Using an energetic cost–benefit approach to identify ecological traps: the case of the African wild dog

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Abstract

In a natural environment, there are high-quality habitats that produce a surplus of animals (sources), facilitating migration into low-quality habitats in which mortality exceeds natality (sinks). Human alterations can increase the attractiveness of a low-quality habitat and/or decrease the suitability of a high-quality habitat, herewith creating an ecological trap. In an ecological trap, animals prefer to stay in habitats where mortality exceeds natality, which can result in extirpation of a population. It is important to distinguish ecological traps from sinks; however, relative population densities do not necessarily give reliable information. In order to identify ecological traps and set appropriate conservation priorities, it is necessary to gain insight into the relationship between habitat preference, quality and suitability. In this study, we used African wild dog hunt data and energetic cost–benefit analysis to determine whether the preferred habitat outside Hwange National Park (HNP) serves as an ecological trap. This analysis enabled us to take several ecological factors into account while assessing habitat quality. Although outside HNP anthropogenic mortality exceeded natality, per capita energetic intake was higher. This indicates that the habitat outside HNP serves as an ecological trap where human alterations have decreased the suitability of the high quality habitat. In order to ensure the recovery of the African wild dog population, conservation efforts should therefore focus on improving the suitability of the habitat outside HNP. This study shows that an energetic cost–benefit analysis can assist with identifying ecological traps and setting conservation priorities. Moreover, in cases of social territorial species, the cost–benefit analysis may also help to identify ecological traps before source populations are depleted, thus increasing the likelihood of population recovery.

Introduction

Demographic variations are associated with differences in habitat quality, with a surplus of animals (natality > mortality) in good-quality habitat and a deficit of animals (natality < mortality) in low-quality habitat (Donovan *et al.*, 1995; Gaona, Ferreras & Delibes, 1998; Vierling, 2000). These variations lie at the basis of classic source–sink theory which predicts immigration of animals from good-quality (source) habitat into lower-quality (sink) habitat when there is not enough source habitat available (Pulliam, 1988). Human activity often reduces habitat quality, which can result in the creation of sinks (Donovan *et al.*, 1995; Gaona *et al.*, 1998; Woodroffe & Ginsberg, 1998; Vierling, 2000). As long as the sink population is maintained by continued immigration from the source, both populations can persist (Pulliam, 1988).

Sometimes, human alterations increase the attractiveness of low-quality habitat (Schlaepfer, Runge & Sherman, 2002), decrease the suitability of high-quality habitat (Delibes, Gaona & Ferreras, 2001) or both (Robertson & Hutto, 2006), herewith creating an equal preference or severe ecological trap (Delibes *et al.*, 2001; Robertson & Hutto, 2006). Equal preference traps occur when the attractiveness of low-quality habitat becomes similar to previously selected high-quality habitat, making it equally likely for animals to settle in low- or high-quality habitat (Robertson & Hutto, 2006). A severe trap occurs when the attractiveness of low-quality habitat or the suitability of high-quality habitat is changed in such a way that animals prefer low-quality habitat over high-quality habitat (Robertson & Hutto, 2006). Within an ecological trap, animals migrate into the sink despite there being enough source habitat available (Kristan, 2003; Battin, 2004). Both

equal preference and severe traps can result in a population decline (Delibes *et al.*, 2001; Robertson & Hutto, 2006). However, the rate of decline is faster in a severe trap, making it more difficult to recognize this kind of ecological trap in time to prevent extirpation (Delibes *et al.*, 2001; Robertson & Hutto, 2006).

Because ecological traps can results in extirpation (Delibes *et al.*, 2001; Kokko & Sutherland, 2001; Kristan, 2003), it is important to be able to differentiate them from sinks. Relative population densities do not necessarily give reliable information (Battin, 2004; Robertson & Hutto, 2006); for example, while there is continuous immigration from the source into the trap, the decline will affect the source first and might not affect the trap for some time; when densities are under the carrying capacity, it is even possible that the population in the trap initially increases (Delibes *et al.*, 2001). In that case, ecological traps are only detected when the source is depleted, making population recovery difficult (Delibes *et al.*, 2001). In addition, reproductive output cannot be used as a surrogate for habitat quality because it might be counterbalanced by compensating effects on survival (Schlaepfer *et al.*, 2002; Battin, 2004). Therefore, to distinguish ecological traps from sinks and correctly manage a habitat, additional knowledge of the relationship between habitat preference, quality and suitability is necessary (Kokko & Sutherland, 2001; Kristan, 2003).

