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Cite this article: Green DS, Farr MT, Holekamp KE, Strauss ED, Zipkin EF. 2019 Can hyena behaviour provide information on population trends of sympatric carnivores? *Phil. Trans. R. Soc. B* **374**: 20180052.
http://dx.doi.org/10.1098/rstb.2018.0052

Accepted: 9 May 2019

One contribution of 19 to a theme issue 'Linking behaviour to dynamics of populations and communities: application of novel approaches in behavioural ecology to conservation'.

Subject Areas:
behaviour, ecology

Keywords:
carnivore conservation, community modelling, hierarchical modelling, hyena, lion, Mara-Serengeti ecosystem

Author for correspondence:
David S. Green
e-mail: david.green@oregonstate.edu

Can hyena behaviour provide information on population trends of sympatric carnivores?

David S. Green[1,2,†,‡], Matthew T. Farr[1,2,†], Kay E. Holekamp[1,2], Eli D. Strauss[1,2] and Elise F. Zipkin[1,2]

[1]Department of Integrative Biology, and [2]Ecology, Evolutionary Biology and Behaviour Program, Michigan State University, East Lansing, MI, USA

DSG, 0000-0001-6031-0076; MTF, 0000-0003-1011-6851

Mammalian carnivores are declining worldwide owing to human activities. Behavioural indicators have the potential to help identify population trends and inform conservation actions, although this area of research is understudied. We investigate whether behaviour is linked to abundance in a community of carnivores in the Masai Mara National Reserve, Kenya. Anthropogenic disturbance increased exponentially in parts of the Reserve between 1988 and 2017, mainly owing to daily incursions by large numbers of livestock and tourists. Previous research showed that hyena behaviour changed markedly during this period. Through a series of vignettes, we inquire whether hyena behaviours correlate with changes in abundance of hyenas themselves, or those of other carnivore species in the region. We find that changes in spotted hyena behaviour in disturbed areas, but not in undisturbed areas, can be linked to changes in their demography (vignette 1). We also find that declines in observed lion–hyena interactions, as well as increases in spotted hyena abundance, are probably caused by competitive release of hyenas from declining lion abundance (vignette 2). Finally, we demonstrate that in some cases, hyena behaviour and demography is linked to the density and distribution of sympatric carnivores, and that behavioural changes in hyenas can provide information on shifts within the carnivore community (vignettes 3 and 4). Our vignettes reveal intriguing relationships between behaviour and demography that should be explored in future research. Pairing behavioural studies with more traditional monitoring efforts can yield useful insights regarding population and community trends, and aid wildlife conservation and management.

This article is part of the theme issue 'Linking behaviour to dynamics of populations and communities: application of novel approaches in behavioural ecology to conservation'.

1. Introduction

There is a pressing need to develop simple methods to document carnivore populations in light of growing threats to mammalian carnivores worldwide [1]. As most carnivores are both elusive and nocturnal, it can be difficult to collect the data necessary to estimate population trends. Innovative approaches, such as behavioural indicators, that complement or enhance traditional monitoring efforts could provide information that is not easily obtained otherwise. Because behaviour is the first line of defence for animals when confronting new threats or stressors associated with environmental change [2–4], behavioural data may contain information on population abundance and possibly even on communities of sympatric species. Yet, behaviour is often ignored in analyses of population and community dynamics (figure 1). If we can determine which behavioural variables are linked to present or future population abundance, behavioural indicators can be paired with traditional population

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[†] Authors contributed equally.

[‡] Present address: Institute for Natural Resources, Oregon State University, Corvallis, OR, USA.

Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.4554134.

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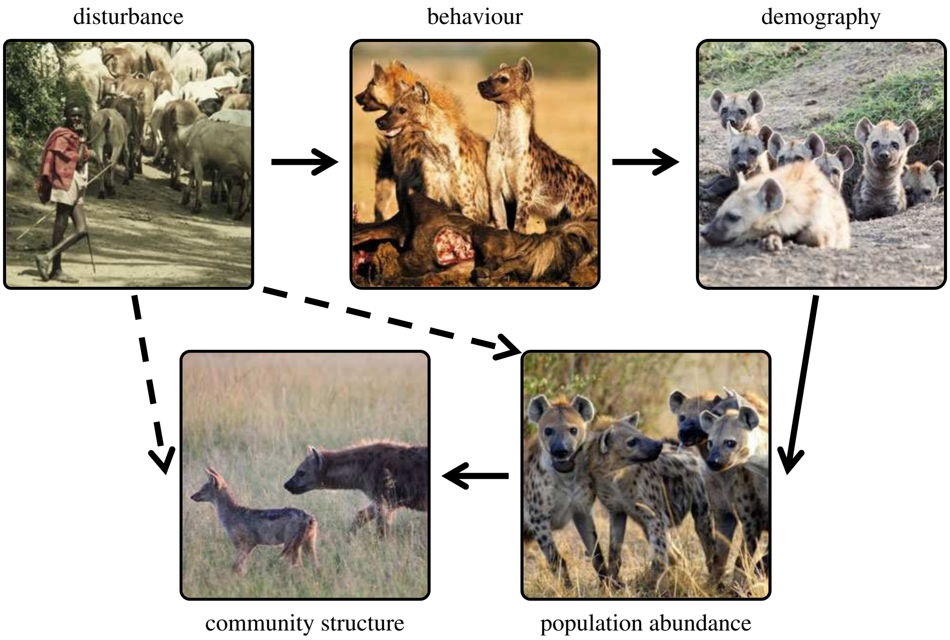


Figure 1. Conceptual diagram showing how anthropogenic disturbance affects behaviour, population abundance and community structure. Most studies directly measure changes in population abundance and community structure after a disturbance event (dashed arrows), but the causal effects of disturbance can be mediated by behavioural and demographic processes, which in turn, are the underlying drivers of population and community level changes (solid arrows). Behaviour may thus provide an early indicator of imminent effects of disturbance.

monitoring to assess demographic responses to environmental factors and offer an auxiliary approach to detecting changes in carnivore populations.

Species vary in their abilities to respond to human-induced environmental change. The spotted hyena (*Crocuta crocuta*) exhibits high levels of behavioural plasticity [5], and recent work suggests this plasticity allows spotted hyenas to survive in areas where other large carnivores have been extirpated, including large cities [6,7]. Here, we inquire whether changes in hyena behaviour correlate with demographic change in hyenas themselves, or with the abundances of sympatric species, using three decades of behavioural data collected from multiple hyena groups in the Masai Mara National Reserve (henceforth ‘the Reserve’), Kenya.

