Spotted hyaena survival and density in a lion depleted ecosystem: the effects of prey availability, humans and competition between large carnivores in African savannahs

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Abstract

Interspecific competition between large carnivores is not well understood due to the complexity of carnivore guild dynamics and the array of ecological and human factors affecting them. The loss of a carnivore guild's dominant species can therefore provide considerable insights. We evaluated spotted hyaena density and demography from Zambia's Liuwa Plain National Park, a recovering ecosystem where the hyaena's main competitor, the African lion, was severely reduced to 3-5 animals. Using data from 233 individuals in five clans and mark-resight robust design models we estimated population size, density, age and sex-specific annual survival rates for the hyaena population from 2010-2013 and tested for the effect of human settlements, prey density, competition with lions and hyaena clan size on mean hyaena survival. We estimated a minimum density of 0.13 hyaenas/km² and maximum density of 0.52 hyaenas/km². Density fluctuated with seasonal migrations of the main prey species, the blue wildebeest. Mean annual survival across all age classes was 0.93 (95%CI: 0.39 - 0.99). With high survival rates across all sex and age classes, we found no detectable effects of ecological or anthropogenic factors on survival. These results suggest that the combination of abundant prey, weak human-carnivore conflict, and weak competition from lions provide very favourable conditions for hyaena survival. Additional investigations of hyaena demography concurrent with lion population recovery efforts can provide considerable insights into the dynamics of carnivore competition and predation in African savannahs and the human and ecological factors affecting them.

Keywords: Spotted hyena; African lion; Survival; Robust design; Anthropogenic effects; Intraguild competition.

1. Introduction

Large carnivores have strong direct and indirect influences on ecosystem structure and function (Estes et al., 2011; Terborgh, 2010); however these apex predators are typically low-density, wide-ranging, elusive and sensitive to a wide array of human impacts (Woodroffe and Ginsberg 1998; Brashares et al 2001). As a consequence large carnivores are extinction-prone and require large areas with sufficient ecological integrity to provide adequate prey and minimize human impacts (Cardillo et al. 2004, Creel et al. 2013). With global declines accelerating (Ripple et al. 2014) demographic data on large carnivore populations is of critical importance. Interspecific competition has long been considered an important factor for large carnivore population dynamics (Creel, 2001; Linnell and Strand, 2000), but is not well understood and hindered by ongoing population declines, loss of intact large carnivore guilds, and the complexity of competitive relationships and how they can be impacted by biological, environmental and anthropogenic factors (Finke and Denno, 2005; Polis and Holt, 1992). Understanding how interspecific competition limits large carnivores is an important component of management and conservation of these species in the face of global carnivore declines (Palomares and Caro, 1999).

The spotted hyaena (*Crocuta crocuta*; hereafter hyaena) is widely regarded as one of Africa's most successful carnivores, inhabiting diverse habitats, persisting in areas facing anthropogenic pressures and attaining high densities in areas with high prey availability (Kruuk, 1972; Mills, 1990; Cardillo et al., 2004, Watts and Holekamp 2008, 2009; Périquet et al., 2015a; Bohm and Honer, 2015). The hyaena's importance to conservation efforts cannot be understated as it is often the last member of the African large carnivore guild to remain in an ecosystem after other species have been eliminated. Within the diverse large carnivore guilds that typify savannah ecosystems in sub-Saharan Africa, the dominant carnivore species, primarily the hyaena and African lion (*Panthera leo*), compete with each other (Périquet et al., 2015a, 2015b) and can have strong limiting effects on the populations of threatened subordinate competitors (e.g., African wild dogs, *Lycaon pictus*, and cheetahs, *Acinonyx jubatus*) (Creel and Creel 1996, 2002; Durant, 1998; Swanson et al., 2014).

An array of ecological factors likely affect the strength of competition between lions and hyaenas, including prey density and composition, lion and hyaena group size, and anthropogenic factors that can affect the distribution, dynamics and behaviour of both species (Kruuk, 1972; Kolowski and Holekamp, 2009; Schuette et al., 2013). However, disentangling the effects of interspecific competition between lion and hyaena is difficult in ecosystems where both species occur (Watts and Holekamp, 2008). The densities of both species correlate positively with ungulate prey density (Laurenson, 1995; Périquet et al., 2015a) and they compete intensely due to overlap in diet and habitat selection (Creel and Creel, 1996; Périquet et al., 2015a; Purchase, 2004; Hayward, 2006; Watts and Holekamp 2008). Lions are behaviourally dominant unless heavily outnumbered, and they frequently kill hyaenas and can limit hyaena numbers (Creel et al., 2001; Kruuk, 1972; Palomares and Caro, 1999; Watts and Holekamp, 2009). Although hyaenas are highly effective hunters (Holekamp et al., 1997), lions also provide them with scavenging opportunities, so the net effect of lions on spotted hyaena demography includes both costs and benefits (Watts and Holekamp 2008).

It is generally expected that the intensity of exploitative and interference competition should decrease as prey availability increases, but this expectation can be altered for large carnivores, where kleptoparasitism can greatly reduce the costs of obtaining carcasses even when prey are abundant (Creel and Creel, 1996). Although hyaenas have adaptations to low prey availability through such behaviour as long-distance movements (Hofer and East 1993a,b), local prey density and distribution is expected to affect juvenile survival, given they are sedentary (Benoit-Bird et al., 2013). Prey size also

affects competitive interactions between hyaenas and lions: ecosystems rich in large prey (> 200kg) favour lions, whereas ecosystems with medium sized prey (100 – 200kg) favour hyaenas (Hayward, 2006; Owen-Smith and Mills, 2008).