A previous study by Van der Meer *et al.* (2013*a*) showed that, within several years, African wild dog packs in Hwange National Park (HNP) moved their territories closer to or beyond the parks border into the surrounding buffer zone where anthropogenic mortality was so severe it exceeded natality (Van der Meer *et al.*, 2013*a*). The African wild dog is an endangered, wide-ranging, social carnivore that hunts and breeds in packs (Woodroffe, Ginsberg & Macdonald, 1997). African wild dogs are territorial and, although boundaries are not actively defended (Grant, Chapman & Richardson, 1992), territories are spatially exclusive with strong temporal avoidance in cases where overlap occurs (Parker, 2010). Therefore, relative African wild dog densities might not be a reliable indicator of habitat quality as, until such a pack is extirpated, small packs can occupy high-quality territories and prevent immigration from larger packs into preferred habitat. Until the source is affected, an African wild dog sink might thus appear to be part of a source–sink system while in actual fact it serves as an ecological trap.

In this study, we revisited our data and used an energetic cost–benefit analysis to gain insight in habitat quality, and the possible discrepancy between habitat quality and habitat suitability, for African wild dogs inside and outside HNP. Several ecological factors have been suggested to play a role in habitat selection of African wild dogs in the Hwange system, for example hunting success (Van der Meer *et al.*, 2013*b*) and kleptoparasitism (Van der Meer *et al.*, 2011). The presented energetic cost–benefit analysis enabled us to bring these ecological factors together and determine its importance. Based on our results, we discuss whether the presented analysis can help to differentiate sinks from eco-

logical traps before the source is depleted and how an energetic cost–benefit analysis assists in setting conservation priorities.

Materials and methods

Study area

HNP covers *c*. 15 000 km^2 in northwest Zimbabwe (19°00′S, 26°30′E). The Hwange region is classified as semi-arid with a mean annual rainfall of 606 mm and a wet season from October to April. Vegetation consists of scattered woodland scrub mixed with grassland. Data were collected along the northern boundary in an area of 5500 km^2, covering part of HNP and its periphery. HNP is a protected wildlife area, without human settlements or main roads. The buffer zone outside HNP is designated for photographic safaris and trophy hunting, with human settlements and a main tar road. African wild dogs experience a high level of anthropogenic mortality outside HNP (Rasmussen, 1997; Van der Meer *et al.*, 2013*a*). As a result, African wild dog densities in and around HNP decreased, from *c*. 150–225 individuals in 1997 (Rasmussen, 1997; Woodroffe *et al.*, 1997) to *c*. 50–70 individuals in 2009 (Zimbabwe Parks and Wildlife Management Authority, 2009; Blinston, Rasmussen & Van der Meer, 2010).

Hunt follows

Hunt follow data from 22 radio-collared African wild dog packs were collected by G.S.A.R. between 1991 and 2002 (study duration 7–72 months per pack). For a detailed overview of the method used see Rasmussen *et al.* (2008) or Van der Meer *et al.* (2013*b*).

Analysis

To compare energetic costs and benefits for African wild dogs inside versus outside HNP, we calculated energetic gain during a successful hunt based on the carcass energetic value of the prey species killed. We calculated energetic costs (chasing + walking + resting) plus losses because of kleptoparasitism. Based on the energetic gain, costs and losses, we determined daily per capita energetic intake for a pack of a given size. Previous analyses provided several parameters for our calculations (Rasmussen *et al.*, 2008; Rasmussen, 2009; Van der Meer *et al.*, 2011, 2013*b*).

We used linear mixed effects models with pack identity as a random factor to test for relationships between the dependent variable (hunt periods per day, hunt period time, energetic gain, energetic costs) and season (denning or nomadic), inside or outside HNP, and pack size. For the analysis of binomial variables (presence of kleptoparasites), we used generalized linear models with binomial distribution and logit link. We tested for differences inside versus outside HNP by including the two-way interactions inside or outside HNP × season and inside or outside HNP × pack

size. As preliminary analysis showed no effect of these inter-actions, they were left out of the final models. To determine whether the costs of a hunt depended on the outcome of the chase, whether or not a chase resulted in a kill was added to the model. With the lack of agreement on the best model approach to analyze behavioral data (Murtaugh, 2009), we decided to present full models.