Anthropogenic disturbance has markedly increased in the eastern portion of the Reserve over the past 30 years, leading to dramatic ecological changes. In particular, unregulated growth of infrastructure for tourism and intense illegal grazing of livestock have had negative effects on wildlife in the eastern portion of the Reserve [8–13]. As anthropogenic disturbance has increased, several aspects of the physiology and behaviour of spotted hyenas have changed as well. For instance, excreted concentrations of glucocorticoid ‘stress’ hormones are higher in hyenas inhabiting disturbed regions of the Reserve than in individuals inhabiting undisturbed regions [14]. Documented behaviour patterns that vary with intensity of disturbance include vigilance [15], use of space and dens [9,16,17], circadian activity patterns [18], maternal behaviour [19], habitat preferences [17], social networks [20] and even personality development [21]. Some of these same behavioural responses to increasing anthropogenic disturbance have also been observed in hyena populations elsewhere in Africa [22].

Our goal here is to explore whether hyena behaviour can inform us about carnivore population and community trends. Specifically, we inquire whether the behaviour of spotted hyenas correlates with demographic change in the hyenas themselves, or with local abundances of lions and other sympatric carnivores. In the first of four vignettes, we use longitudinal data collected over 30 years to examine whether subgroup sizes of hyenas found at ungulate kills correlate with overall clan size the following year. In the second, we use longitudinal records of behavioural interactions between hyenas and lions to assess trends in lion numbers over time [9]. In our third vignette, we use a cross-sectional approach comparing the movement speeds of hyenas between areas of the Reserve exposed to high or low levels of anthropogenic disturbance to predict densities of sympatric carnivores [8]. Finally, in the fourth vignette, we evaluate carnivore population trends, and trends in carnivore group size, with hierarchical distance sampling models [23].

2. General methods

(a) Study area

The Reserve is primarily composed of open, rolling grassland that supports herds of resident and migrant herbivores and several species of mammalian carnivores that are present year-round [24–27]. Rainfall in the Reserve is bimodal, with most rain falling in November to December and March to May [28]. There is considerable variation in the exposure of carnivores to anthropogenic disturbance in the Reserve owing to the presence of two different management regimes within Reserve boundaries. The eastern portion of the Reserve, managed by the Narok County Government, has undergone massive increases in the number of human settlements and tourist facilities immediately outside the Reserve [8,29], as well as exponential growth in numbers of livestock grazing daily within Reserve boundaries [9,16,17,29]. The Talek region in particular, which is situated in the eastern

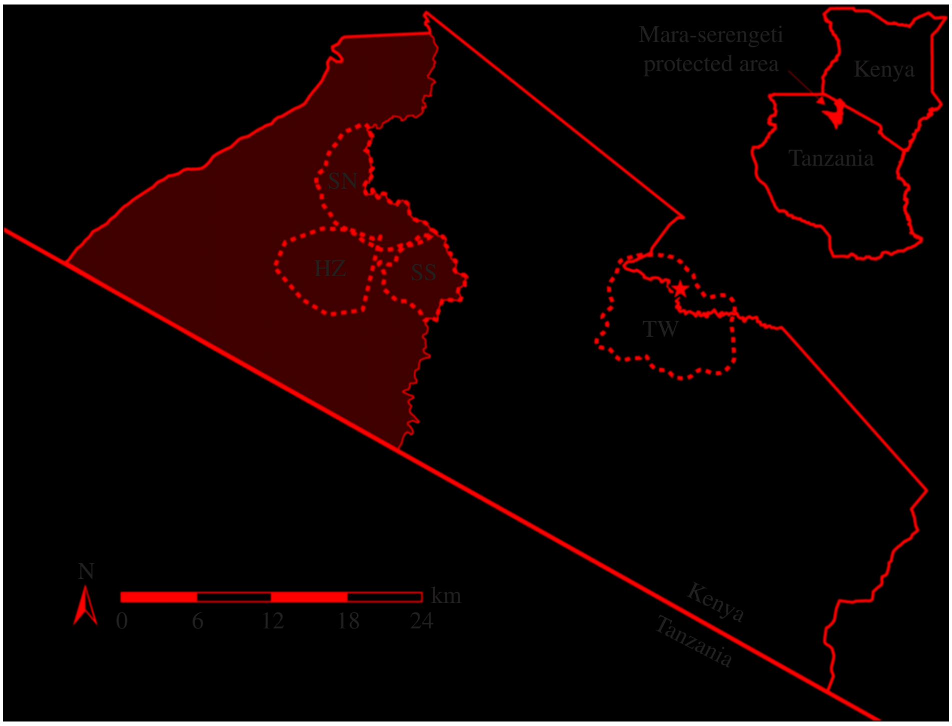


Figure 2. Map showing the territories of the four hyena clans used in our analyses located in the Masai Mara National Reserve within the Mara-Serengeti ecosystem: TW is the territory of the Talek West clan, SN is that of the Serena North clan, SS is that of the Serena South clan and HZ is that of the Happy Zebra clan. The grey shaded region indicates the Mara Triangle, the section of the Reserve that experiences relatively little disturbance, while the white region indicates the section of the Reserve that experiences higher levels of disturbance especially near Talek Town (star ★). The two regions are separated by the Mara River.

portion just inside the Reserve's northern boundary (figure 2), has been heavily affected by these forms of human activity. In contrast to the Talek region, however, other portions of the Reserve are largely unaffected by anthropogenic activity, and thus remain remarkably pristine. For example, the western portion of the Reserve, called the 'Mara Triangle,' has been managed by the Mara Conservancy since 2000 [30], and animals there encounter no livestock, and experience no anthropogenic activity other than limited visitation by tourist vehicles [8].

(b) Study animals

Spotted hyenas live in social groups, called clans, composed of adult females, their juvenile offspring, and one to several immigrant males. Each clan is structured by a linear dominance hierarchy, and an individual's position in its hierarchy determines its priority of access to food and other resources [31]. Clan members defend a shared territory [32]. Clans are fission–fusion societies in which hyenas spend much of their time alone or in small subgroups, and all members of the clan are seldom found together [33]. We used data collected from four monitored clans: one clan exposed to a high level of anthropogenic disturbance in the northeastern portion (the 'Talek region') of the Reserve (the 'Talek West' clan; figure 2) and three clans in the Mara Triangle exposed to relatively little anthropogenic disturbance ('Serena North', 'Serena South' and 'Happy Zebra'; figure 2). The Talek West clan has been monitored continuously from 1988 to the present and the other three clans have been monitored since 2008. All members of each study clan were known individually by their unique spots. We located and observed hyenas daily by systematically driving one to two vehicles throughout the territories of one or more study clans during morning (05.00–10.00 h) and evening (16.00–21.00 h) observation periods in both disturbed and undisturbed areas. Each time we found one or more hyenas separated from others by at least 200 m, we referred to the hyenas present there as a 'subgroup' of the clan. When a natal animal was seen for the first time, its birthdate was estimated to ± 7 days [34]; cubs are defined as animals less than 1 year old, juveniles are animals greater than or equal to 1 and less than 2 years old, and adults are animals greater than or equal to 2 years old. Mean monthly clan sizes were calculated as the total number of individuals in all age classes present during each month in which a particular clan was observed, and we calculated annual clan size as the mean of the monthly clan sizes. Standardized social ranks were calculated for all natal clan members ranging from 1 to -1 based on outcomes of dyadic aggressive interactions [35].

