideal' PECs, emphasizing the need to target rural pastoralists that are most directly affected by carnivores by reducing the costs and increasing the benefits, thereby supporting human-carnivore coexistence in circumstances where the decision to extirpate carnivores is economically driven. These guidelines include methods that (i) minimize conflict by targeting payments to those most directly affected, (ii) reduce the costs of human-carnivore coexistence, (iii) provide local people with additional revenue directly linked to carnivores, (iv) avoid moral hazard and perverse incentives, (v) do not require significant additional revenue, (vi) link payments to desired conservation outcomes, and (vii) are likely to reduce (local) human poverty.

However, the 'hidden' or indirect costs of human-wildlife conflict have not been widely considered (Barua et al., 2012). Nelson (2009) emphasizes the importance of determining the monetary payment that will exceed both the actual and the opportunity costs of living with large carnivores. But what are the opportunity costs of living with lions? Because lions are unequally distributed across the landscape (Schaller, 1972; Mosser et al., 2009; Mosser et al., 2015; Namibia MET, 2017), efficient PES/PEC programs addressing opportunity costs will account for differentiated lion presence. Remote monitoring using satellite and/or GPS tracking technologies is a universally accepted form of recording wildlife movements (Benson, 2008). Where spatially explicit data are available, Aguilar-Gómez et al. (2018) have created a framework for developing efficient differentiated payments schemes for ecosystem services (DPES). We have adopted Aguilar-Gómez et al.'s (2020) definition of DPES: "monetary or in-kind payment transactions, between the buyer or allocator and the provider of environmental services, aiming at maximizing efficiency in order to achieve the objects of PES, where the payment is differentiated according to the environmental, social, and economic characteristics in a given scale and according to the sector." To identify the relevant stages for creating a DPES approach, we have applied Aguilar-Gómez et al.'s (2018) DPES framework which identifies four separate stages necessary for identifying DPES. These include: 1) collection of relevant environmental data, 2) measurements of the relative influence of each affected community, 3) development of an index for payments, and 4) application of the index to creating a differentiated payment scheme, for distributing funds to communities according to their respective contributions. Applying this framework, and based on the insights from Dickman et al.'s (2011) guidelines for ideal PEC's, and Nelson's (2009) consideration of opportunity costs, we have developed a novel approach for estimating the costs lions impose upon communal conservancies in northwest Namibia both directly (via livestock losses) and indirectly (via the loss of prey animals that could otherwise be utilized as game meat). Using GPS collar data, we quantify the time lions spend within a given conservancy and use prey-selection data to estimate the market value of prey consumed by lions (Fig. 1). This approach diversifies the mechanisms for assessing the costs of living with lions, which is an important part of moving towards a more comprehensive framework for assessing the pervasive challenges of human-lion interactions, particularly among low-income Africans. Using available lion population data, we show how these estimates could be scaled-up to account for the costs imposed by a conservancy's lion population or for the regional lion population and linked to conservation payments. We then show how this concept could be applied to other human-wildlife scenarios. Our objective was to show that the costs of living with lions are spatially differentiated, and to develop an approach based on lion movements and predation under ideal circumstances (lions preying upon wildlife) within the given system that could provide a robust foundation for quantifying the opportunity costs of living with lions and tie these to appropriate PES to local communities.

1.1. Lions in Northwest Namibia

Following record levels of drought and high levels of wildlife poaching in the 1980s (Reardon, 1986; Bollig, 2020), locally-centered wildlife conservation efforts led to the formation of communal conservancies in the late 1990s–early 2000s in northwest Namibia. Since that time, communal conservancies have "successfully" unified rural development and wildlife conservation (Dressler et al., 2010; Owen-Smith, 2010). Since 1996, Namibians inhabiting communal land can receive benefits from wildlife by forming a communal conservancy. Thirty-six such conservancies have since been created in northwest Namibia (Namibian Association of CBNRM Support Organizations (NACSO), 2018b). To receive official recognition, each conservancy must draft a constitution that includes a government-approved benefit-allocation plan and borders that have been negotiated with its neighbors. Within their respective jurisdictions, communal conservancies have conditional rights over wildlife occurring within conservancy boundaries, including sustainable-use quotas that are negotiated between conservancies and Namibia's Ministry of Environment, Forestry and Tourism (NACSO,