We used two-tailed Pearson's correlations to test whether the energy an African wild dog spent, gained and lost changed over the study years inside or outside HNP. Statistical analyses were performed using SPSS software release 20.0 (SPSS Inc., Chicago, IL, USA).

For the cost–benefit calculations, we determined the relationship between pack size and energetic costs of chasing, and pack size and gain during a successful chase for the different seasons by seeking best fit regressions using GraphPad Prism version 6.02 (GraphPad Software Inc., La Jolla, CA, USA). We used Akaike information criteria corrected for small sample size (AICc) to determine the best model fit, with the smallest value representing the best fit. A t-test was used to test whether there was a difference in per capita daily gain and energetic costs of resting, successful hunts, failed hunts and kleptoparasitism inside and outside HNP.

Hunt periods per day and hunt period time

For the analysis of the number of hunt periods per day and time spent hunting, pack size was defined as the number of adults + yearlings + pups in the nomadic season (n_{AYP}) and the number of adults + yearling in the denning season (n_{AY}) (Rasmussen et al., 2008). In accordance with Rasmussen et al. (2008), number of hunt periods per day depended on pack size ($F_{1,218} = 5.17$, $P = 0.02$) and season ($F_{1,227} = 3.93$, $P = 0.05$). We therefore based number of hunt periods per day on the same values (nomadic: hunt periods per day = $0.27 + 0.14 \times n_{AYP} - 0.006 \times n_{AYP}^2 + 0.000083 \times n_{AYP}^3$, denning: hunt periods per day = $0.16 + 0.23 \times n_{AY} - 0.014 \times n_{AY}^2 + 0.00028 \times n_{AY}^3$) (Rasmussen et al., 2008). Pack size and whether the hunt took place inside or outside HNP did not affect hunt period time. In accordance with Rasmussen et al. (2008), hunt period time depended on season ($F_{1,428} = 5.71$, $P = 0.02$) therefore, we used the same values (nomadic: 2.20 h, denning: 2.51 h) (Rasmussen et al., 2008).

Hunting costs

Chase distances ($n = 132$) were multiplied by 1.3 to allow for zigzagging (Rasmussen et al., 2008). African wild dogs spent 15 156.66 KJ km^{-1} chasing its prey (Rasmussen, 2009). To determine energetic expenditure during the chase, chase distance (kilometer) was multiplied by 15 156.66 KJ. Time spent walking was calculated by dividing chase distance (kilometer) by 60 km h^{-1}, the maximum speed at which African wild dogs chase prey (Creel & Creel, 1995; Woodroffe et al., 1997), and subtracting this value from the hunt period time. African wild dogs spent 3119.40 KJ h^{-1} walking (Rasmussen et al., 2008). Time spent walking was
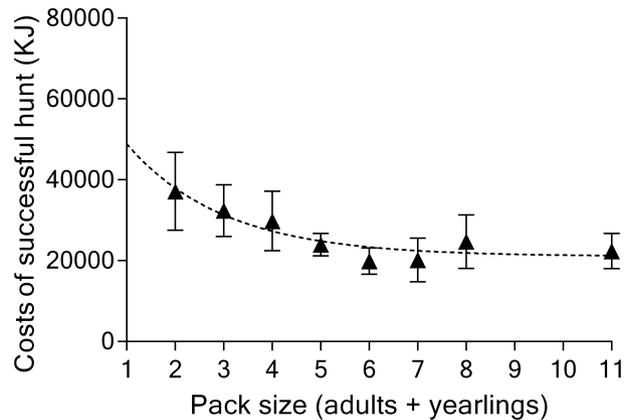

Figure 1 Energetic costs of a successful hunt (energy spent chasing + energy spent walking) in relation to pack size (costs = 21 027 + (45 766 × exp$^{(-0.4973*pack\ size)}$).

multiplied by 3119.40 KJ to determine energy spent walking. Total energetic costs of a hunt period were calculated by adding the energy spent walking and chasing.