(c) Model analyses

Unless otherwise noted, analyses for each of the models presented in the vignettes were conducted using a Bayesian framework with Markov chain Monte Carlo in R with JAGS accessed with the 'JagsUI' package [36–38]. We used uninformative priors for all analyses and standardized continuous variables to have a mean of 0 and a standard deviation of 1. We assessed model convergence by visually inspecting the chains, and with the Gelman–Rubin statistic ($\hat{R}$) to ensure that all values were less than 1.1 [39,40]. We calculated probabilities (used in some vignettes) as the percentage of posterior draws above zero for given parameters. Further information regarding the modelling methods for each vignette can be found in the electronic supplementary material.

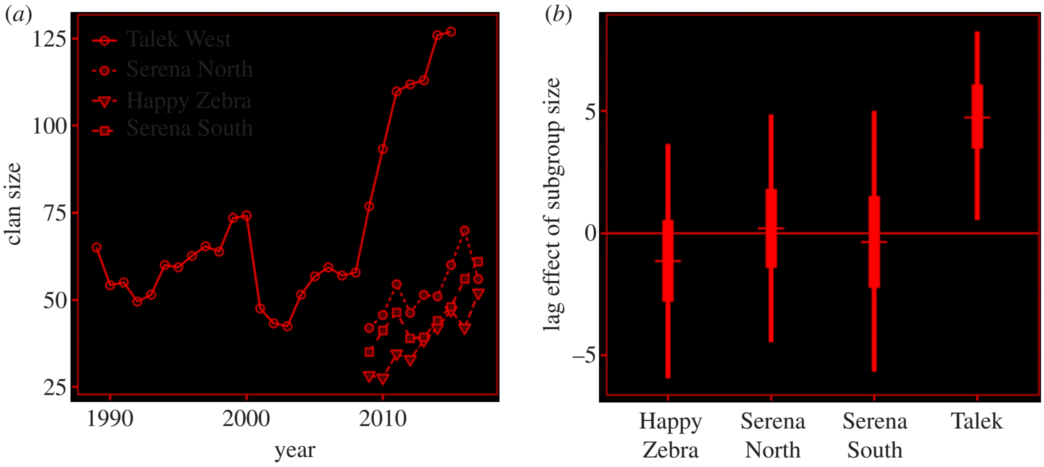


Figure 3. (*a*) Annual mean estimates of the total size of each of the four hyena clans monitored. (*b*) One year lag effect of the mean hyena subgroup size found at kills on clan size for each of the four clans. We estimated a 99.8% probability that subgroup size had a positive lag effect on clan size in Talek, but no effect was estimated on the other clans.

3. Vignettes: specific methods and results

(a) Vignette no. 1: hyena subgroup size at kills correlates with clan size in disturbed, but not undisturbed, areas

A prior study documented a rapid increase in hyena subgroup size at fresh ungulate kills immediately preceding a clan fission event that occurred in Talek West in 1989 [41]. This occurred as clan size increased owing to an influx of juveniles before the clan fission. Based on these findings, we hypothesized that changes in average subgroup size at kills might serve as an early behavioural indicator of future population abundance. We thus examined whether mean hyena subgroup size at kills in 1 year correlated with clan size the following year in Talek West (1989–2015) and each of the three Mara Triangle clans (2009–2017). All clans increased in size over time, although the Talek West clan, which was consistently the largest, increased most rapidly (figure 3*a*). We developed a hierarchical regression model to estimate annual mean size of each clan as a function of the previous year's mean clan size, the previous year's mean subgroup size at kills and an annual random effect.

Average yearly clan sizes in the Reserve ranged from 28 to 127 individuals (mean ± s.e.: 58.12 ± 3.12). Average yearly subgroup size of hyenas at kills ranged from 2.6 to 11.34 (mean ± s.e.: 7.19 ± 0.25). We found that subgroup size at kills the previous year was correlated with overall size of the Talek West clan (mean and 95% credible interval (CI) on the normal scale: 4.73; 0.55–8.25). However, we found no effect in any of the three study clans in the undisturbed region of the Reserve (figure 3*b*). The estimated relationship in the disturbed region is probably owing to the exceptionally high levels of sustained population growth in the Talek West clan. External factors specific to this region, such as human disturbance and lion declines, may also be responsible for the correlation between subgroup size at kills and clan size in the Talek region. Future research should investigate how subgroup sizes of hyenas at kills are also affected by factors such as prey size, seasonality and the presence of other carnivores, as this may elucidate the mechanisms linking behaviours with clan size.

(b) Vignette no. 2: monthly rates of lion–hyena interactions correlate with relative lion abundance

Anthropogenic disturbance is known to affect lion populations negatively [9,23]. Decreasing lion numbers appear to have a positive effect on hyena populations, as indicated by significant increases in survival of young hyenas to sexual maturity, reproductive success, and clan size [9,42]. A previous distance sampling analysis revealed that lion densities between 2012 and 2014 were lower in Talek West than in the Mara Triangle, whereas spotted hyena densities were higher in Talek West than the Mara Triangle [23]. Because we did not systematically monitor lions as we did spotted hyenas since 1988, we inquired whether a behavioural index might be useful in tracking lion populations in the territory of the Talek West clan.

Between 1988 and 2013, we monitored the number of times lions were found within 200 m of spotted hyenas in the Talek West clan. We recorded each time at least one lion was found with hyenas, deemed a 'lion–hyena interaction' (figure 4). Although this monitoring approach does not allow for direct estimation of the total number of lions in our study area, the method used to track lion–hyena interactions was consistent throughout the study period. We thus assumed that a change in the number of observed lion–hyena interactions reflects a true change in lion density [9]. To assess variation in lion–hyena interactions in the Talek West territory over time, we modelled temporal trends in their monthly frequency using a generalized linear mixed-effects model.