In hyaenas and other large carnivores, group size has a strong effect on the outcome of interference competition (Creel and Creel, 1996, 2002; Fanshawe and FitzGibbon, 1993; Palomares and Caro, 1999), and thus on survival (Holekamp et al., 2012; Watts and Holekamp, 2009). Large hyaena clans are more effective in food acquisition (Kruuk, 1972), and clan size has a positive effect on cub survival (Watts and Holekamp, 2009). Nonetheless, kills made by bigger clans are attended by more individuals, which reduces the provisioning of food by lower ranking females to their cubs (Frank, 1986; Kolowski et al., 2007), so the benefits of large group size are not apportioned equally to all individuals, as is true for other social carnivores (e.g., African wild dogs: Creel and Creel, 2015).

Conflict with people is a major cause of mortality of large carnivores, even in protected areas (Balme et al., 2009; Woodroffe and Ginsberg, 1998). Human activities affect survival of large carnivores most obviously through direct killing (Becker et al., 2013; Rosenblatt et al., 2014; Watson et al., 2013), but also by reducing habitat quality and prey availability (Ripple et al., 2015; Watson et al., 2014), and by constraining space utilisation and activity patterns (Boydston et al., 2003; Kolowski and Holekamp, 2009; Kolowski et al., 2007; Schuette et al., 2013). Carnivores residing close to human settlements are expected to experience stronger anthropogenic effects than those inhabiting the interior of protected areas. For example, hyaenas close to human activity in the Maasai Mara National Reserve spent far less time attending to cubs at the den, compared to clans distant from human activity (Kolowski et al., 2007).

As densities for both species are tightly linked to ungulate densities, few ecosystems provide information on the dynamics of hyaenas or lions when the other species is absent or rare. Western Zambia's Greater Liuwa Ecosystem (GLE), centred on Liuwa Plain National Park (LPNP) experienced substantial human induced reductions of wildlife populations, including the near-complete extirpation of lions. As a consequence, hyaenas are the dominant large carnivore in the ecosystem, with 3-5 lions and >150 hyaenas (see Results). We used intensive photographic monitoring and robust design mark-resight models to assess population density and survival of spotted hyaenas in LPNP from 2010-2013. This analysis provides the first methodologically and statistically rigorous estimates of hyaena density in a severely lion-depleted ecosystem, and evaluates the effects of a broad range of ecological and anthropogenic effects on survival. Juxtaposed with prior studies in ecosystems with typical and ecologically effective lion densities, our results help to understand interactions between the two dominant carnivores in African savannah ecosystems.

2. Materials and Methods

2.1. Study Area

The GLE is located in western Zambia and is comprised of LPNP and the Upper West Zambezi Game Management Area (UWZGMA). The LPNP covers 3660 km² of seasonally flooded grassland with isolated patches of open broad-leaved woodlands. The GLE experiences extensive rains and flooding during the wet season (Nov–Apr) and isolated seasonal and permanent water sources remain during the dry season (May – Oct).

Declared a National Park in 1972, LPNP has been a conservation area since the 1880s, when it was declared by the Lozi King as a royal hunting ground. Following park designation, settlements were permitted and the human population within LPNP numbered approximately 10 000 people during this

study (APN, 2009a). The GLE currently holds one of the largest remaining wildebeest (*Connochaetes taurinus taurinus*) populations in Africa at an estimated 46 000 animals, which move seasonally between the southern portion of LPNP in the rains and the UWZGMA and northern LPNP during the dry season (APN, 2013). It also contains an unknown but large number of oribi (*Ourebia ourebi*) and approximately 9000 migratory zebra (*Equus burchelli*), as well as smaller numbers of red lechwe (*Kobus leche leche*), tsessebe (*Damaliscus lunatus lunatus*), reedbuck (*Redunca arundium*), common duiker (*Sylvicapra grimmia*), and eland (*Tragelaphus oryx*) as potential prey species (APN, 2009b, 2011, 2013).

Due to depletion by poaching and conflict, the GLE carnivore guild is unusual because of its relative lack of lions and dominance of spotted hyaena. By 2003 the lion population was reduced to a single lioness, with subsequent reintroductions of two males and two females in 2009 and 2011, respectively, so that the park held 3-5 adult lions (a density of only 0.25-0.42 lions/100km²) in one pride during this study. Small, recovering populations of wild dogs (1-2 packs of 15-22 dogs total during this study) and cheetahs (17 known individuals) were also present. Concurrent studies of prey selection by all large carnivores in LPNP ($N = 517$ kills) indicated that wildebeest are the primary prey for all carnivores in LPNP, although oribi are also an important prey species for cheetahs and wild dogs, but not lions or hyaenas. Zebras were very rarely killed and only by lions and hyaenas. While hyaenas were present throughout the GLE, we confined our investigations to an approximately 1200 km² intensive study area in the southern portion of LPNP, which held the majority of the park's hyaena population and fully contained the territories of five clans (Fig. 1).

2.2. Study Design

We used restricted stratified random sampling to collect observations of individually-recognized hyaenas in the study area. These observations yielded a record of monthly detection/non-detection for 233 individuals over a period of 38 months from October 2010 to November 2013. We used these detection histories to fit robust design mark-resight models, providing estimates of population size and annual survival and testing how survival was affected by a set of demographic, ecological and anthropogenic factors.

2.2.1. Observations of Recognized Individuals

Because hyaena clans are highly social (Kruuk, 1972) and radio-collars strongly facilitate intensive mark-resight studies for social carnivores (Rosenblatt et al., 2014), we equipped 20 female and 3 male adult hyaenas from 5 clans with VHF (15) and GPS (8) radio collars (Telonics, Telemetry Solutions and Advanced Telemetry Solutions). Because hyaena societies are strongly matriarchal, we focused our collaring effort on females, who provide better monitoring of uncollared clan-mates. We typically maintained collars on at least three adult female in each clan throughout the study.