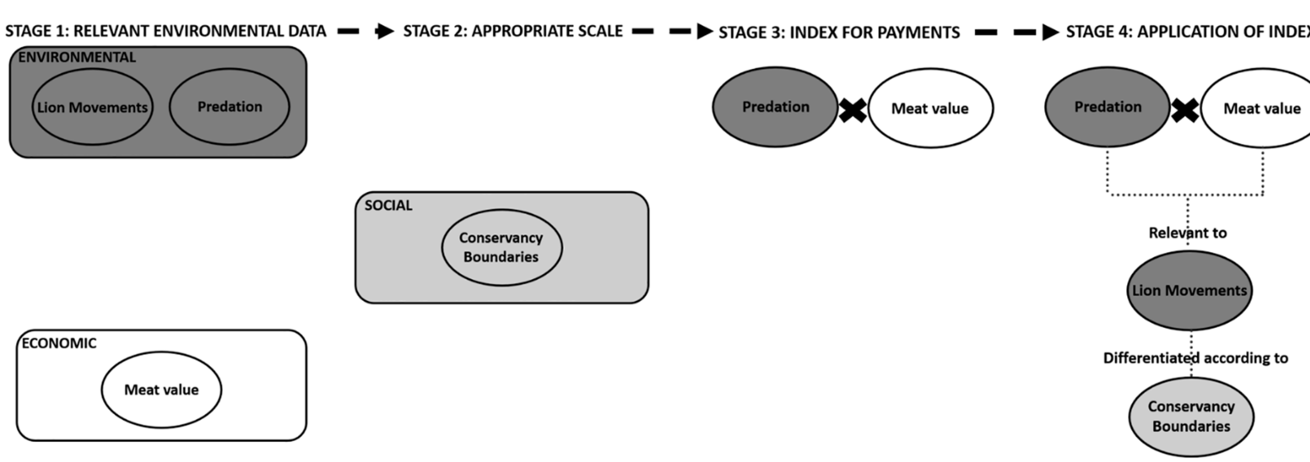

Fig. 1. conceptual schematic for DPES of desert-adapted lions, adapted from Aguilar-Gómez et al. (2018). Potential PES in this scheme differentiated according to environmental, social, and economic characteristics (see Methods).

2018b). Within these sustainable-use quotas, conservancies can harvest animals, either as trophies, own-use (consumed by conservancy members), shoot-and-sell (meat and other products sold to a buyer), or capture-and-sell (live animal sold to a buyer). In certain cases, individual animals may also be destroyed as a Ministry-declared ‘problem animal,’ in which case the meat and other products belong to the conservancy – with the exception of elephant (*Loxodonta africana*) ivory or rhino (*Diceros bicornis*) horn, which are kept by government.

The growth of communal conservancies coincided with herbivore population recoveries in the early 2000s (NACSO, 2018a). A growing prey base coupled with increased local involvement in wildlife conservation led to lion numbers increasing on communal lands; from 20 individuals in 1990 to ~180 in 2015 across communal lands in northwest Namibia. Once confined to fewer than 7000 km^2, lions ranged across nearly 40,000 km^2 by 2017, much of which is communal land (Stander, 2018). However, since the mid-2010s, severe and sustained drought conditions have resulted in a decreasing prey base (NACSO, 2018b), and lions are increasingly preying upon livestock (Lion Rangers, 2020; J.H. unpublished data). HLC killings now account for >80% of recorded adult lion mortality and 100% of recorded sub-adult mortality (Namibia MET, 2017). This growing conflict is endangering the success of community conservation in the region (Owen-Smith, 2017; Hartmann, 2018; Heydinger, 2019). While consumptive and non-consumptive benefit streams, such as trophy hunting and eco-tourism, currently exist, our approach demonstrates one means for complementing these benefits.

In a recent survey, examining the livelihood effects of lion predation on pastoralists’ livestock, as well as their attitudes towards lions, Heydinger et al. (2019) found while 75.9% of local pastoralists state they want to continue to have lions in their conservancy, 84.3% say they do not receive any benefits from lions. During outreach activities with conservancy members, we found a certain willingness to live alongside “not too many” lions (G.S.H, unpublished). Heydinger et al. (2019) also found that lions have been responsible for a mean loss of US$ 2985 worth of livestock per household during the recent drought (2014–2017). In an area where 40% of the population live on ≤US$ 1/day and 23% live on ≤US$ 0.73/day (Namibia National Planning Commission, 2012), such losses erode families’ assets and undermine their ability to meet basic needs. Additionally, 92.7% of communal pastoralists felt a recent government-sponsored livestock-loss offset program was ineffective, attributing its failure to the program inadequately replacing the full value of lost livestock (see Heydinger, 2019, pp. 184–215).

2. Methods

2.1. DPES stage 1: relevant environmental data – lion collaring data

To assess lion presence within different communal conservancies we examined satellite collar data tracking the movement of five lions, provided by the local NGOs Desert Lion Conservation (DLC) and Namibian Lion Trust (NLT). All five lions were fitted with satellite collars primarily for research and monitoring purposes and their movements had not previously been measured. Data from these five individuals were selected for their longevity and relative completeness. DLC provided data for three lions: the Hoanib pride female (collared 05/05/2008 to 06/06/2017, representing 2791 nights), the Oruwao male (collared 29/08/2012 to 07/12/2016, 907 nights), and XPL-73 (male) (08/08/2010 to 02/07/2014, 1195 nights). NLT provided collar data for two lions: HPL-1 (female) (01/02/2016 to 09/02/2018, 734 nights), and HPL-12 (female) (15/04/2016 to 09/03/2018, 668 nights). GPS locations were plotted onto area maps comprising all protected and other land-use areas these lions entered as well as riverbeds, with locations taken at 21:00 each night. Since lions are primarily nocturnal, nighttime locations more accurately indicate areas of hunting behavior (Schaller, 1972; Stander, 2009). Gaps in data occurred when collars malfunctioned or were inoperable.