We recorded a total of 1188 lion–hyena interactions in 303 months of observations between 1988 and 2013. The number of lion–hyena interactions seen per month ranged from 0 to 18 (mean ± s.e.: 3.92 ± 0.23). The frequency of lion–hyena interactions in the territory of the Talek West clan declined significantly between 1988 and 2013 (intercept and (95% CI) mean estimate on the normal scale: 5.81 (4.34, 7.66); change per year mean estimate and (95% CI) −0.15 (− 0.32, −0.03)). Our results agree with a cross-sectional distance sampling analysis showing lower lion density in the Talek West region than in the Mara Triangle [23]. Thus, using the rate of lion–hyena interactions as a crude indicator of local lion abundance appears to work reasonably well.

Figure 4. An example of a lion–hyena interaction. (Online version in colour.)

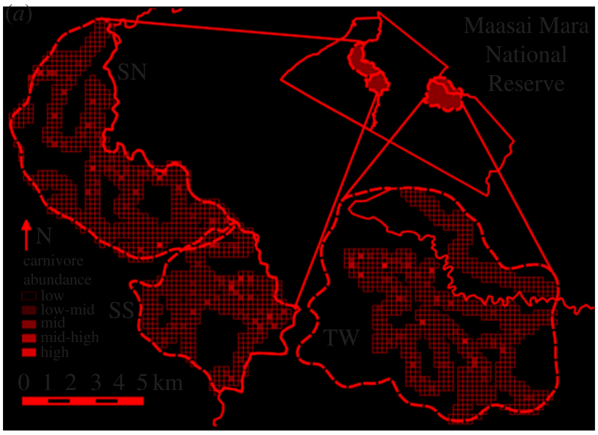
We ran an additional analysis on hyena demographic data to further examine links between lion–hyena interaction rates, declining lion abundance, and increasing hyena abundance. Using data from a complete census of hyenas for both the Talek West clan and the combined clans of the Mara Triangle, we separated the hyena recruitment process into fecundity (i.e. the number of cubs born), cub survival (i.e. survival probability of cubs to 1 year old), juvenile survival (i.e. survival probability of cubs to 2 years old) and adult survival (i.e. annual adult survival probability). We found that cub and juvenile survival of hyenas most strongly correlated (Pearson correlation: 0.50 and 0.42, respectively) with the growth rate of the Talek West clan, whereas fecundity was the strongest correlate of hyena clan growth rate in the Mara Triangle (Pearson correlation: 0.35). The large increases in clan size in Talek West after 2008 (figure 3*a*) may be attributable to increased cub and juvenile survival, possibly resulting from a decline in lions, which often kill young hyenas [43]. These results provide additional evidence that, in the presence of few lions (e.g. Talek region), cub and juvenile survival may drive clan growth, whereas in the presence of many lions (e.g. Mara Triangle), competition and intra-guild predation prevent cub and juvenile survival from driving clan growth.

(c) Vignette no. 3: hyena movement correlates with abundances of sympatric carnivores

Preliminary research suggests that the behaviour of spotted hyenas changed in response to disturbance a few years before changes in their population dynamics became apparent [17]. Thus, hyenas might emit early warning signals about their own future welfare. Here, we examine whether the behaviour of spotted hyenas might also correlate with abundances of sympatric carnivores. Hyenas are a top predator in the Reserve and we hypothesized that hyena movements, such as their speed, might influence other sympatric carnivore species. Furthermore, hyena movement speeds reflect variations in prey availability and avoidance of anthropogenic disturbance, and these factors are also likely to affect the demography and subsequent abundances of sympatric carnivore species. To inquire whether hyena movement behaviour is predictive of the future abundances of sympatric carnivores, we paired hyena movement speeds with systematic sampling of local-level sympatric carnivores.

We fitted six to eight spotted hyenas in each of three clans (Talek West, Serena North and Serena South) with GPS radio collars (Vectronic Aerospace, Berlin, Germany) in 2012. Collars were deployed on parous females of low and high ranks (i.e. only in the lowest and highest thirds, respectively, of the female rank hierarchy for that clan). We set the collars to record GPS locations of hyenas at hourly intervals from 1600 h to 1000 h, and once again at 1300 h. Hyena travel speeds were then calculated between successive hourly locations in the movement paths of the hyenas with the package ‘adehabitatLT’ in R [38,44].

We next estimated variation in abundance and distribution of carnivores by delineating a grid of 200 × 200 m cells within each hyena territory, and calculated the estimated abundance of each of the following species within cells every four to six weeks between July 2012 and March 2014: banded mongoose (*Mungos mungo*), bat-eared fox (*Otocyon megalotis*), black-backed jackal (*Canis mesomelas*), caracal (*Caracal caracal*), cheetah (*Acinonyx jubatus*), spotted hyena, leopard (*Panthera pardus*), lion, side-striped jackal (*Canis adustus*) and slender mongoose (*Galerella sanguinea*). Briefly, we defined sampling loop transects (henceforth, ‘loops’) within each territory to allow for maximum coverage and minimal opportunities for double counting wildlife, and estimated the abundance of carnivores using distance sampling, starting at sunrise ([45]; electronic supplemental material).



(*b*)

parameter	estimate (s.e.)	*Z*	*p*-value
14 weeks			
intercept	−2.604 (0.063)	−41.64	≤0.001
speed	**−0.281 (0.048)**	**−5.9**	**≤0.001**
rank (low)	**−0.722 (0.093)**	**−7.77**	**≤0.001**
20 weeks			
intercept	−2.709 (0.073)	−37.01	≤0.001
speed	**−0.158 (0.048)**	**−3.31**	**≤0.001**
rank (low)	**−0.216 (0.091)**	**−2.37**	**0.018**

Figure 5. (*a*) Variation in the abundance and distribution of carnivores within the Serena North (SN), Serena South (SS) and Talek West (TW) territories during the entire study. Darker shades indicate higher carnivore abundance within the 200 m × 200 m grid cell than within lighter cells. Non-gridded areas within territory boundaries indicate regions with no sampling effort. (*b*) Results from the generalized linear mixed-effects models that estimated carnivore abundance within grids as a function of the speed and rank of spotted hyenas during previous time steps (weeks 14 and 20). Significant parameter estimates (excluding the intercepts) are indicated in bold font ($p < 0.05$).