We employed restricted stratified random sampling to ensure an unbiased distribution of observation effort amongst the respective clans. We randomly selected the order in which clans were observed, and within each clan we randomized the order of search for collared individuals. We typically observed one clan per day, and all clans were sampled before beginning a new randomized sample. This procedure also allowed for unbiased estimates of home range sizes. When searching for collars or observing a collared animal, we recorded the identity of all hyaenas that we encountered, including the location (using GPS), group size, sex, habitat type and activity. We regularly visited communal dens in the clan to assess reproduction and record identities of all individuals present. We attempted to photograph both sides of all individuals at all sightings and utilized spot patterns and markings for identification. During the 4 years of study we used > 25 000 such photos to develop a photographic identification file of 233 individual hyaenas in 5 clans. Clan membership was determined through association and behaviour and

was typically unambiguous (Kruuk, 1972). Sex determination was accomplished through a composite of differences in body outline (Frank, 1986), reproductive status, and from the third month onwards using the shape of the phallic glans (Frank et al., 1990). We also assigned known or estimated age to each individual, using five biologically meaningful age classes: Young Cub (0-3 months), Old Cub (4-12 months), Subadult (1-2 years), Young Adult (3-4 years), Adult (4-6 years) and Old Adult (>6 years). Assignment to categories was based on a composite of characteristics relating to size, coat color and wear, and tooth wear. Over the course of the study we were able to assign many individuals known ages based on the emergence from the den and backdating photographs of identified individuals from years prior to the study. These known-aged animals provided comparisons for assigning estimated ages. Finally, given the uncertainties inherent in estimating ages (particularly for adults), we also analysed hyena survival using a reduced set of age classes to detect if aging errors had any detectable effect on our estimates of effects on survival (see below).

2.3. Estimating Hyaena home range

From the observations described above, we obtained 4405 locations from hyaenas in the five focal clans, primarily from VHF locations using restricted stratified random sampling, because GPS collar failures resulted in fewer locations than expected. The size of each clan's home range and core area were determined from these locations using the 90% isopleth and 70% isopleth from a kernel utilisation distribution, respectively, created using the fixed Gaussian Kernel Density Estimate (KDE) function in Geospatial Modelling Environment (GME; Beyer, 2012). Kernel bandwidth was determined by least squares cross-validation (LSCV) (Gitzen et al., 2006). We used these home ranges to determine the total area occupied by the five focal clans (represented by the 90 % contour in figure 1), and used this total area in conjunction with estimated population size to produce an upper bound on population density.

2.4. Evaluating Ecological and Anthropogenic Factors Affecting Hyaena Survival

From studies of hyaenas in other ecosystems and our knowledge of this system we hypothesized that survival may be affected by hyaena age class and sex, competition with lions, prey density, and proximity to human settlements.

2.4.1. Competition with lions

We hypothesized that hyaena survival would be lower in areas of higher lion use. We intensively monitored the single GLE pride using VHF and GPS radio-collars. These lions occupied our focal study area when migratory wildebeest and zebra were present at high densities (from mid-October to mid-July) and moved north-east outside the main study area following migratory prey from mid-July to mid-October, making occasional forays back into the main study area.

Using 5697 GPS and VHF lion locations from 2010-2013 we created a kernel utilisation distribution in the same manner as for hyaenas, and rasterized this distribution (cell size: 100 x 100 m) so the value of each pixel of the raster map represented the likelihood of encountering a lion within that cell. We used the 90th percentile of the distribution of lion daily movement distances as the bandwidth for this utilisation distribution so that it had relatively strong smoothing, and thus our inferences about differences between locations in lion use were conservative. We used the "lsectpolyrst" tool in GME (Beyer, 2012) to intersect the lion raster with the 70% isopleth 'core' area for each of the hyaena clans, providing a quantitative measure of variation among hyaena clan territories in the intensity of use by lions (Fig. 1).

2.4.2. Prey Density

Prey density was determined from distance sampling models fit to data from systematic line transects located in eight survey quadrats distributed evenly across the study area (Fig. 1). Detailed methods and results for these data are presented elsewhere (M'soka et al., in review), but each quadrat was 8 km x 8 km with two transect lines running east-west at 2 km and 6 km along the north-south axis, for a total of 128 km of transects that we surveyed 10 times between June and December from 2010 to 2013. Transects were surveyed five times in 2010, once in 2011, once in 2012 and three times in 2013. Of these transects, 83 km fell within the territories of the 5 hyaena clans (Fig. 1). Because wildebeest comprised over 90% of all hyaena kills, and were by far the most common ungulates in the study area (with estimated densities ~4X higher than oribi, the next most common species: M'soka et al., in review), we restricted our analysis of prey availability to wildebeest. We estimated wildebeest density (corrected for detection probability) for each clan's home range using the distance-sampling model that was best-supported by AIC scores. This model included effects of vegetation type, grass height, the presence of water and burned areas, season, local hyaena density, distance to the park boundary and distance to the nearest village (M'soka et al., in review).

2.4.3. Proximity to human settlements

We quantified the effect of human settlements on hyaena survival by calculating the distance from the geometric centre (or 'centroid') of each clan's home range to the nearest village, hypothesizing that hyaenas closer to settlements are likely to have higher mortality due to conflict with humans and livestock. Centroid locations were calculated in ArcGIS 10.2.2 (ESRI, Redlands, California, USA) using the locations of all females in a clan, each weighted by the number of hyaenas observed at that location. We used data only for females because occasional extra-territorial forays by males include locations that are rarely (if ever) used by most individuals in the same clan. We then used ArcGIS 10.2.2 (ESRI, Redlands, California, USA) to determine the distance from each centroid to the nearest village, which were mapped systematically from the air. These distances ranged from 4.2 km to 13.8 km.