2.2. DPES stage 2: appropriate scale – communal conservancies

By measuring lion occupancy at a local scale, this approach differentiates the relative contribution of each conservancy to the conservation of the lion population. Conservancies are the official means through which residents receive benefits from wildlife, and thus represent the appropriate, legally-recognized, social scale for DPES on communal land. Conservancy legislation dictates that benefits be allocated to members based upon the conservancy’s constitution. Thus, each conservancy can decide how possible DPES would be distributed to its members. Because lions in northwest Namibia have home ranges among the largest ever recorded (4726 km^2; Stander, 2019) accounting for lion movements between different areas is essential to assessing their effects on conservancy-level prey and livestock numbers. While we recognize prey species are also mobile, our approach aims to contribute to the benefits conservancy members receive from lions within the given protected area structure of northwest Namibia. (For conservancy size, human population, and annual income see Supporting Information.)

2.3. DPES stage 3: index for quantifying relative importance – cost of prey consumption

In Namibia commercial markets exist for prey species. Thus, meat consumed by lions represents an opportunity cost for the affected conservancy. We have used the meat price of lion prey species as a conservative estimate of their market value to conservancies (Table 1). To calculate annual meat consumption by lions we used the following equations:

$$\text{annual individual lion consumption} = \text{daily meat consumption} \times \text{number of days/yr}$$

Adult female lions consume an estimated 5 kg of meat per day, while adult males consume an estimated 7 kg per day (Schaller, 1972). In northwest Namibia, Stander (2018, pp. 96–7) found female groups contain an average of 1.59 adults, so we adjusted the amount of meat consumed per collared female to 7.95 kg (5 × 1.59 = 7.95).

$$\text{annual male lion consumption} = 7\ \text{kg} \times 365.25$$

$$\text{annual female group consumption} = (5\ \text{kg} \times 1.59) \times 365.25$$

Of the five lions considered here, three were female (Hoanib pride female, HPL-1, and HPL-12), and two were male (the Oruwao male and XPL-73). Note that this female:male ratio (3:2) over-represents males within the communal land in northwest Namibia, where the overall female:male ratio is 5.5:1 (Stander, 2010).

In order to assess the relative contribution of each prey species to lion prey consumption, the proportion of prey species consumed by the collared lions was estimated from predation data collected by Stander (2018). The cost per kilogram of each game species was derived from the prices a local butcher would pay for each prey species based on an in-person interview (Impala Meat Market & General Dealer – Kamanjab, 2020). Namibian dollars were converted to US dollars (US$) at a rate of 15 to 1. Note that the conservancies in which lion presence was recorded

Table 1
Contribution of individual prey species to lion diet within communal lands in northwest Namibia and meat-value opportunity costs of female groups (1.59 lions) and individual male lions. Contribution of edible biomass of each prey species is taken from Stander (2018). (Species recorded comprise 97.2% of lion diet – remaining 2.8% is comprised of species with no market value, such as porcupine (*Hystrix africaeaustralis*), and/or were consumed in such small quantities as to have no relevant market value, such as steenbok (*Raphiceros campestris*)).

species	biomass (%)	yearly biomass/ female group (kg/ female group)	yearly biomass/ male (kg/male)	cost/kg meat (US$/kg)	annual cost/female group (US$)	annual cost/male (US$)
gemsbok (*Oryx gazella*)	27.4	794.25	699.34	1.67	1326.4	1167.90
mountain zebra (*Equus zebra*)	18.7	542.85	477.98	1.04	564.56	497.10
ostrich (*Struthio camelus*)	5.2	149.86	131.95	5.33	798.75	703.30
giraffe (*Giraffa camelopardalis*)	38.4	1113.64	980.56	1.00	1113.64	980.56
springbok (*Antidorcas marsupialis*)	2.0	57.76	50.86	1.67	96.46	84.93
kudu (*Tragelaphus strepsiceros*)[1]	2.7	79.85	70.31	1.80	143.72	126.55
donkey (*Equus asinus*)[2]	2.1	61.82	54.43	1.04	64.29	56.61
cattle (*Bos taurus*)	0.7	21.06	18.56	2.67	56.27	49.54
total	97.2	2821.1	2483.98		4164.1	3666.5

[1] Kudu are defined as “high-value” and have not been available for shoot-and-sell in northwest Namibia since 2012. The price per kg of kudu meat was derived from recent game-auction information from private game farms in other parts of Namibia (R.D. unpublished data).

[2] Donkey are not formally sold at butcheries but are sold informally among community members. There was general agreement among interviewees that donkey meat has the same value as zebra meat (J.H. pers. obs).