Abundances of carnivores varied among grid cells in our loops (figure 5*a*). To estimate the relationship between spotted hyena movement and local abundances of sympatric carnivores, we used the ‘glmmADMB’ package in R [38,46,47]. The abundance of carnivores in each cell was modelled as a function of the speeds at which collared hyenas moved in that same cell before the sampling event. We inquired how the movement of hyenas over the course of two weeks might correlate with the abundance of sympatric carnivores in our samples 14 and 20 weeks later. We investigated other time steps in preliminary analyses, but settled on these two-time points because loops were performed every four to six weeks and we wanted to look far enough into the future such that any environmental changes affecting hyena behaviour would have time to manifest in the abundances of sympatric carnivores. All speeds of hyena movement were standardized to have a mean of 0 and a standard deviation of 1. We also included social rank in our models to inquire how movements of low- and high-ranking hyenas might correlate differently with the abundance of sympatric carnivores.

From 22 adult female hyenas fitted with GPS collars, we collected a total of 138 751 locations that were separated by 1 h (mean number of locations ± s.e. per hyena: 6306.9 ± 619.4) on 953 nights (mean number of nights ± s.e. per hyena: 498.4 ± 38.5) between April 2012 and November 2014. We recorded 1838 individuals of 11 carnivore species while running loops 16 times in the Talek region and Mara Triangle. Cells in which spotted hyenas moved faster were correlated with fewer sympatric carnivores at both 14 and 20 weeks in the future ($p < 0.05$; figure 5*b*). Social rank of the collared hyenas was also a significant negative predictor of numbers of sympatric carnivores; cells in which hyenas of low rank were more likely to be found contained fewer carnivores 14 and 20 weeks later ($p < 0.05$; figure 5*b*) than did cells in which high-ranking hyenas occurred. Although the exact mechanisms mediating this effect are unclear, future research should investigate whether these results may be associated with anthropogenic disturbance or ecological change and determine whether this relationship is robust, occurring in other environments and ecosystems.

(d) Vignette no. 4: disturbance affects carnivore behaviour and abundance

Species may alter their behaviour in response to disturbance, which may eventually lead to shifts in abundance and community structure (figure 1). Carnivores within the Reserve were previously shown to have varying responses to anthropogenic disturbance with regard to both their behaviour (i.e. subgroup size) and abundance [23]. Most carnivore species had lower abundances in the disturbed Talek region, with the only exceptions being black-backed jackal and spotted hyena (figure 6*a*). Additionally, only spotted hyenas showed no effect of disturbance on subgroup size, whereas all other carnivore species had smaller subgroup sizes in the disturbed Talek region than in the undisturbed Mara Triangle (figure 6*b*). Here, we further explored the unique responses of spotted hyena and black-backed jackal to disturbance, and evaluated whether changes in behaviour (i.e. subgroup size) are linked to changes in abundance (i.e. number of subgroups).

We applied a single-species version of the multi-species distance sampling model developed by Farr *et al.* [23] using the loop transect data described in vignette no. 3 to examine why the subgroup size of hyenas was larger in the disturbed area while the subgroup size of jackals was larger in the undisturbed area, despite both species having higher numbers of subgroups in the disturbed region. We included effects of lions (i.e. the apex predator), domestic cattle, and domestic sheep and goat densities (estimated via distance sampling and standardized; electronic supplementary material) as potential factors related to the variation in numbers of subgroups and subgroup size of hyenas or black-backed jackals in addition to an indicator variable of disturbance (electronic supplementary material). As expected, the single-species models showed that spotted hyenas had a 99.1% probability (mean and 95% CI (log-scale): 1.14 (0.21, 2.09)) and black-backed jackals had a 92.2% probability (0.94 (−0.33, 2.49)) of having a greater number of subgroups in the Talek region than in the Mara Triangle. Spotted hyenas had a 98.1% probability of having larger subgroup sizes (0.66 (0.33, 1.35)) in the Talek region than in the Mara Triangle, but black-backed jackals had a