2.5. Estimating Hyaena Survival

We used the monthly detection histories of 233 individually identified hyaenas in a robust design mark-resight analysis. We used the robust design model to estimate population size and annual survival rates while accounting for imperfect detection, and to test the demographic, ecological and anthropogenic factors affecting survival. The robust design estimates population size within 'primary' periods for which the population is assumed to be demographically closed (by analysis of secondary periods nested within primary periods), and survival rates by comparisons across the intervals between primary periods. We compiled monthly detections for each hyaena over the study period from October 2010 to November 2013. We partitioned this study period of 38 months into a set of seven primary periods for which demographic closure was reasonably approximated and field effort was high, separated by periods considered demographically open (during which field effort was lower) to allow estimation of survival rates. Closed primary periods were Oct - Dec 2010, Apr - Jul 2011, Oct 2011 - Jan 2012, May - Jul 2012, Oct 2012 - Jan 2013, Apr - Jul 2013, and Oct - Nov 2013. The intervening six open periods were Jan - Mar 2011, Aug - Sep 2011, Feb - Apr 2012, Aug - Sep 2012, Feb - Mar 2013, and Aug - Sep 2013. Small differences between years in the timing of open and closed periods reflected variation in the timing of intensive efforts to locate hyaenas in the radio-collared clans.

We fit robust design models (Kendall et al., 1995; Kendall and Nichols, 1995; Kendall et al., 1997) to these data using the **RMark** package (Laake, 2013) in R (R Core Team, 2014). Our original intent was to use Akaike's Information Criterion corrected for small sample size and extrabinomial variation (QAICc)

to compare a set of *a priori* models, but this approach could not be implemented because some parameters could not be estimated in some of the *a priori* models. Consequently, we used a sequential model-fitting process to obtain QAICc scores for a set of models that yielded precise estimates of population size and annual survival, and allowed tests of the factors affecting survival. We adjusted for extrabinomial variation by estimating median $\hat{c}$ using a Cormack-Jolly-Seber model in Program Mark (White and Burnham, 1999) with our dataset collapsed to primary occasions, as recommended by Laake (2015). This analysis showed that over dispersion was minor in these data (median $\hat{c} = 1.4$). In our first step, we determined the best-supported parameterization of temporary emigration, defined as γ' (the probability of remaining unavailable) and γ'' (the probability of becoming unavailable). Because hyaenas in some ecosystems are known to leave their typical home ranges for extended periods when following migratory prey (Kruuk, 1972; Hofer and East, 1993a, b) we assumed that the likelihood that an individual would be present and available for detection each primary period was affected by a Markovian process of temporary emigration. QAICc model selection between robust design models varying only by Markovian and no-movement temporary emigration indicated higher support for Markovian models. In our second step, we determined that models allowing detection probability (p) to vary within and between primary periods consistently received more support than otherwise-identical models that held p constant or only considered differences between primary periods. Finally, we combined these models of detection probability and Markovian temporary emigration with nine candidate models of ecological and anthropogenic effects on survival, shown in Table 1. We annualized the survival estimates from these models using the *time.intervals* function in **RMark**, and used model-averaging to estimate anthropogenic and ecological effects on survival, using the *model.avg* and *model.sel* functions of the **MuMIn** package.

Not all of the above models could be fit to data partitioned by sex and age-classes, so we fit a final model to estimate mean annual survival for each sex in each of five age classes (young cubs, old cubs, sub adults, adults and old adults). For this model, $\hat{p}$, $\hat{\gamma}'$ and $\hat{\gamma}''$ were modelled as described above.

2.6. Estimating Population size and density

Estimates of population size were obtained from the top ecological model, which had the effects of distance to human settlements. For comparison to other estimates of hyaena population density, we converted population size to population density in two ways. For comparison to estimates that include unused locations within a broad area (e.g. from call-up surveys or spoor counts), we divided the population estimate by the area of our focal study site (1200 km²). For comparison to more localized estimates (e.g. from intensive study of radio-collared clans), we divided the average population estimate by the area known to have been used by these hyaenas (291.1 km²).

3. Results and discussion

Our robust design models yielded precise estimates of population size and survival rates, largely because the intensity of sampling was high enough that very few individuals went undetected (mean $f_0 = 0.44$, upper 95% CL = 1.52) and monthly detection probabilities were high ($\hat{p} = 0.51$, range = 0.33 to 0.71). Model-averaged estimates of Markovian temporary emigration were $\hat{\gamma}'' = 0.13$ (95% CI: 0.09 – 0.19) and $\hat{\gamma}' = 0.75$ (95% CI: 0.71 – 0.78). While the parameters just described were not of direct interest, they must be estimated to obtain unbiased estimates of population size and survival. These results also indicate that the excellent visibility of this population and intensive monitoring combined to allow detection of almost all individuals over the study period.

3.1. Hyaena Population size and Density

Averaged across the seven primary periods, we observed 136.4 individuals and estimated an average population size of 151.2 ± 5.9 (SE) individuals per primary period (Table A1). We estimated a minimum density of 0.13 hyaenas/km² and maximum density of 0.52 hyaenas/km². For comparison, Périquet et al. (2015a) comprehensively reviewed estimates of hyaena density and reported values ranging from 0.005 to 1.8 individuals/km² (mean = 0.39 ± 0.10 individuals/km²). While the density of hyaenas in LPNP is not comparable to the >1 individual/km² that has been reported for some prey-rich systems (e.g. Serengeti NP: Kruuk, 1972), our density estimates indicates a healthy and stable population.