Previous analyses show that hunting success is determined by whether the chase takes place inside or outside HNP (inside HNP 62.9% success, outside HNP 78.4% success) but not by season or pack size (Van der Meer et al., 2013b). Hunting costs were calculated by adding the costs of chasing and walking and depended on whether or not the hunt was successful ($F_{1,126} = 6.70$, $P = 0.01$) [successful: chase = $18\ 638.55 \pm 2037.83$ KJ ind^{-1} hunt^{-1}, walking = 7414.05 ± 46.05 KJ ind^{-1} hunt^{-1} (mean $\pm$ SE); failed: chase = 9267.72 ± 1677.13 KJ ind^{-1} hunt^{-1}, walking = 7431.47 ± 88.19 KJ ind^{-1} hunt^{-1} (mean $\pm$ SE)]. The costs of failed hunts did not depend on pack size, season or whether the chase took place inside or outside HNP; we therefore used a mean value in the calculations (mean $\pm$ SE = $16\ 699.19 \pm 1659.85$ KJ ind^{-1} hunt^{-1}). Costs of successful hunts depended on pack size ($F_{1,47} = 3.29$, $P = 0.05$), but was not affected by season or whether the chase took place inside or outside HNP. An exponential one-phase decay fit provided the best model for the costs of successful hunts in relation to pack size (Fig. 1) and was used in the final calculations.

Gain

We based kilojoules gained during successful hunts ($n = 127$) on prey mass-related energetic values (see Rasmussen et al., 2008). Prey mass was divided by the number of individuals feeding from the carcass (nomadic season: adults + year-lings + pups, denning season: adults + yearlings + in cases where pups were feeding from the carcass, pups weighed by a factor 0.5) and multiplied by the energetic value of the prey killed (KJ kg^{-1}) to calculate per capita kilojoules gained. The maximum stomach capacity of African wild dogs was set at 10 kg (Rasmussen et al., 2008).

Energetic gain on successful hunts depended on pack size (adults + yearlings) ($F_{1,122} = 22.81$, $P < 0.001$) and season
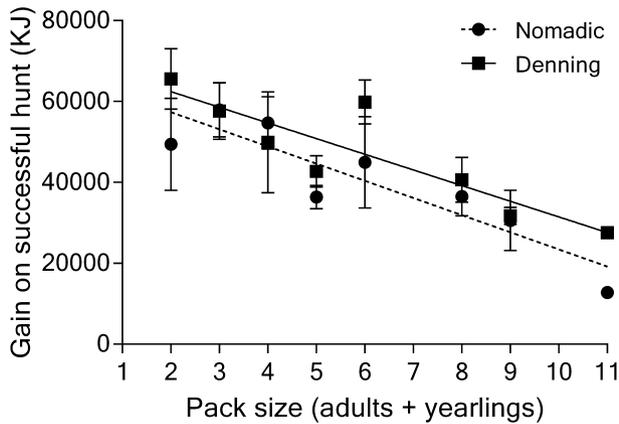
Figure 2 Energetic gain from the prey item killed during a successful hunt per season in relation to pack size (adults + yearlings), gain$_{nomadic}$ = 65 854 + (–4242 × pack size), gain$_{denning}$ = 70 194 + (–3873 × pack size).

($F_{1,122}$ = 3.67, P = 0.05). A straight line fit provided the best model for gain in relation to season and pack size (Fig. 2) and was used in the final calculations.

Losses because of kleptoparasitism

Losses because of kleptoparasitism were taken into account by calculating per capita food intake for a given pack size, before lions or spotted hyenas stole the kill, using the following equation by Carbone *et al.* (2005):

$$\text{Carcass intake} = (\text{CEV}/\text{N})\left(1 - e^{-6808(\text{N}/\text{CEV})\text{tk}}\right)$$

Carcass intake is measured in kilojoules, with N being the number of individuals feeding from the carcass (nomadic season: adults + yearlings + pups, denning season: adults + yearlings + in cases where pups were feeding from the carcass, pups weighed by a factor 0.5), CEV is the total energetic value of the carcass and tk is the time before kleptoparasites steal the kill (min). When intake exceeded stomach capacity, total energetic value of the carcass was set at 10 kg multiplied by the energetic value (KJ kg^{-1}) of the prey species killed. Kilojoules lost to kleptoparasites were calculated by subtracting per capita carcass intake before the kill was stolen, from the number of kilojoules an African wild dog could have gained if it had not been stolen. Negative values meant the pack was able to devour the carcass before kleptoparasites arrived and were set to zero.