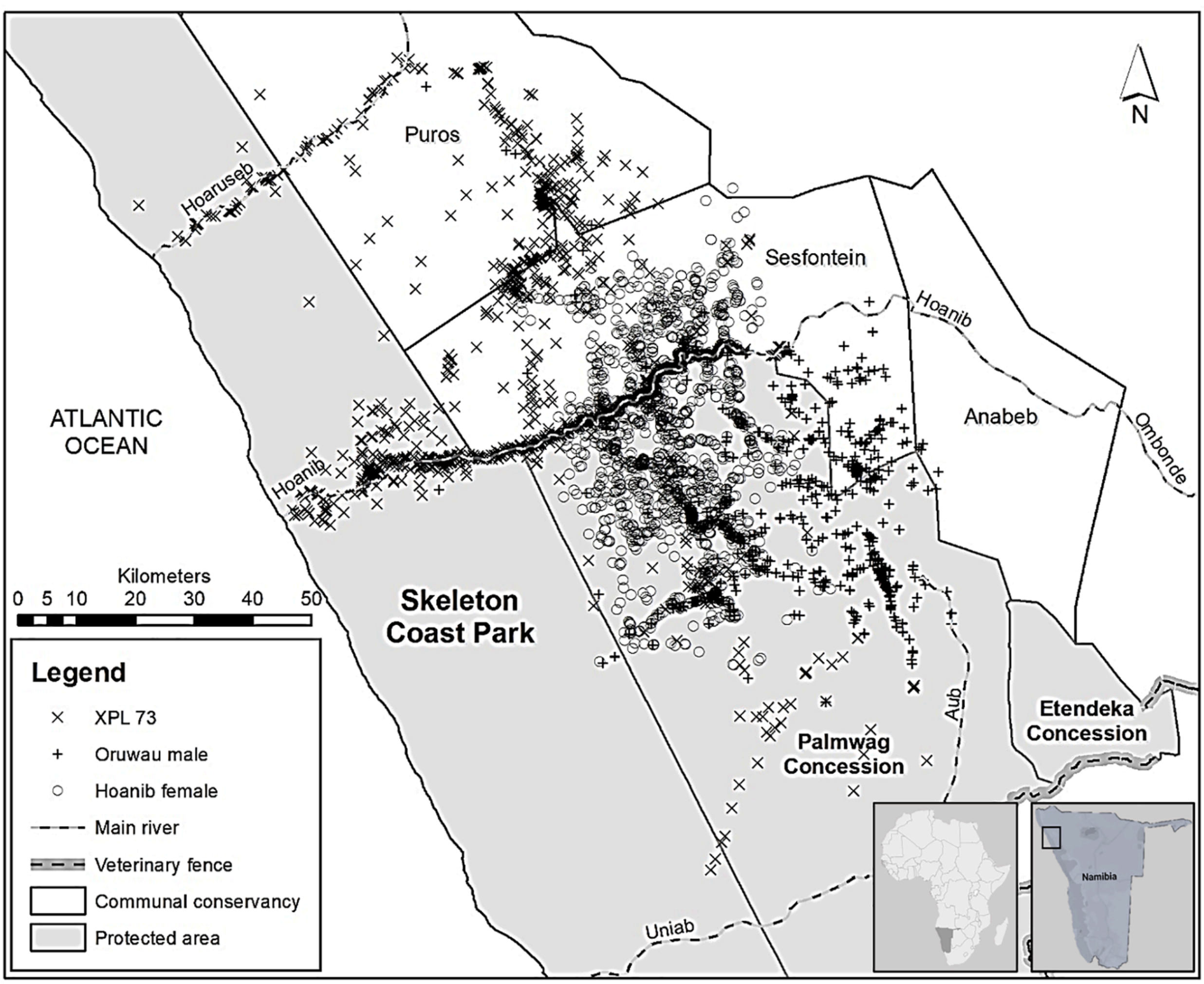

Fig. 2. collared lion movements (05/05/2008 to 07/12/2016) for three lions collared by Desert Lion Conservation (DLC). Map created using ArcGIS (Environmental Systems Research Institute (ESRI), 2020).

fall along both sides of Namibia's Veterinary Control Fence, colloquially known as the Red Line. Since meat from north of the Red Line cannot be exported south of the Red Line (or to international markets such as the European Union) without undergoing extensive quarantine, this may reduce its value (Miescher, 2012; Millennium Challenge Corporation, 2014), though the local butcher did not differentiate meat value for prey species falling north or south of the Red Line. Also note that the trophy value of each species greatly exceeds the value of its meat, so our estimates are conservative.

$$\text{prey species' contribution to annual consumption} = \text{annual individual male lion (or female group) consumption} \times \text{species' proportional biomass contribution}$$

Because not all lions in the population were collared, we estimated ranges for total cost by extrapolating lion presence from these collars in two ways: lion density across the six conservancies based on regional density estimates (Namibia MET, 2017) and overall population of free-ranging lions west of Etosha (Stander, 2018) (Supporting Information).

2.4. DPES stage 4: Application of index to environmental data for DPES - cost of lion presence

Between 1999 and 2017, Stander (2018) recorded 363 individual animals preyed upon by lions, and estimated the amount of biomass consumed from each carcass. By totaling lions' food intake across all prey, we are able to estimate the proportion that each species contributes to lions' diet. After Schaller (1972), we estimated that females consume 1826.25 kg/yr ($5 \times 365.25 = 1826.25$), while males consume 2556.75 kg/yr ($7 \times 365.25 = 2556.75$). Because females typically move in groups of 1.59 adults, we adjusted the amount of meat consumed by female groups to 2903.74 kg/yr. Multiplying the percentage that each species contributed to a lion's annual meat consumption, we arrived at the amount of meat from each species per year. For example, since gemsbok (*Oryx gazella*) contributed 27.4% of biomass consumed, female groups would consume 795.62 kg of gemsbok meat annually ($0.274 \times 2903.74 = 795.62$). In contrast, a male lion would consume 699.34 kg of gemsbok meat annually ($0.274 \times 2556.75 = 699.34$). Having derived the annual cost of female groups (US$ 4164.1) and males (US$ 3666.5) we estimated the cost per lion night for female groups (US$ 11.4 = 4164.1/365.25) and males (US$ 10.4 = 3666.5/365.25) (Table 1).