Our estimates indicate that the Liuwa hyaena population was stable over the duration of the study period (Fig. 2a). There is an apparent increase in the Liuwa hyaena population after the first primary period (Oct-Dec 2010; Table A1), largely due to the number of known individuals increasing after the first primary period. In one clan (Mutata) only 8 individuals were detected in the first primary period; this increased to between 29 and 40 individuals detected in subsequent periods. Because we did not estimate detection independently for each clan in each period, we believe that detection for this clan was overestimated in the first primary period, so that the size of this clan (and thus total population size) was underestimated in the first primary period. Although population size did not trend systematically upward or downward over the long-term, the population estimates over the 6 primary periods (excluding the first primary period, for reasons just explained) fluctuated systematically with the estimates of the Oct – Jan periods generally higher than the estimates of the May – Jul periods (Fig. 2a; Table A1). This pattern is probably due to the migratory nature of the prey species in this ecosystem, with wildebeest being locally more abundant in the wet season (Nov-Apr) than the dry season (May-Oct) (M'soka et al. in review). When wildebeest migrate out of the study area densities of available prey drop significantly and hyaena remaining in their clan territories must focus primarily on resident territorial wildebeest bulls that remain. Migratory prey movements drive temporary immigration in other hyaena populations (Hofer and East, 1993a, b), and provide a logical explanation for this observed pattern in the size of the Liuwa hyaena population. This is further supported by the proportional change in population size between primary periods loosely matching our estimates of $\hat{\gamma}'$ and $\hat{\gamma}''$, further suggesting that temporary immigration driven by prey availability plays a role in the dynamics of this hyaena population, as elsewhere (Hofer and East, 1993a,b; Höner et al., 2005).

3.2. Prey Density and Hyaena Density in LPNP

Prior research has established that hyaena density is positively correlated with prey density (Hayward, 2006; Höner et al., 2005). Périquet et al. (2015a) used data from 20 studies to describe this relationship quantitatively as

$$\log(\text{hyaena density}) = -4.11 + 0.97 \times \log(\text{prey biomass})$$

Wildebeest were by far the most common ungulates in the study area, with a density that ranged from 60.8 ± 2.34 (SE) individuals/km² to 11.3 ± 0.67 individuals/km² in the wet and dry season respectively (M'soka et al., in review). With this prey base, and a sample of 516 kills in Liuwa, wildebeest comprised 92% of hyaena kills (95% CI: 85-96%) and 90% of lion kills (95% CI: 85-96%). For the ungulate prey community of LPNP (with estimated mean prey mass = 180 kg) the relationship described by Périquet et al. (2015a) predicts a hyaena density of 0.17 individuals/km² based on dry season prey densities, and 0.88 individuals/km² based on wet season prey densities. Our estimates of hyaena density in LPNP are comparable to the mean of these two seasonal estimates, suggesting that the prey base of LPNP supports the hyaena population that would be expected on the basis of data from other protected areas.

3.3. Clan Size and home range size

Mean clan size in LPNP during the study period was 48.6 hyaenas. Though somewhat smaller than the clan sizes supported by the ungulate migrations across the Serengeti and Mara populations, LPNP clans tend to be larger than comparably-sized parks in Southern Africa, and larger than the mean clan size of 30.84 ± 7.39 reported by Périquet et al. (2015a). Hyaena home range sizes ranged from 52.2 km² to 102.4 km², and tended to be smaller than the mean of 178 ± 79.19 km² from 15 other studies (Périquet et al., 2015a), but well within the reported range of 24.5 - 1095 km².

3.4. Survival: Variation among Age-Sex Classes

On the basis of relatively high prey density and low levels of competition with lions, we hypothesized that hyaena survival would be high. Supporting this hypothesis, estimated annual survival rates were high, and varied little across age-sex classes (Fig. 2b, Table A3). Frank et al (1995), reported little variation in survival between sexes up to 24 months old in the Mara in Kenya, however the small variation in estimated differences between the sexes in the adult age classes in our data is somewhat unusual (Clutton-Brock and Isvaran, 2007), but hyaenas are relatively monomorphic, have very low reproductive rates, and reproductive effort by females is offset by female dominance, all of which predict that survival should show less age-sex variation in hyaenas than in most large carnivores. This could also be a reflection of our ability to track adult males beyond their natal clans after dispersal. Male dispersal hinders the estimation of survival rates in most ecosystems as fates of dispersed males are rarely known (Holekamp and Smale, 1995).

3.5. Ecological Effects on Survival

Comparison of QAICc scores shows distributed support for models that include effects of clan size, prey density within the home range, proximity to people, and local competition with lions (Table 1). However, as Fig. 2b shows, the confidence intervals for all of these effects overlap substantially with zero, suggesting that none of these variables had significant effects on the survival of hyaenas in LPNP.

Despite the high survival rates that we found for all age-sex classes, this hyaena population appears to be stable (Figure 2a; Table A1). This could possibly be attributed to dispersal or source sink dynamics in this hyena population resulting in a population that is stable rather than increasing. We could not detect any significant effects of proximity to people on hyaena survival, even though people are allowed to reside within the park with their livestock, and human-wildlife conflict surveys conducted throughout the GKE indicate that despite human presence, carnivore conflict is low, owing in part to good livestock husbandry practices that include use of effective bomas and herders (M'soka unpublished data). Thus negative anthropogenic impacts are relatively low and likely ameliorated by the high density of prey and low levels of competition from lions in the intensive study area. Studies in other African ecosystems have shown that hyaena survival and abundance are closely related to prey abundance (Hofer and East, 1993a; Kruuk, 1972; Watts and Holekamp, 2009). Thus, the patterns observed in LPNP suggest that hyaenas can compensate for any negative effects of anthropogenic activities if prey density remains high and competition from lions is low. More generally, this result confirms that finding ways to promote coexistence of people and livestock with ungulate prey is a strong determinant of the persistence of large carnivores in human dominated ecosystems (Schuette et al., 2013).