In accordance with Van der Meer *et al.* (2011), the presence of kleptoparasites depended on whether the kill was made inside or outside HNP ($P < 0.001$), but not on pack size or season. The risk of kleptoparasitism was thus based on previous analysis (inside HNP: spotted hyenas 6.28%, lions 3.14%, outside HNP: spotted hyenas 2.66%, lions 0.00%) (Van der Meer *et al.*, 2011). Losses because of kleptoparasitism depended on whether the kill was made inside or outside HNP ($F_{1,13}$ = 4.08, P = 0.05), but not on pack size or season. Therefore, mean values for losses inside (mean ± SE = 39 639.18 ± 8408.52 KJ ind^{-1} hunt^{-1}) and outside HNP (mean ± SE = 10 838.08 ± 6072.43 KJ ind^{-1} hunt^{-1}) were used in the final calculations.

Cost–benefit calculations

Calculations were made per season, for pack sizes of 2–11 adults + yearlings (pack sizes for which the outcome of a sufficient number of chases was known), inside and outside HNP.

With 92% of the packs inside HNP and 93% of the packs outside HNP consisting of 2–11 adults + yearlings, this gives a reliable reflection of the situation in the study area. Packs (adults + yearlings) ≤ 5 den for 112 days, packs > 5 den for 84 days (Rasmussen *et al.*, 2008). To determine the number of hunts per season per pack size, the number of days denning and nomadic for a given pack size were multiplied by the season-dependent number of hunt periods per day for this pack size. Based on a chase success of 62.9% inside HNP and 78.4% outside HNP (Van der Meer *et al.*, 2013*b*), we calculated the number of successful and failed hunts per season per pack size inside and outside HNP. The number of failed hunts was multiplied by the energetic costs of failed hunts. The number of successful hunts was multiplied by the pack size-dependent costs of successful hunts (Fig. 1). Energetic costs of resting were determined by multiplying the number of hunt periods per season per pack size by the season-dependent hunt period time. This figure was subtracted from 24 h and multiplied by 217.5 KJ (the energy African wild dogs spent per hour resting, see Gorman *et al.*, 1998) and the pack size-dependent number of days in a season to determine the costs of resting per season per pack size. Losses because of kleptoparasitism were calculated based on the number of successful hunts per season per pack size inside and outside HNP, with a kleptoparasitism risk of 9.42% inside HNP and 2.66% outside HNP (Van der Meer *et al.*, 2011). The number of kleptoparasitized hunts per season per pack size inside and outside HNP was multiplied by mean energetic losses because of kleptoparasitism inside and outside HNP.

Energetic intake was calculated per season by subtracting the costs of resting, successful and failed hunts and losses because of kleptoparasitism from the gain. Intake in the denning season was added to intake in the nomadic season and divided by 364 to determine daily energetic intake per African wild dog, in a pack of a given size, inside and outside HNP.

Results

The energy an individual African wild dog spent, gained and lost because of kleptoparasitism inside or outside HNP did not change over the study years (all $P > 0.05$). Regardless of pack size, daily per capita intake was higher outside HNP (Fig. 3). On average, inside HNP packs did not gain energy, while outside HNP packs ≤ 8 individuals did. A pack of five seemed to be an optimal size for maximized per capita intake. For African wild dogs, the chase is the most ener-

getic costly part of the hunt (Rasmussen *et al.*, 2008), with failed chases being shorter than successful chases (Van der Meer, 2011), the majority of the energetic costs were related to successful hunts.

Outside HNP, energetic gain ($t_{(18)} = -3.57$, $P < 0.01$) and intake ($t_{(18)} = -2.70$, $P = 0.02$) were higher so were the energetic costs of successful hunts ($t_{(18)} = -5.60$, $P < 0.01$). There was no difference in the energetic costs of resting ($P > 0.05$). Energetic costs of failed hunts ($t_{(18)} = 4.66$, $P < 0.01$) and kleptoparasitism ($t_{(9.17)} = 11.60$, $P < 0.01$) were lower outside HNP. Both inside and outside HNP losses because of kleptoparasitism were relatively low (0.53–9.19% of the daily energetic costs). For an overview of mean values of energetic costs and benefits, see Table 1.