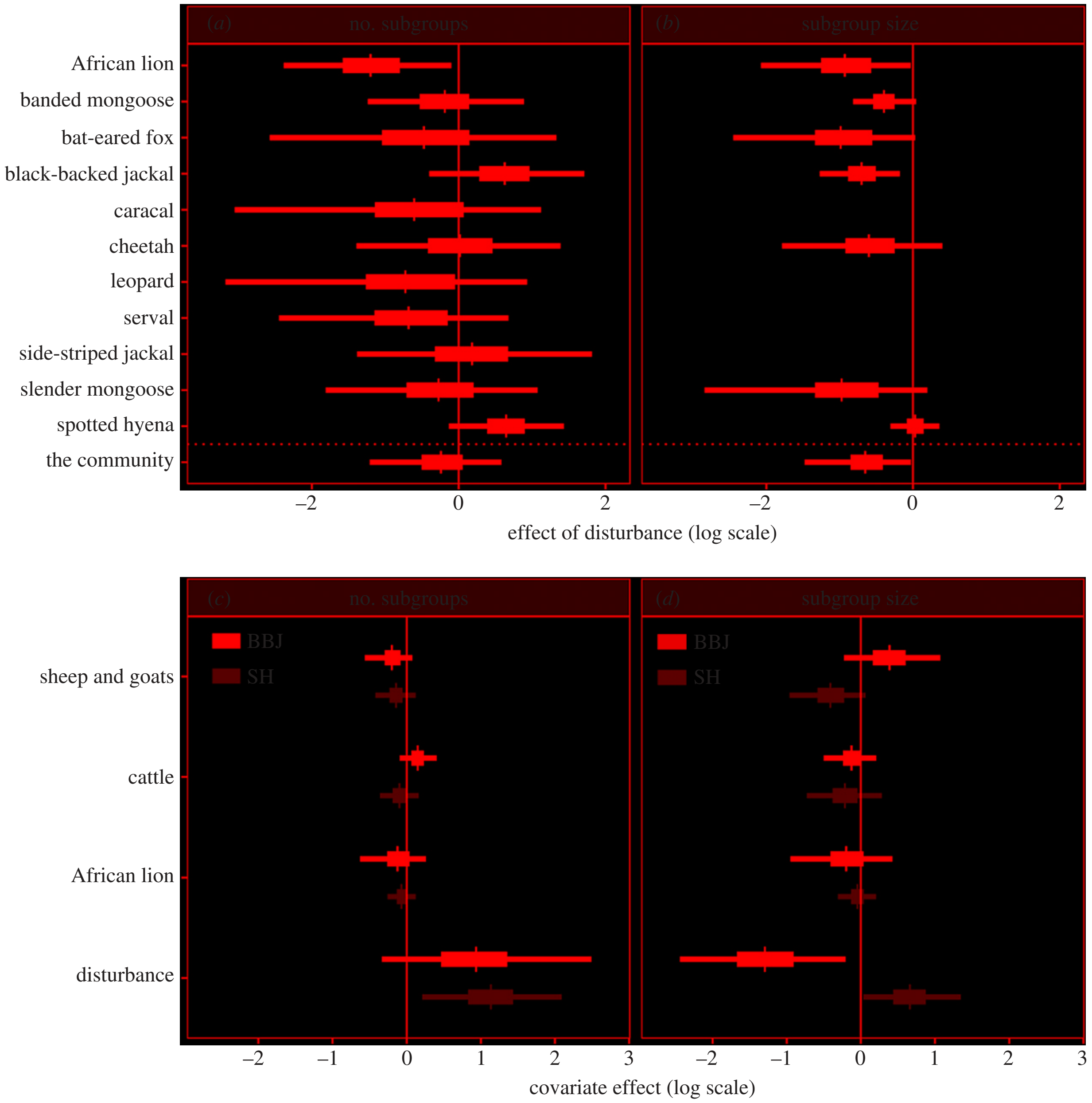


Figure 6. Parameter estimates from a community model (*a*,*b*) and a single-species model for black-backed jackal and spotted hyena (*c*,*d*) showing the effects of disturbance (log scale) on the number of subgroups and subgroup sizes. Note that a positive effect of disturbance is interpreted as a higher value in the Talek region than in the Mara Triangle. Mean values are indicated with small vertical bars; 50% and 95% credible intervals are shown with thick and thin horizontal bars, respectively. (*a*) Effect of disturbance on the expected number of individuals or subgroups for all species as estimated using a community model. (*b*) Effect of disturbance on the expected subgroup size for each species estimated with a community model. (*c*) Estimates of the effects of disturbance, African lion, cattle and sheep/goats on the expected number of black-backed jackal (BBJ) and spotted hyena (SH) subgroups estimated in single-species models. (*d*) Estimates of the effects of disturbance, African lion, cattle and sheep/goats on the expected subgroup size of black-backed jackal and spotted hyena estimated with single-species models.

98.9% probability of having smaller subgroup sizes (−1.30 (−2.44, −0.21)) in the Talek region than in the Mara Triangle.

As for the mechanisms driving hyena and jackal abundance and behaviour: lion, cattle, and sheep and goat densities had slight negative to virtually no effects on the number of hyena subgroups and subgroup size (figure 6*c*,*d*). The effects of these variables on black-backed jackal abundance varied, but were also all weak. In this case, our results highlight the difficulty of determining exactly how behavioural change is linked to change in abundance. The spotted hyena's unique response to disturbance, and the variable response of black-backed jackals, makes it difficult to directly link changes in hyena behaviour to unidirectional changes in abundances of sympatric carnivores.

4. Discussion

Our vignettes revealed a series of interesting relationships between hyena behaviours and the population trends of both hyenas and other sympatric species within the carnivore community. However, our results also suggest that using behavioural indices to infer trends in the abundance and demography of carnivores has its challenges. Some of our results suggest relationships between hyena behaviours and demographic parameters (e.g. subadult survival, fecundity, and the abundances of hyenas and other sympatric species), but we did not find this in all our analyses. Nevertheless, we believe our vignettes represent an important initial step in exploring links between behaviour, population size, and community structure. More work should be done to investigate the robustness of such relationships, and to determine whether it is feasible and advisable to integrate behavioural studies into long-term carnivore monitoring.

The results from our four vignettes suggest that certain hyena behaviours may be useful for providing information on demographic trends in hyenas themselves and sympatric carnivores. The sizes of hyena subgroups found at ungulate kills were related to overall clan size the following year in the disturbed Talek West territory, but not in the territories of undisturbed clans. Because we observed only one clan living in a disturbed area, we cannot assume that this relationship will necessarily hold in other clans. The estimated relationship, however, is nonetheless intriguing, and future research might continue to explore how subgroup sizes at kills change relative to hyena abundance across a gradient of habitat variables. Monthly rates of lion–hyena interactions appeared to correlate with local lion abundance, and we found that growth rates among hyena clans are driven by cub and juvenile survival in the presence of few lions, but by fecundity in the presence of many lions. Interestingly, movement speeds of collared female hyenas correlated with the abundance of sympatric carnivores roughly five months in the future. We can only speculate as to why hyenas move faster in areas later found to contain fewer sympatric carnivores. It may be that these areas contain lower prey densities or are exposed to more anthropogenic disturbance, or it is possible that the occurrence and movement of hyenas deters other species. It is impractical to collar hyenas solely to assess population trends in sympatric carnivores from hyena behaviour, but where behaviour monitoring is already underway, our results suggest that such data can provide useful auxiliary information on the community. In our final vignette, we found variable responses to disturbance across the carnivore community. This variation, in addition to the difficulty in identifying explicit mechanisms linking changes in behaviour to changes in abundance, presents a challenge to using hyena behaviour to assess sympatric species abundances and highlights the need for additional research in this area.

For many animals, a critical element of their success, or lack thereof, is their behavioural response to human-induced environmental change [4]. As with other large African carnivores, the range of the spotted hyena has shrunk considerably in recent decades owing largely to human population growth and associated changes in land-use patterns [48]. Whereas many other carnivores are declining, the spotted hyena is currently listed by the International Union for Conservation of Nature as a species of ‘Least Concern’ [49], and it appears to cope successfully with human disturbance owing to its enormous behavioural and ecological plasticity [5]. Our results suggest that this plasticity in spotted hyenas may aid in understanding the status of sympatric species, and that anthropogenic disturbance may disproportionately affect less plastic species (e.g. lions). Any restructuring of the carnivore community may have important ramifications with respect to conflicts between carnivores and humans or their livestock. Around the Masai Mara National Reserve, spotted hyenas represent one of the major sources of such conflicts [50], and reduced lion populations may have unforeseen negative consequences for local communities owing to competitive release of hyenas.

Methods for documenting carnivore population trends should ideally be easy and cost-effective to implement, and integrate well with existing monitoring initiatives suggested by international conservation organizations (e.g. Convention on International Trade in Endangered Species of Wild Fauna and Flora). Spotted hyenas occur throughout sub-Saharan Africa, and their behaviour is easier to observe than that of many other carnivore species living sympatrically with them, and they may thus be useful in this regard. We found links between hyena subgroup sizes and clan sizes, lion–hyena interactions and relative lion numbers, and hyena movement speeds and sympatric carnivore abundance. These relationships, however, did not occur consistently in both disturbed and undisturbed areas. We also must validate our methods on a wider spatial scale before behavioural results can be integrated into ongoing monitoring efforts. Nevertheless, we suggest that behavioural analyses, such as those presented in our vignettes, can be used in conjunction with more standard trend assessment techniques to improve understanding of changing carnivore populations and communities as well as their conservation and management.