$$\text{cost per lion night} = \frac{\text{total annual cost}}{365.25}$$

3. Results

Collared lion movements are summarized in Figs. 2 and 3 (the area in Fig. 2 lies directly west of the area in Fig. 3). DLC collars recorded lion movements within and between communal, government-concession, and national park land across the western part of the region (Fig. 2) whereas the NLT collars recorded lion movements across comparable areas in the eastern part of the region (Fig. 3). Otjikandivirongo Conservancy and Wildeck 626 farm recorded the fewest total number of collared lion nights (n = 1 each), while Palmwag Concession had the

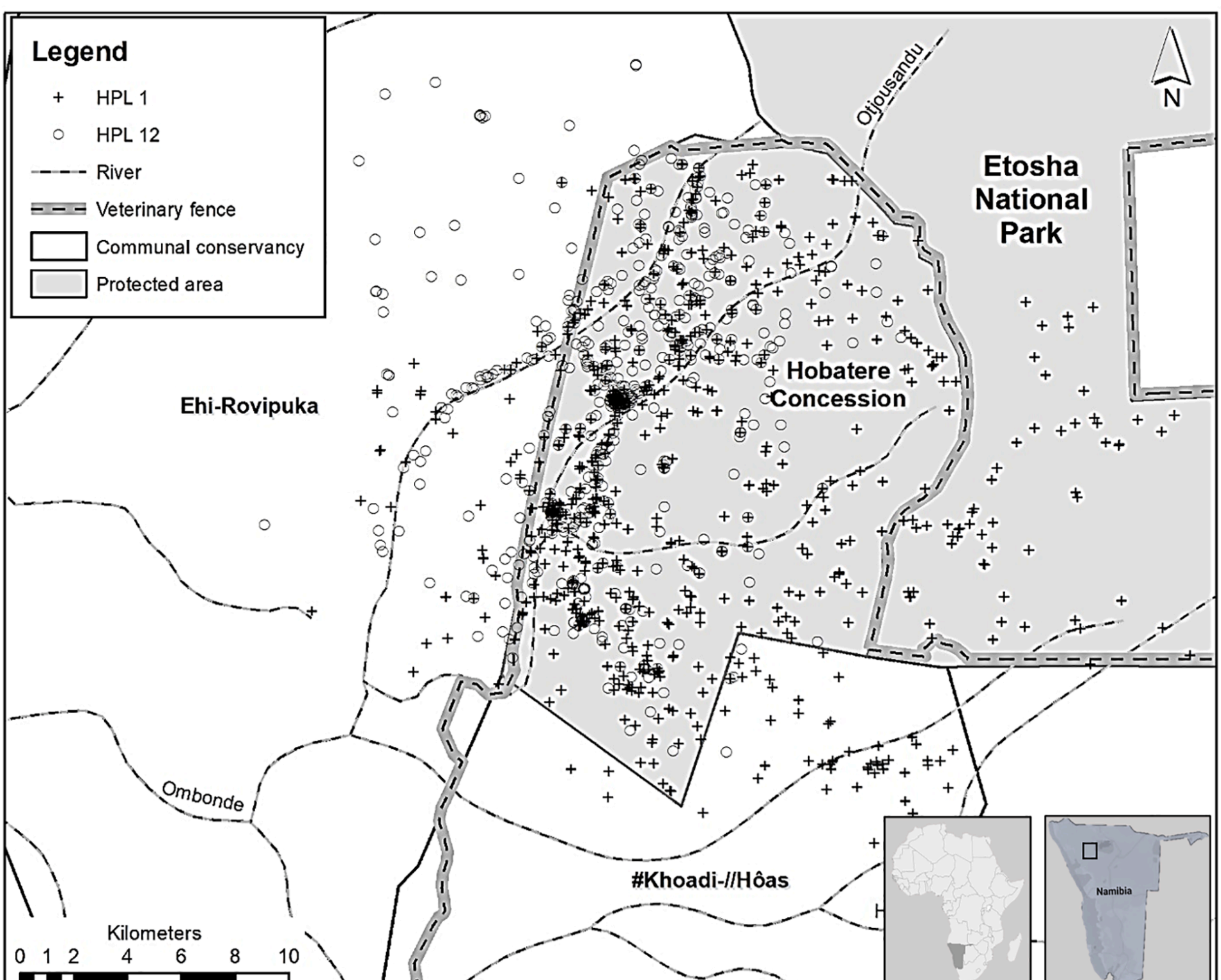

Fig. 3. collared lion movements (01/02/2016 to 09/03/2018) for three lions collared by Namibian Lion Trust (NLT). Map created using ArcGIS (ESRI 2020).

Table 2
Number of nights collared lions spent within indicated boundaries each year. μ nights/yr is the mean number of nights across all years with available data.