We were not able to detect any effect of the Liuwa lion pride on hyaena survival (Fig. 2c), most likely due to seasonal movements of lion and/or the small lion population in LPNP. During the course of our study, lions consistently occupied the study area when migratory wildebeest were present at high

densities (From mid-October to mid-July) and moved north-east outside the main study area following migratory prey from mid-July to mid-October, making occasional forays back into the main study area. It is possible that lions shift their range during this period not only to follow prey, but also to reduce interference competition with spotted hyaenas during this time of reduced prey availability. However, this behaviour of lions has been reported in other ecosystems with migratory prey species (Schaller, 1972, Hanby et al., 1995). Additionally, given that lions are ambush predators the prevalence of fires reducing grass height and providing subsequent vegetation flushes tracked by wildebeest in their winter range (M'soka et al. In Review) may reduce vulnerability of wildebeest to lion predation at this time, leading lions to concentrate in more woodland areas with greater prey vulnerability rather than abundance (Hopcraft et al., 2005). As coursing predators hyaena would likely be unaffected by changes in ambush cover due to fires. Temporal variation in prey availability may ameliorate the competitive interactions between hyaena and lion in this ecosystem, though this possibility must be evaluated with the recognition that a single lion pride occupied the study area, at a density much lower than many other populations, making this the only hyaena population studied in such a state; thus the effect of lions is expected to be weak.

The relatively constant survival across age classes, particularly cubs, contrasts with results from other studies of hyaenas (Frank et al 1995; Watts and Holekamp 2009). In this study, hyaenas of all classes had very high detection rates throughout the study period and the resulting confidence intervals on survival were quite narrow (Fig. 2), so the difference in results is unlikely to be methodological. Type II survivorship curves with constant survival across age classes are most common among medium-sized mammals, and have been seen in studies of other large carnivores using long-term observation of known individuals (Creel et al. 2004). We interpret the relatively high and constant survival (across years, age classes and clans) in the Liuwa population as a manifestation of nearly ideal conditions with low lion density, weak anthropogenic impacts, and good prey availability. Where one or more of these limiting factors are strong, they are likely to affect age classes differently, but where all of these limiting factors are weak, survival is uniformly high across age classes.

3.6. Top-down Impacts of Hyaena in the Absence of Strong Lion Competition

To our knowledge the GLE is the only ecosystem where hyena demography has been rigorously studied using mark-resight methods with known individuals, with a very high density of hyaena and a severely depleted lion population. How hyaena populations respond in the absence of strong competition from lions is of key interest, and the impact of these hyaena dynamics on prey populations is also unknown and likely significant, particularly since Liuwa hyaenas rely almost exclusively on predation versus scavenging for food acquisition. Several investigators have found complex relationships between lion and hyaena abundance and the relative proportion of scavenging and kleptoparasitism versus predation (Watt and Holekamp 2008, Périquet et al., 2015b) and this is likely to be dynamic in a recovering ecosystem. Liuwa's keystone species, the wildebeest, has recovered rapidly from years of poaching; however a strong selection for wildebeest by hyaena, coupled with what may constitute a numerical response by hyaena populations to a growing wildebeest population, is likely to exert a strong limiting influence on the net growth rate and recovery of wildebeest. How lion recovery and increased competition with hyaena will impact these dynamics is unknown and continued studies of hyaena and lion demography and predation in LPNP will provide additional insights on the dynamics of competition and predation in large mammal systems, as well as the ecological and anthropogenic factors affecting them.

4. Conclusions

Overall, our results show that the migratory wildebeest population that has recovered in LPNP over the last decade supports a healthy and stable hyaena population. Survival is an important demographic component of population growth and for modelling ecological and anthropogenic risk to the viability of species. Annual survival is uniformly high for all age-sex classes, with no detectable effects of variation in prey density, local variation in utilisation by lions, or proximity to people (and their livestock). If recovery of the lion population continues competitive effects on hyaenas and other carnivores may increase, and this should be a focus for ongoing monitoring. With the relatively high availability of wildebeest as prey, very low competition with lions, hyaena survival was high and was not affected by proximity to villages, even though settlement are allowed within the National Park itself. This is an encouraging pattern which suggests that, as elsewhere (Schuette et al., 2013), maintenance of native prey populations allows coexistence between humans and large carnivores in Africa; however in this instance high hyaena survival is also likely to be a result of low lion competition. Despite being well-studied and abundant there are few reliable estimates of hyaena density and survival in the absence of their main competitor, and as both species continue to be heavily impacted by human activities, understanding large carnivore guild dynamics and the factors affecting them will help inform management and conservation efforts.

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Table 1. QAICc scores for a set of models of ecological effects on annual survival rates of LPNP hyaenas.

model	npar	QAICc	DeltaQAICc	weight	QDeviance	c-hat
S(~village)	21	405.81	0	0.20	363.27	1.4
S(~lion)	21	406.18	0.37	0.16	363.65	1.4
S(~size)	21	406.24	0.44	0.16	363.71	1.4
S(~prey)	21	406.27	0.46	0.16	363.74	1.4
S(~size + village)	22	407.37	1.56	0.09	362.79	1.4
S(~lion + village)	22	407.78	1.97	0.07	363.20	1.4
S(~prey + village)	22	407.84	2.04	0.07	363.26	1.4
S(~prey + size)	22	408.23	2.42	0.06	363.65	1.4
S(~lion + size + village)	23	409.08	3.27	0.04	362.44	1.4

Village = distance to the nearest settlement, lion = probability of lion presence, size = clan size, prey = prey density.