Discussion

The presented energetic cost–benefit calculations are by no means flawless, for example they do not take into account costs of hunts at which chases were not initiated, costs of regurgitation or costs of defense of kills against

kleptoparasites. We do feel that the calculations nevertheless give an indication of differences in habitat quality and would therefore like to draw some conclusions.

Animals generally utilize habitats in which they yield the highest rate of energy (Rosenzweig, 1991). However, an animal establishing a territory is unlikely to be able to predict the energetic costs and benefits the territory provides. Instead, animals base their choice on physical characteristics (settlement cues) that reflect habitat quality (Schlaepfer *et al.*, 2002; Kristan, 2003; Fig. 4). In this study, African wild dogs that move their territory outside HNP, indeed, showed a preference for habitat in which they yield the highest rate of energy. With no differences in prey densities and hunting parameters (Van der Meer *et al.*, 2013*b*), this preference seems to be based on settlement cues that are related to a higher hunting success (Van der Meer *et al.*, 2013*b*) and a smaller chance of interspecific competition outside HNP (Van der Meer *et al.*, 2011). With interspecific killing by lions being a common cause of death (Woodroffe *et al.*, 1997), African wild dogs perceive lions as an immediate predation risk (Webster, McNutt & McComb, 2012) which they actively avoid (Cozzi *et al.*, 2013; Vanak *et al.*, 2013). Although within our study energetic losses because of kleptoparasitism were relatively little, a higher risk of (aggressive) interactions with lions (Van der Meer *et al.*, 2011, 2013*a*) might nevertheless have influenced African wild dog habitat preference.

Habitat preference of African wild dogs for the buffer zone outside HNP is based on sound ecological cues but because of human interference, these cues are no longer associated with the anticipated fitness outcome. Despite a higher reproductive output outside HNP, anthropogenic mortality is so high it exceeds natality (Van der Meer *et al.*, 2013*a*), turning the buffer zone into unsuitable habitat. However, African wild dogs perceive this unsuitable habitat as the more attractive habitat in which they prefer to establish territories. A preference for unsuitable habitat indicates this habitat serves as an ecological trap rather than a sink (Kristan, 2003; Battin, 2004; Fig. 4). The higher habitat quality and unidirectional movement of African wild dog territories outside HNP (Van der Meer *et al.*, 2013*a*) further suggest a severe ecological trap rather than an equal preference trap.
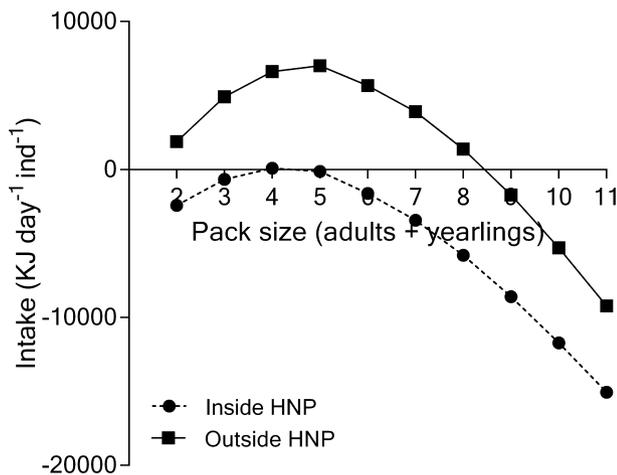

Figure 3 Per capita energetic intake in relation to pack size (adults + yearlings) inside Hwange National Park (Inside HNP) and in the trap habitat in the buffer zone outside HNP (Outside HNP).