Conservancies	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	total	μ nights/yr
Anabeb									4			4	0.36
Ehi-Rovipuka									40	105	4	149	13.55
#Khoadi-//Hôas									6	49	4	59	5.36
Otjikandivirongo										1		1	0.09
Puros					123	95	96					314	28.55
Sesfontein	113	206	27	138	221	140	69	181	293	103		1491	135.54
Total	113	206	27	138	344	235	165	181	343	258	8	2018	183.45
Other Areas	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**total**	**μ nights/yr**
ENP									1	46	18	65	5.91
Hobatere									525	530	73	1128	102.55
Palmwag	127	135	174	392	478	424	310	373	260	54		2727	257.55
SCNP			54	198	30	46	28					356	32.36
Wildeck 626											1	1	0.09
Total	127	135	228	590	508	470	338	373	786	630	92	4277	398.45

Table 3
Cost of the five collared lions each year (US$) by conservancy. Yearly costs reflect nightly costs multiplied by the number of lion nights (in parentheses) spent within each conservancy.

Hoanib group cost	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	total	μ annual cost
Otjikondavirongo										11.4 (1)	11.4 (1)	1.14
Sesfontein	1288.28 (113)	2348.54 (206)	34.2 (3)	741.04 (65)	900.65 (79)	216.91 (19)	364.82 (32)	1140.07 (100)	2280.13 (200)	1174.27 (103)	10488.62 (920)	1048.86
total	1288.28 (113)	2348.54 (206)	34.2 (3)	741.04 (65)	900.65 (79)	216.91 (19)	364.82 (32)	1140.07 (100)	2280.13 (200)	1185.67 (104)	10500.02 (921)	1050

Oruwao male cost	2012	2013	2014	2015	2016	total	μ annual cost
Anabeb					40.15 (4)	40.15 (4)	8.03
Puros		70.27 (7)	10.04 (1)			80.31 (8)	16.06
Sesfontein		722.76 (72)	80.31 (8)	813.10 (81)	933.56 (93)	2549.73 (254)	509.95
total	0.00	793.03 (79)	90.34 (9)	813.10 (81)	973.72 (97)	2670.19 (266)	534.04

XPL-73 cost	2010	2011	2012	2013	2014	total	μ annual cost
Puros			1234.71 (123)	883.37 (88)	953.64 (95)	3071.73 (306)	614.35
Sesfontein	240.92 (24)	732.80 (73)	1425.44 (142)	491.88 (49)	291.11 (29)	3182.15 (317)	636.43
total	240.92 (24)	732.80 (73)	2660.15 (265)	1375.25 (137)	1244.75 (124)	6253.87 (623)	1250.78

HPL-1 group cost	2016	2017	2018	total	μ annual cost
Ehi-Rovipuka	273.62 (24)	273.62 (24)		547.23 (48)	182.41
#Khoadi-//Hôas	45.6 (4)	535.83 (47)	45.6 (4)	627.04 (55)	209.01
total	319.22 (28)	809.45 (71)	45.6 (4)	1174.27 (103)	391.42

HPL-12 group cost	2016	2017	2018	total	μ annual cost
Ehi-Rovipuka	182.41 (16)	923.26 (81)	45.6 (4)	1151.47 (101)	383.82
#Khoadi-//Hôas	22.8 (2)	22.8 (2)		45.6 (4)	15.2
total	205.21 (18)	946.26 (83)	45.6 (4)	1197.07 (105)	399.02

greatest total number of collared lion nights (n = 2727) (Table 2). Out of a total 6295 collared lion nights, 4277 (67.9%) were recorded on government, government-concession, or privately controlled land, and the remaining 2018 nights (32.1%) were recorded on communal land (Table 2). The number of nights recorded for collared individual lions over the entire study period ranged from 668 (the female XPL-12) to 2791 (Hoanib pride female). Though four of the five collared lions spent only 14.0–32.9% nights on communal land, the male XPL-73 spent 52.1% of nights on communal land (Supporting Information).

Because lions are unevenly distributed across the landscape and highly mobile, the cost of lion presence is borne unequally by conservancies. Based upon recorded presence, the HPL-1 group of females cost the conservancies the least (total: US$ 1174.27, annually: US$ 391.42) while the Hoanib female group cost the most (total: US$ 10,500.02, annually US$ 1050) (Table 3). Lion use of communal land differed greatly from year to year. For example, in 2009, the Hoanib group spent 206 nights within the Sesfontein conservancy, representing an estimated opportunity cost of US$ 2348. The following year, the Hoanib group spent three nights in the Sesfontein conservancy, representing an estimated opportunity cost of US$ 34.2. Across the 11 years of data, Otjikandavirongo Conservancy recorded only one collared-lion night, and therefore had a total expected cost of only US$ 11.4. In contrast, 1625 collared-lion nights were recorded in Sesfontein Conservancy, totaling a cost of US$ 16,220. Sesfontein Conservancy also experienced the greatest average cost (US$ 1475/yr) and the single greatest year cost (2016: US$ 3214). In total, the five groups of lions cost the six conservancies an estimated US$ 21,795 over the 11-year period; a mean-average of US$ 1981 annually (Table 4).