Ethics. This work was approved by the Michigan State University Institutional Animal Care and Use Committe most recently in approval no. 05/14/087-00.

Data accessibility. Data and code are publicly available at https://github.com/farrmt/Green_etal_2019_PTRS.

Authors’ contributions. K.E.H. and D.S.G. provided the data, then M.T.F., D.S.G., E.D.S. and E.F.Z. analysed the data and performed the modelling. All authors contributed to writing the manuscript and gave final approval for publication.

Competing interests. We declare we have no competing interests.

Funding. This work was supported by NSF grant nos DEB1353110, OISE1556407, OISE1853934 and IOS1755089 to K.E.H. and E.F.Z., by an award from the Kenya Wildlife Trust to K.E.H., and by Graduate Research Fellowships from NSF to E.D.S. and D.S.G. M.T.F. was supported by Fellowships from the Quantitative Biology program and also from the program in Ecology, Evolutionary Biology and Behaviour at Michigan State University.

Acknowledgements. We thank the many former graduate students and research assistants on the Mara Hyena Project who contributed to data collection. The Kenyan National Commission for Science, Technology and Innovation, the Narok County Government, The Mara Conservancy and the Kenya Wildlife Service provided permission to conduct this work. We thank Brian Heath for allowing us to study carnivores in the Mara Triangle, and for maintaining the Mara Triangle in such pristine condition. We also thank Jakob Bro-Jørgensen and two anonymous reviewers for many useful comments on the paper.

References

1. Ripple WJ *et al.* 2014 Status and ecological effects of the world’s largest carnivores. *Science* **343**, 1241484. (doi:10.1126/science.1241484)
2. Wong BBM, Candolin U. 2015 Behavioral responses to changing environments. *Behav. Ecol.* **26**, 665–673. (doi:10.1093/beheco/aru183)
3. Sih A. 2013 Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Anim. Behav.* **85**, 1077–1088. (doi:10.1016/j.anbehav.2013.02.017)
4. Sih A, Trimmer PC, Ehlman SM. 2016 A conceptual framework for understanding behavioral responses to HIREC. *Curr. Opin.*

Behav. Sci. **12**, 109–114. (doi:10.1016/j.cobeha.2016.09.014)