Table 1 Mean per capita values for the daily energetic costs, benefits and intake for African wild dogs inside and in the trap habitat outside Hwange National Park (HNP)

| Energetic values (KJ ind^{-1} day^{-1})		Benefits	Costs				Balance
		Gain	Resting	Successful hunt	Failed hunt	Kleptoparasitism	Intake
Inside HNP	Mean	22 440.31	4745.87	14 489.55	5902.07	2237.49	−4934.66
	SE	969.17	36.18	399.31	457.70	173.51	1662.62
	Minimum	16 573.33	4607.91	12 863.97	3338.34	1265.57	−15 063.17
	Maximum	25 931.29	4950.42	16 479.42	7649.30	2899.87	91.11
Outside HNP (Trap)	Mean	27 970.12	4745.87	18 060.10	3436.25	215.32	1512.59
	SE	1207.99	36.18	497.71	266.48	16.70	1710.54
	Minimum	20 657.38	4607.91	16 033.95	1943.61	121.79	−9223.41
	Maximum	32 321.35	4950.42	20 540.32	4453.50	279.06	7012.51
Significant difference		Yes	No	Yes	Yes	Yes	Yes
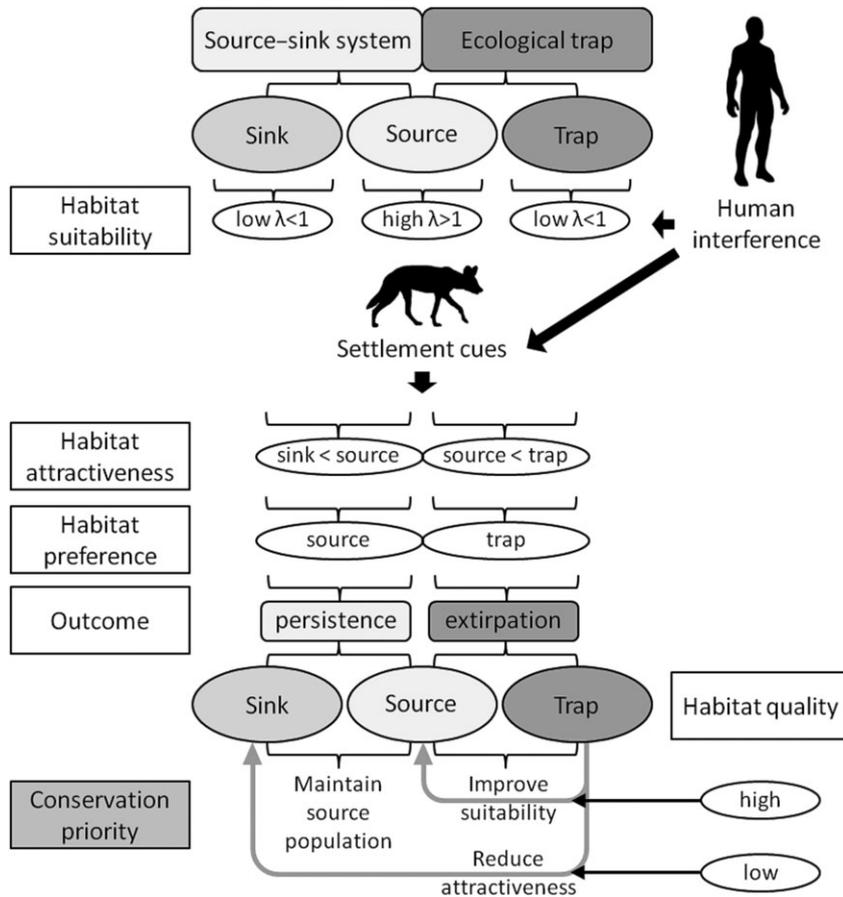
Figure 4 Graphical representation of the relationship between habitat suitability, attractiveness and preference in a source–sink system and a severe ecological trap. Sinks occur when unsuitable habitat is avoided. Traps occur when, because of human interference, the suitability of high-quality habitat is decreased and/or settlement cues have changed so that the attractiveness of low-quality habitat is increased and unsuitable habitat is preferred. In a source–sink system, conservation efforts should focus on maintaining the source population. Depending on the quality of the trap habitat, in an ecological trap, conservation efforts should either focus on improving the suitability of high-quality trap habitat or reducing the attractiveness of low-quality trap habitat.

Ecological traps occur when human alterations decrease the suitability of high-quality habitat (Delibes *et al*., 2001; Robertson & Hutto, 2006) and/or change settlement cues so that the attractiveness of low-quality habitat increases (Schlaepfer *et al*., 2002; Robertson & Hutto, 2006; Fig. 4). Within the buffer zone of HNP, high anthropogenic mortality did not only reduce suitability (Van der Meer *et al*., 2013*a*), it may have also simultaneously increased attractiveness, as because of trophy hunting, lion densities in the buffer zone were very low (2.7 lions per 100 km^2 inside HNP, 0.06 lions per 100 km^2 outside HNP) (Davidson, 2009). With smaller carnivores trying to avoid interspecific competition with larger predators (Fedriani *et al*., 2000; Linnell & Strand, 2000), an ecological trap where anthropogenic mortality decreases suitability of a buffer zone surrounding a protected area, while at the same time increasing its attractiveness by anthropogenic elimination of larger competitors, might be relatively common.