Because movement data for the entire lion population was not available, we estimated the total costs to all six conservancies and for the region, using aggregate estimates based upon two different approaches (Table 5) (Supporting Information). First, the estimated lion density (0.48–0.62/100 km^2) (Namibia MET, 2017) across the six conservancies yields an expected number of 67–87 lions, and a female:male ratio of

Table 4
Total cost per conservancy from collared lions representing female groups and individual males. μ annual cost is the average across years where data were available.

conservancy cost	2008	2009	2010	2011	2012	2013	2014
Anabeb							
Ehi-Rovipuka							
#Khoadi-//Hôas							
Otjikandivirongo							
Puros					1235	954	964
Sesfontein	1288	2349	275	1474	2326	1431	736
Total	1288	2349	275	1474	3561	2385	1700
	2015	2016	2017	2018	total	μ annual cost	
Anabeb		40			40	4	
Ehi-rovipuka		456	1197	46	1699	154	
#Khoadi-//Hôas		68	559	46	673	61	
Otjikandivirongo			11		11	1	
Puros					3152	286	
Sesfontein	1953	3214	1174		16,220	1475	
total	1953	3778	2941	91	21,795	1981	

Table 5
Estimated total cost for all lions across all six conservancies. Annual presence on conservancy land based upon recorded minimum (14%), percentage of recorded time across all five collars (32.1%), recorded maximum (52.1%), and 100% presence. Density based upon estimated number of lions within all six conservancies (Namibia MET 2017). Estimated total population for all lions in northwest Namibia from Stander (2018).

annual presence	conservancy density (US$)	total population (US$)
14%	26,325–33,739	43,631–54,260
32.1%	60,360–77,341	100,039–124,419
52.1%	97,968–125,556	162,369–201,925
100%	188,039–240,991	311,649–387,572

5.5:1 (Stander, 2018) would predict a total of 55–71 females and 12–15 males, suggesting an overall cost ranging from US$ 46,237–59,687 per annum ($2618.92 \times 55 \times 0.321 = 46237.03$; $2618.92 \times 71 \times 0.321 = 59687.81$) for females, and US$ 14,123–17,654 per annum ($3666.5 \times 12 \times 0.321 = 14123.36$; $3666.5 \times 15 \times 0.321 = 17654.2$) for males, assuming the population spent 32.1% of nights on conservancy land.

Second, a female to male ratio of 5.5:1 combined with Stander's (2018) population estimate of between 112–139 individuals for the region, suggests a total of 91–113 females and 20–25 males, yielding overall annual costs of US$ 76,501–94,996 ($2618.92 \times 91 \times 0.321 = 76501.27$; $2618.92 \times 113 \times 0.321 = 94996.09$) for females, US$ 23,538–29,423 ($3666.5 \times 20 \times 0.321 = 23538.93$; $3666.5 \times 25 \times 0.321 = 29423.66$) for males, given 32.1% presence on conservancy land (Table 5). As with the prior calculation these values can be altered to reflect different presence on conservancy land, either by individuals, groups, or as estimates for the entire population (Table 5). With more comprehensive population data these estimates could be refined. A more complete accounting would also allow for meat consumption by cubs, juveniles, and subadults.

4. Discussion

The spatial data presented here show lion presence can be meaningfully differentiated by conservancy. By combining the monetary value of meat eaten with lion movement data, we have shown that the opportunity costs imposed by lions differ by conservancy. Though the costs of collared lions from this study would have been relatively small when compared to conservancy annual income (with the exception of Otjikandivirongo, which reported no income), total costs vary widely. For example, at low density (0.48 lions/100 km^2) and 14% lion presence, the opportunity cost for Anabeb Conservancy would have been 1.3% of annual conservancy income. In contrast, at high density (0.62 lions/100 km^2) and 52.1% lion presence, the opportunity cost for Ehi-Rovipuka Conservancy would have been 50.3% of annual conservancy income. Total cost estimates, based upon estimated lion density within the six conservancies or population size across the region, stratified by different lion occupancy, also demonstrate the effect of lion movements on the range of these costs. It is worth noting that these data record lion movements during years of drought, when livestock may be more at risk of being preyed-upon. During periods of greater or less rainfall, the ratio of livestock to wild prey losses will likely change, though our approach of deriving costs based on proportion of consumed prey will still be viable. However, more data are needed to assess the changes in such ratios.

As the data show, these collared lions spent the majority of their time on government and government-concession land. (Note here that, per their government-issued research permits, DLC and NLT primarily collar and monitor lions within government and government-concession land.) Historically, lion densities within government and government-concession lands have been greater than within communal areas (Stander, 2004). Given that lion prides maintain exclusive home ranges when possible (Packer et al., 1990; Packer and Pusey, 1997) it is reasonable to expect that lions whose home ranges fall primarily within communal land will spend more time within communal conservancies. This highlights the importance of generating more comprehensive lion movement data to refine the measurement of differentiated costs to different conservancies.

Efficient PES will be differentiated according to each conservancy's relative contribution to the lion population. As a proxy for conservation performance, lion movement is an imperfect measure. Though the approach we have outlined is not intended to replace other means of providing payments for living alongside lions, it does provide a framework for assigning lion conservation payments. By linking the movements recorded by satellite collars (or similar spatially explicit monitoring methods such as camera traps) with predation data, opportunity costs can be differentiated by conservancy. However, the collar data presented here may not represent a random sample of the overall population. If DPES are to accurately represent the differentiated opportunity costs of the entire population, a representative sample is needed. We present aggregated estimates (Table 5) merely to indicate the scale of payments necessary to cover the costs of all the lions in the region. When collar data capture a representative sample of the population, our approach could be implemented to deliver population-level DPES; contributing to a more complete measure of the cost of living with lions. Future estimates of the full costs of predation should also consider movements and wildlife consumption by other large predators, such as leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), brown hyena (*Hyaena brunnea*), and spotted hyena (*Crocuta crocuta*). Finally, note that "surplus killing," where predators kill greater numbers of prey than they consume, could further increase the total costs incurred by conservancies. Though lions in northwest Namibia have been recorded killing dozens or even hundreds of livestock in a single night (e.g., Hartmann 2017), always within livestock enclosures, Stander (2018) did not record instances of surplus killing of wild prey.