Figure Legends

Figure 1. Contour lines represent the 70% and 90% isopleths of the 5 resident hyaena clans. Lion use of the area during the period July 2010 – November 2013 is shown by colour: the darker an area, the higher the probability of lion presence. Straight lines represent transects along which prey was monitored. Black triangles indicate village locations.

Figure 2. (a) LPNP hyaena population estimates from the robust design model with the probability of detection allowed to vary across primary and secondary sampling sessions. (b) Estimated annual survival was above 0.90 for all age-sex classes, with a very small and non-significant tendency for males to survive better than females, and adults to survive better than younger age classes. (c) Model-averaged effects of ecological variables on annual survival rates of LPNP hyaenas. Variables were standardized as z-scores so that effect sizes could be compared directly. Point estimates and 95% confidence intervals are shown.

Table A1: Population estimates for the seven primary periods.

Primary period	Number of Hyaenas observed	Population estimate	se	sd	lcl	ucl
Wet 2010	102	119.01	6.70	73.12	112.31	125.71
Dry 2011	142	147.55	3.25	39.48	144.30	150.80
Wet 2011	161	167.64	3.45	44.70	164.18	171.09
Dry 2012	131	152.70	6.65	82.20	146.05	159.35
Wet 2012	155	165.60	4.33	55.66	161.27	169.92
Dry 2013	127	143.31	5.61	67.18	137.70	148.92
Wet 2013	137	162.54	7.89	100.61	154.65	170.43

Table A2: Coefficient estimates for model averaged effects on survival of distance to human settlement (Village), clan size, Prey availability (Prey) and competition with lions (Lions)

	effect	Beta	beta.lcl90	beta.ucl90
1.00	Village	0.95	-2.17	4.08
2.00	Clan Size	-0.32	-3.57	2.93
3.00	Prey	-0.35	-3.63	2.93
4.00	Lions	-1.15	-6.88	4.58

Table A3: Estimates of annual survival across age and sex classes for the Liuwa hyena population.

	SEX	AGE	ESTIMATE	SE	95 % LCL	95 % UCL
1	f	Young Cub	0.9051	0.1698	0.1654	0.9978
2	f	Young Cub	0.9056	0.1666	0.1742	0.9977
3	f	Young Cub	0.9059	0.1645	0.1800	0.9976
4	f	Young Cub	0.9063	0.1615	0.1885	0.9975
5	f	Young Cub	0.9066	0.1597	0.1940	0.9975
6	f	Young Cub	0.9070	0.1579	0.1995	0.9974
7	f	Young Cub	0.9054	0.1676	0.1712	0.9977
8	f	Young Cub	0.9062	0.1625	0.1857	0.9976
9	f	Young Cub	0.9065	0.1606	0.1913	0.9975
10	f	Young Cub	0.9057	0.1655	0.1771	0.9977
11	m	Young Cub	0.9245	0.1779	0.0764	0.9994
12	m	Young Cub	0.9249	0.1768	0.0774	0.9994
13	m	Young Cub	0.9252	0.1761	0.0779	0.9994
14	m	Young Cub	0.9255	0.1752	0.0785	0.9994
15	m	Young Cub	0.9258	0.1747	0.0788	0.9995
16	m	Young Cub	0.9260	0.1742	0.0790	0.9995
17	m	Young Cub	0.9248	0.1772	0.0771	0.9994
18	m	Young Cub	0.9254	0.1755	0.0783	0.9994
19	m	Young Cub	0.9257	0.1749	0.0786	0.9994

20	m	Young Cub	0.9250	0.1765	0.0776	0.9994
21	f	Old Cub	0.9082	0.1515	0.2192	0.9971
22	f	Old Cub	0.9086	0.1495	0.2257	0.9971
23	f	Old Cub	0.9089	0.1483	0.2297	0.9970
24	f	Old Cub	0.9094	0.1466	0.2350	0.9970
25	f	Old Cub	0.9097	0.1455	0.2382	0.9969
26	f	Old Cub	0.9100	0.1446	0.2411	0.9969
27	f	Old Cub	0.9085	0.1502	0.2236	0.9971
28	f	Old Cub	0.9092	0.1471	0.2333	0.9970
29	f	Old Cub	0.9095	0.1460	0.2367	0.9969
30	f	Old Cub	0.9088	0.1489	0.2277	0.9970
31	m	Old Cub	0.9270	0.1727	0.0786	0.9995
32	m	Old Cub	0.9274	0.1723	0.0781	0.9995
33	m	Old Cub	0.9276	0.1721	0.0776	0.9995
34	m	Old Cub	0.9280	0.1719	0.0767	0.9995
35	m	Old Cub	0.9283	0.1719	0.0760	0.9995
36	m	Old Cub	0.9285	0.1719	0.0752	0.9995
37	m	Old Cub	0.9273	0.1724	0.0783	0.9995
38	m	Old Cub	0.9279	0.1720	0.0770	0.9995
39	m	Old Cub	0.9281	0.1719	0.0763	0.9995
40	m	Old Cub	0.9275	0.1722	0.0779	0.9995
41	f	Sub-Adult	0.9112	0.1417	0.2489	0.9969
42	f	Sub-Adult	0.9116	0.1410	0.2503	0.9969
43	f	Sub-Adult	0.9119	0.1407	0.2507	0.9969
44	f	Sub-Adult	0.9123	0.1403	0.2506	0.9969
45	f	Sub-Adult	0.9126	0.1401	0.2501	0.9970
46	f	Sub-Adult	0.9129	0.1400	0.2492	0.9970
47	f	Sub-Adult	0.9115	0.1412	0.2499	0.9969
48	f	Sub-Adult	0.9122	0.1404	0.2508	0.9969
49	f	Sub-Adult	0.9125	0.1402	0.2504	0.9969
50	f	Sub-Adult	0.9118	0.1408	0.2505	0.9969
51	m	Sub-Adult	0.9295	0.1722	0.0711	0.9996
52	m	Sub-Adult	0.9298	0.1725	0.0693	0.9996
53	m	Sub-Adult	0.9301	0.1727	0.0680	0.9996
54	m	Sub-Adult	0.9304	0.1732	0.0660	0.9996
55	m	Sub-Adult	0.9307	0.1735	0.0646	0.9996
56	m	Sub-Adult	0.9309	0.1739	0.0631	0.9996
57	m	Sub-Adult	0.9297	0.1724	0.0699	0.9996
58	m	Sub-Adult	0.9303	0.1730	0.0667	0.9996
59	m	Sub-Adult	0.9305	0.1733	0.0653	0.9996
60	m	Sub-Adult	0.9299	0.1726	0.0687	0.9996
61	f	Young Adult	0.9141	0.1405	0.2419	0.9972
62	f	Young Adult	0.9145	0.1410	0.2377	0.9973