5. Holekamp KE, Dloniak SM. 2010 Chapter 6 - intraspecific variation in the behavioral ecology of a tropical carnivore, the spotted hyena. *Adv. Study Behav.* **42**, 189–229. (doi:10.1016/S0065-3454(10)42006-9)
6. Abay GY, Bauer H, Gebrihiwot K, Deckers J. 2011 Peri-urban spotted hyena (*Crocuta crocuta*) in Northern Ethiopia: diet, economic impact, and abundance. *Eur. J. Wildl. Res.* **57**, 759–765. (doi:10.1007/s10344-010-0484-8)
7. Yirga G, Leirs H, De Iongh HH, Asmelash T, Gebrehiwot K, Vos M, Bauer H. 2017 Densities of spotted hyaena (*Crocuta crocuta*) and African golden wolf (*Canis anthus*) increase with increasing anthropogenic influence. *Mamm. Biol.* **85**, 60–69. (doi:10.1016/j.mambio.2017.02.004)
8. Green DS. 2015 Anthropogenic disturbance, ecological change, and wildlife conservation at the edge of the Mara-Serengeti ecosystem. PhD thesis, Michigan State University, MI, USA. (doi:10.25335/M5V139)
9. Green DS, Johnson-Ulrich L, Couraud HE, Holekamp KE. 2018 Anthropogenic disturbance induces opposing population trends in spotted hyenas and African lions. *Biodivers. Conserv.* **27**, 871–889. (doi:10.1007/s10531-017-1469-7)
10. Ogutu JO, Piepho H-P, Dublin HT, Bhola N, Reid RS. 2009 Dynamics of Mara–Serengeti ungulates in relation to land use changes. *J. Zool.* **278**, 1–14. (doi:10.1111/j.1469-7998.2008.00536.x)
11. Ogutu JO, Owen-Smith N, Piepho HP, Said MY. 2011 Continuing wildlife population declines and range contraction in the Mara region of Kenya during 1977–2009. *J. Zool.* **285**, 99–109. (doi:10.1111/j.1469-7998.2011.00818.x)
12. Ogutu JO, Piepho H-P, Said MY, Ojwang GO, Njino LW, Kifugo SC, Wargute PW. 2016 Extreme wildlife declines and concurrent increase in livestock numbers in Kenya: what are the causes? *PLoS ONE* **11**, e0163249. (doi:10.1371/journal.pone.0163249)
13. Veldhuis MP *et al.* 2019 Cross-boundary human impacts compromise the Serengeti-Mara ecosystem. *Science* **363**, 1424–1428. (doi:10.1126/science.aav0564)
14. Van Meter PE, French JA, Dloniak SM, Watts HE, Kolowski JM, Holekamp KE. 2009 Fecal glucocorticoids reflect socio-ecological and anthropogenic stressors in the lives of wild spotted hyenas. *Horm. Behav.* **55**, 329–337. (doi:10.1016/j.yhbeh.2008.11.001)
15. Pangle WM, Holekamp KE. 2010 Lethal and nonlethal anthropogenic effects on spotted hyenas in the Masai Mara National Reserve. *J. Mamm.* **91**, 154–164. (doi:10.1644/08-MAMM-A-359R.1)
16. Boydston E, Kapheim KM, Watts HE, Szykman M, Holekamp KE. 2003 Altered behaviour in spotted hyenas associated with increased human activity. *Anim. Conserv.* **6**, 207–219. (doi:10.1017/S1367943003003263)
17. Kolowski JM, Holekamp KE. 2009 Ecological and anthropogenic influences on space use by spotted hyaenas. *J. Zool.* **277**, 23–36. (doi:10.1111/j.1469-7998.2008.00505.x)
18. Kolowski JM, Katan D, Theis KR, Holekamp KE. 2007 Daily patterns of activity in the spotted hyena. *J. Mamm.* **88**, 1017–1028. (doi:10.1644/06-MAMM-A-143R.1)
19. Greenberg JR. 2017 Developmental flexibility in spotted hyenas (*Crocuta crocuta*): the role of maternal and anthropogenic effects. PhD thesis, Michigan State University, MI, USA. (doi:10.25335/M5B87K)
20. Turner JW. 2018 Social development and its influence on adult traits in the spotted hyena. PhD thesis, Michigan State University, MI, USA. (doi:10.25335/M5SJ19T6G)
21. Greenberg JR, Holekamp KE. 2017 Human disturbance affects personality development in a wild carnivore. *Anim. Behav.* **132**, 303–312. (doi:10.1016/j.anbehav.2017.08.023)
22. Belton LE, Cameron EZ, Dalerum F. 2018 Social networks of spotted hyaenas in areas of contrasting human activity and infrastructure. *Anim. Behav.* **135**, 13–23. (doi:10.1016/j.anbehav.2017.10.027)
23. Farr MT, Green DS, Holekamp KE, Roloff GJ, Zipkin EF. 2019 Multispecies hierarchical modeling reveals variable responses of African carnivores to management alternatives. *Ecol. Appl.* **29**, e01845. (doi:10.1002/eap.1845)
24. Bell RHV. 1971 A grazing ecosystem in the Serengeti. *Sci. Am.* **225**, 86–93. (doi:10.1038/scientificamerican0771-86)
25. Sinclair ARE, Norton-Griffiths M. 1979 *Serengeti: dynamics of an ecosystem*. Chicago, IL: The University of Chicago Press.
26. Stelfox JG, Peden DG, Epp H, Hudson RJ, Mbugua SW, Agatsiva JL, Amuyunzu CL. 1986 Herbivore dynamics in southern Narok, Kenya. *J. Wildl. Manage.* **50**, 339–347. (doi:10.2307/3801925)
27. Craft ME, Hampson K, Ogutu JO, Durant SM. 2015 Carnivore communities in the greater Serengeti ecosystem. In *Serengeti IV: sustaining biodiversity in a coupled human-natural system* (eds ARE Sinclair, KL Metzger, SAR Mduma, JM Fryxell), pp. 419–447. Chicago, IL: University of Chicago Press.
28. Ogutu JO, Piepho HP, Dublin HT, Bhola N, Reid RS. 2008 Rainfall influences on ungulate population abundance in the Mara-Serengeti ecosystem. *J. Anim. Ecol.* **77**, 814–829. (doi:10.1111/j.1365-2656.2008.01392.x)
29. Lamprey RH, Reid RS. 2004 Expansion of human settlement in Kenya's Maasai Mara: what future for pastoralism and wildlife? *J. Biogeogr.* **31**, 997–1032. (doi:10.1111/j.1365-2699.2004.01062.x)
30. Walpole MJ, Leader-Williams N. 2001 Masai Mara tourism reveals partnership benefits. *Nature* **413**, 771. (doi:10.1038/35101762)
31. Tilson RL, Hamilton III WJ. 1984 Social dominance and feeding patterns of spotted hyaenas. *Anim. Behav.* **32**, 715–724. (doi:10.1016/S0003-3472(84)80147-5)
32. Kruuk H. 1972 *The spotted hyena: a study of predation and social behavior*. Chicago, IL: University of Chicago Press.
33. Smith JE, Kolowski JM, Graham KE, Dawes SE, Holekamp KE. 2008 Social and ecological determinants of fission-fusion dynamics in the spotted hyaena. *Anim. Behav.* **76**, 619–636. (doi:10.1016/j.anbehav.2008.05.001)
34. Holekamp KE, Smale L, Szykman M. 1996 Rank and reproduction in the female spotted hyaena. *Reproduction* **108**, 229–237. (doi:10.1530/jrf.0.1080229)
35. Holekamp KE, Smale L. 1993 Ontogeny of dominance in free-living spotted hyaenas: juvenile rank relations with other immature individuals. *Anim. Behav.* **46**, 451–466. (doi:10.1006/anbe.1993.1214)
36. Plummer M. 2003 JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. See https://www.r-project.org/conferences/DSC-2003/Drafts/Plummer.pdf.
37. Kellner K. 2017 jagsUI: a wrapper around 'rjags' to streamline 'JAGS' analyses. R package version 1.4.8. See https://CRAN.R-project.org/package=jagsUI.
38. R Core Team. 2017 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See http://www.R-project.org/.
39. Gelman A, Meng XL, Stern H. 1996 Posterior predictive assessment of model fitness via realized discrepancies. *Stat. Sinica* **6**, 733–760.
40. Gelman A, Carlin JB, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin DB. 2013 *Bayesian data analysis*, 3rd edn. Boca Raton, FL: Chapman and Hall/CRC.
41. Holekamp KE, Ogutu JO, Dublin HT, Frank LG, Smale L. 1993 Fission of a spotted hyena clan: consequences of prolonged female absenteeism and causes of female emigration. *Ethology* **93**, 285–299. (doi:10.1111/j.1439-0310.1993.tb01210.x)
42. Watts HE, Holekamp KE. 2008 Interspecific competition influences reproduction in spotted hyenas. *J. Zool.* **276**, 402–410. (doi:10.1111/j.1469-7998.2008.00506.x)
43. Périquet S, Fritz H, Revilla E. 2015 The lion king and the hyaena queen: large carnivore interactions and coexistence. *Biol. Rev.* **90**, 1197–1214. (doi:10.1111/brv.12152)
44. Calenge C. 2006 The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Modell.* **197**, 516–519. (doi:10.1016/j.ecolmodel.2006.03.017)
45. Buckland ST, Anderson D, Burnham KP, Laake JL. 1993 *Distance sampling: estimating abundance of biological populations*. Oxford, UK: Oxford University Press.
46. Fournier DA, Skaug HJ, Ancheta J, Ianelli J, Magnusson A, Maunder MN, Nielsen A, Sibert J. 2012 AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optim. Methods Softw.* **27**, 233–249. (doi:10.1080/10556788.2011.597854)
47. Skaug H, Fournier D, Bolker B, Magnusson A, Nielsen A. 2016 glmmADMB: Generalized linear mixed models using 'AD Model Builder'. R package version 0.8.3.3. See http://glmmadmb.r-forge.r-project.org.
48. Mills M, Hofer H. 1998 *Hyaenas: status survey and conservation action plan*. Gland, Switzerland: IUCN.
49. Bohm T, Höner OR. 2016 Crocuta crocuta. *The IUCN Red List of Threatened Species* 2015, e. T5674A45194782. See https://www.iucnredlist.org/species/5674/45194782.
50. Kolowski JM, Holekamp KE. 2006 Spatial, temporal, and physical characteristics of livestock depredations by large carnivores along a Kenyan reserve border. *Biol. Conserv.* **128**, 529–541. (doi:10.1016/j.biocon.2005.10.021)