Because ecological traps can result in extirpation of a species (Delibes *et al*., 2001; Kokko & Sutherland, 2001; Kristan, 2003), it is important to detect them at the earliest possible stage, as once the source becomes depleted population recovery is increasingly difficult (Delibes *et al*., 2001). Especially for social territorial animals such as African wild dogs, an energetic cost–benefit analysis in combination with

information on relative densities could assist with an early detection of a trap. Before the source is affected, small packs occupy preferred territories in the trap habitat and relative densities are likely to be lower in the trap habitat outside HNP. If based on energetic costs and benefits, the habitat with the low density is the high-quality habitat, this might indicate that this habitat serves as an ecological trap; as within a classic source–sink system, high-quality habitat is expected to hold high population densities (Pulliam, 1988). If additional demographic data show that within the high-quality habitat mortality exceeds natality, this further suggests it serves as trap habitat and conservation action needs to be taken accordingly.

An energetic cost–benefit analysis can also help to determine conservation priorities (Fig. 4). When setting conservation priorities, it is important to be able to identify high-quality habitat, as failure to do so can influence the ability of the population to reach its maximum size (Gilroy & Sutherland, 2007). Within a natural heterogeneous environment, high-quality habitats (source) provide a surplus which facilitates migration into low-quality habitats (sink) (Pulliam, 1988). Although sinks can promote larger population sizes and longevity, they cannot persist without continued immigration from the source (Howe, Davis & Mosca, 1991; Dias, 1996). It is therefore important to focus

conservation efforts on source habitats as without them the population as a whole will not survive (Howe *et al.*, 1991; Dias, 1996).

Contrary to a source–sink system, within an ecological trap, the source population cannot sustain the trap population because of an animal's preference for trap habitat, ultimately resulting in local extinction (Delibes *et al.*, 2001; Kokko & Sutherland, 2001; Kristan, 2003). Within an ecological trap, conservation efforts should therefore focus on trap habitats. The quality of the trap habitat can assist in determining the cause of action. If the quality is high but the trap habitat has become unsuitable because of human alterations, the focus should be to improve suitability, which could potentially turn the trap into a source. If the quality of the trap habitat is naturally low but human interference has increased its attractiveness, conservation efforts should focus on reducing the attractiveness of the trap, which would turn it into a sink (Fig. 4).

In the case of the African wild dogs in HNP, conservation efforts should focus on improving suitability and reducing the attractiveness of the buffer zone. In 2005, a moratorium on trophy hunting of lions was implemented outside HNP. This has resulted in an increase in the lion population and relative lion densities have become similar inside and outside HNP (Davidson, 2009), which might have reduced the attractiveness of the trap habitat. Increasing habitat suitability by preventing anthropogenic mortality in the buffer zone is therefore likely to ensure a relative quick recovery of the African wild dog population.

Although an energetic cost–benefit analysis in combination with demographic data assists to detect ecological traps and set conservation priorities, additional insight in possible settlement cues (e.g. carnivore and prey densities) is useful. When energetic losses because of kleptoparasitism are low, energetic cost–benefit calculations underestimate the role of competing carnivores by not taking the risk and impact of aggressive interactions into account. Relative densities of competing carnivores might therefore be a better indicator. However, prey densities were not an indicator of differences in hunting success. Furthermore, although this was not the case in this study, a higher hunting success could be negatively balanced by longer chase distances or smaller prey items. Therefore, an energetic cost–benefit analysis might be the only way to reliably detect differences in foraging efficiency. The effort and resources needed to collect sufficient data to carry out such an analysis depend on the number of study packs, distribution of pack sizes, terrain and sample intensity. Although it might not be necessary to collect data for several succeeding years, it is necessary to at least follow one reproductive cycle to collect demographic data on annual reproduction and mortality.

Acknowledgments

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