63	f	Young Adult	0.9148	0.1414	0.2345	0.9973
64	f	Young Adult	0.9152	0.1422	0.2292	0.9975
65	f	Young Adult	0.9155	0.1428	0.2253	0.9975
66	f	Young Adult	0.9158	0.1434	0.2211	0.9976
67	f	Young Adult	0.9144	0.1408	0.2392	0.9973
68	f	Young Adult	0.9151	0.1419	0.2310	0.9974
69	f	Young Adult	0.9154	0.1425	0.2273	0.9975
70	f	Young Adult	0.9147	0.1412	0.2361	0.9973
71	m	Young Adult	0.9318	0.1757	0.0570	0.9997
72	m	Young Adult	0.9322	0.1765	0.0546	0.9997
73	m	Young Adult	0.9324	0.1771	0.0530	0.9997
74	m	Young Adult	0.9327	0.1781	0.0505	0.9997
75	m	Young Adult	0.9330	0.1787	0.0489	0.9997
76	m	Young Adult	0.9332	0.1794	0.0473	0.9997
77	m	Young Adult	0.9321	0.1763	0.0554	0.9997
78	m	Young Adult	0.9326	0.1777	0.0513	0.9997
79	m	Young Adult	0.9329	0.1784	0.0497	0.9997
80	m	Young Adult	0.9323	0.1768	0.0538	0.9997
81	f	Adult	0.9169	0.1467	0.2023	0.9979
82	f	Adult	0.9173	0.1481	0.1945	0.9980
83	f	Adult	0.9176	0.1491	0.1892	0.9981
84	f	Adult	0.9180	0.1507	0.1810	0.9982
85	f	Adult	0.9183	0.1519	0.1754	0.9983
86	f	Adult	0.9186	0.1530	0.1698	0.9984
87	f	Adult	0.9172	0.1476	0.1972	0.9980
88	f	Adult	0.9179	0.1502	0.1838	0.9982
89	f	Adult	0.9182	0.1513	0.1782	0.9983
90	f	Adult	0.9175	0.1486	0.1919	0.9981
91	m	Adult	0.9341	0.1823	0.0409	0.9998
92	m	Adult	0.9344	0.1835	0.0386	0.9998
93	m	Adult	0.9347	0.1843	0.0371	0.9998
94	m	Adult	0.9350	0.1856	0.0349	0.9998
95	m	Adult	0.9352	0.1865	0.0335	0.9998
96	m	Adult	0.9354	0.1873	0.0321	0.9998
97	m	Adult	0.9343	0.1831	0.0394	0.9998
98	m	Adult	0.9349	0.1852	0.0357	0.9998
99	m	Adult	0.9351	0.1860	0.0342	0.9998
100	m	Adult	0.9346	0.1839	0.0379	0.9998
101	f	Old Adult	0.9196	0.1581	0.1472	0.9987
102	f	Old Adult	0.9201	0.1602	0.1388	0.9988
103	f	Old Adult	0.9203	0.1616	0.1333	0.9988
104	f	Old Adult	0.9207	0.1637	0.1252	0.9989
105	f	Old Adult	0.9210	0.1652	0.1198	0.9990

106	f	Old Adult	0.9212	0.1667	0.1146	0.9991
107	f	Old Adult	0.9199	0.1595	0.1416	0.9988
108	f	Old Adult	0.9206	0.1630	0.1278	0.9989
109	f	Old Adult	0.9209	0.1645	0.1225	0.9990
110	f	Old Adult	0.9202	0.1609	0.1361	0.9988
111	m	Old Adult	0.9363	0.1910	0.0268	0.9999
112	m	Old Adult	0.9366	0.1925	0.0250	0.9999
113	m	Old Adult	0.9369	0.1935	0.0238	0.9999
114	m	Old Adult	0.9372	0.1949	0.0222	0.9999
115	m	Old Adult	0.9374	0.1959	0.0211	0.9999
116	m	Old Adult	0.9376	0.1970	0.0201	0.9999
117	m	Old Adult	0.9365	0.1920	0.0256	0.9999
118	m	Old Adult	0.9371	0.1944	0.0227	0.9999
119	m	Old Adult	0.9373	0.1954	0.0216	0.9999
120	m	Old Adult	0.9367	0.1930	0.0244	0.9999