Improving metrics for linking social and ecological factors remains a challenge within the ecosystem services framework (Vaz et al., 2021), so too in large carnivore conservation. Our approach provides a way to incorporate relevant environmental, social, and economic factors into a variety of potential DPES program, serving as a proof of concept. The four stages we have adapted from Aguilar-Gómez et al. (2018) (Fig. 1) could similarly be applied to assessing the opportunity costs of living with other wildlife species, where environmental information such as movement data, and monetary values of resources are available, such as consumption of browse and grasses by large herbivores that would otherwise be available to livestock, or loss of timber stocks to elephants. Our approach for assigning monetary value to prey species could also be applied to other socioeconomic contexts such as high-value trophy hunting, where the price of each prey animal would be adjusted upwards to reflect trophy, rather than meat, value. Alternatively, the value of each prey species could be reduced where communities derive no direct benefits from consumptive utilization, while still linking these animals to other forms of monetary valuation, e.g., receipts from photo-tourism. Furthermore, by emphasizing a community's successful conservation performance (Zabel and Holm-Müller, 2008), our approach could complement existing approaches to mitigate HLC and provide a broader perspective on wildlife as economic actors within multi-use landscapes. Finally, lion movement data can provide greater insight into high and low value landscape features for lions (Mosser et al., 2009; Mosser et al., 2015). Where more comprehensive data on habitat use are available, DPES approaches for conserving landscape features and processes could then be implemented using GIS.

Our approach addresses the guidelines for designing ideals PECs to foster human-carnivore coexistence (Dickman et al., 2011). It works towards identifying costs based upon lion presence within differentiated areas. When paired with offset and HLC mitigation programs (e.g. Lion angers, 2020), our approach can reduce costs, provide the framework for additional revenue, and link potential payments to desired outcomes. By emphasizing the ideal scenario of lions capturing wild prey, this approach is more likely to reduce human poverty than would offsets for lost income. It provides an objective metric for developing appropriately scaled and efficient financial support. Additional revenue can be made available through partnerships with donors and tourism operators, such as one already being adapted based-upon an existing wildlife credits program (Community Conservation Namibia 2019). We do not regard moral hazards or perverse incentives as pertinent. If scaled up to encompass the entire lion population, our approach may help combat local poverty.

While existing scholarship linking ecosystem services and opportunity costs focuses on landscape-use transformations (Ruijs et al., 2017; Schröter et al., 2014), our approach reveals the need to account for the spatial differentiation of opportunity cost within a given system. Other opportunity costs, such as time spent herding, or time and money spent constructing enclosures (kraals), have proven difficult to quantify. In northwest Namibia, livestock herding often occurs by young children and adolescents who otherwise earn no income. Enclosures are often constructed of available woody materials or, when they are made of 'modern' materials such as metal and chain-link, are donated by local NGOs. Furthermore, herding and kraals are infrequently relied upon, due to seminomadic pastoral movements and unwillingness to place livestock in enclosures during certain periods of limited rainfall (J.H., pers obs).

5. Conclusion

Our DPES approach incorporates environmental, social, and economic factors in a spatially explicit format that rewards conservation performance, utilizes types of data available in other conservation scenarios, and provides a system for designing efficient community benefits. We have shown that existing but heretofore disparate environmental (lion movement and predation), social (conservancy boundaries and benefit legislation) and economic (prey values) data can be creatively combined to link the array of costs of living with lions to potential benefits. Because they are unevenly distributed across the landscape, lions spend unequal amounts of time in different conservancies. The realized and opportunity costs of living with lions are thus spatially differentiated. For PES to be efficiently allocated among communities living with lions, payments must be spatially differentiated. When it comes to supporting communities living alongside lions, payments are themselves an end. But when it comes to increasing tolerance for living with lions, payments or other incentives are a means. The importance of diverse conservation payment mechanisms to locals living alongside potentially destructive wildlife has been underscored by the dramatic slowdown in global tourism from the COVID-19 pandemic (Lindsey et al., 2020). Though monetary incentives may not, on their own, lead to full tolerance of living with lions (Dickman et al., 2014), incentives covering a broader array of the costs of coexistence may *improve* tolerance while helping to support a wider array of human-wildlife conflict mitigation measures (Barua et al., 2012; de la Torre et al., 2021). As long as HLC is the key direct driver of lion mortality, innovating approaches to support local tolerance of lions may have important conservation outcomes. Our approach to DPES can also be adapted to a variety of other wildlife and land-use settings where spatial data, relevant boundaries, and monetary values are known.

6. Consent to participate

All authors consented to participate.

7. Consent to publish

All authors consented to publication.

8. Code availability

Not applicable.

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Ethical statement

Data were collected under relevant permits provided by the Namibia Ministry of Environment, Forestry and Tourism.

Authors contributions

All authors contributed to article write-up. KD created maps. JH performed statistical analyses.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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