

# Group formation stabilizes predator–prey dynamics

John M. Fryxell<sup>1</sup>, Anna Mosser<sup>2</sup>, Anthony R. E. Sinclair<sup>3</sup> & Craig Packer<sup>2</sup>

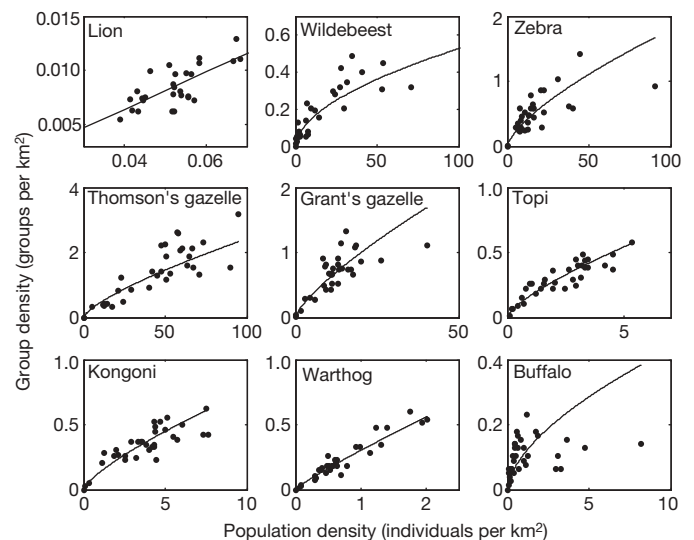
Theoretical ecology is largely founded on the principle of mass action, in which uncoordinated populations of predators and prey move in a random and well-mixed fashion across a featureless landscape. The conceptual core of this body of theory is the functional response, predicting the rate of prey consumption by individual predators as a function of predator and/or prey densities<sup>1–5</sup>. This assumption is seriously violated in many ecosystems in which predators and/or prey form social groups. Here we develop a new set of group-dependent functional responses to consider the ecological implications of sociality and apply the model to the Serengeti ecosystem. All of the prey species typically captured by Serengeti lions (*Panthera leo*) are gregarious, exhibiting nonlinear relationships between prey-group density and population density. The observed patterns of group formation profoundly reduce food intake rates below the levels expected under random mixing, having as strong an impact on intake rates as the seasonal migratory behaviour of the herbivores. A dynamical system model parameterized for the Serengeti ecosystem (using wildebeest (*Connochaetes taurinus*) as a well-studied example) shows that grouping strongly stabilizes interactions between lions and wildebeest. Our results suggest that social groups rather than individuals are the basic building blocks around which predator–prey interactions should be modelled and that group formation may provide the underlying stability of many ecosystems.

Although the adult population of Serengeti lions has shown considerable variation in total abundance over the past 27 years (ref. 6), most of this variation is accommodated by changes in the number of prides in a given area (Fig. 1;  $y = -1.0939 + 0.173x$ ,  $R^2 = 0.524$ ,  $F_{1,26} = 28.59$ ,  $P < 0.001$ ). As a consequence, the mean number of adult lions per pride ( $G$ ) has not varied significantly with population abundance ( $F_{1,26} = 0.002$ ,  $P = 0.844$ ), averaging 6.3 adults per group. During periods when lions are abundant, variation in pride size tends to increase as a result of the successful recruitment of offspring as well as the formation of smaller prides by fission<sup>6</sup>.

All eight of the lions' most common prey species are gregarious; thus, the rate at which lions encounter their prey depends on the density of herds rather than individuals. We estimated the lions' prey encounter rates by driving 33 ground censuses across the lion study area between 2004 and 2007, recording the density of prey groups per unit area and relating group density to individual density, with prey groups operationally defined as any individuals occurring within a 2-ha area. Although the frequency of encounter with prey groups was positively associated with prey density (Fig. 1), the best fit ( $R^2 = 0.76–0.98$ ) was always provided by a simple power function ( $y = cN^b$ ), where  $y$  is herd density per km<sup>2</sup>,  $c$  and  $b$  are the intercept and exponent of the power curve, and  $N$  is the prey density per km<sup>2</sup>. In each species, the best-fit estimate of the exponent  $b$  was significantly less than 1 (see Supplementary Information), implying that each doubling of prey density leads to a much more modest increase in encounter frequency with groups.

We used the Serengeti data to develop four alternative functional responses by lions feeding on wildebeest (Box 1): a null response, assuming that lions forage solitarily and prey are randomly distributed (equation (1) in Box 1), a grouped lion functional response (equation (2)), a grouped prey response (equation (3)), and a functional response assuming group formation both by lions and their prey (equation (4)). Group formation by either species depresses the attack rate at a given population density, but group formation by both lions and wildebeest is especially effective (Fig. 2).

If we assume that both species were solitary, local stability analysis confirms that a lion–wildebeest system with parameters taken from Serengeti would be unstable for most combinations of conversion efficiency ( $\epsilon$ , which is defined as the rate with which wildebeest biomass is converted to lion biomass) and lion mortality rate ( $d$ ) (Fig. 3a). The potential for local stability is increasingly enhanced by group formation by lions (Fig. 3b), by wildebeest (Fig. 3c) and by both lions and wildebeest (Fig. 3d). Nonlinear relationships between group density and prey population density are not essential for stabilization. For example, a linear relationship between wildebeest group density and population density data would be even more strongly stabilizing than the nonlinear best-fit model shown in Fig. 1. The key requirement for a stabilizing effect is that prey-group density is lower than individual density.



**Figure 1 | Group density in relation to population density for Serengeti lions and their predominant eight prey species.** Herbivore prey include wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*), Thomson's gazelle (*Gazella thomsoni*), Grant's gazelle (*Gazella granti*), topi (*Damaliscus korrigum*), kongoni (*Alcelaphus buselaphus*), warthog (*Phacochoerus aethiopicus*) and Cape buffalo (*Syntherus caffer*). Lines show best-fit power functions for herbivores and the best-fit linear function for lions, based on least-squares minimization.

<sup>1</sup>Department of Integrative Biology, University of Guelph, 50 Stone Road East, Guelph, Ontario, Canada, N1G 2W1. <sup>2</sup>Department of Ecology, Evolution, and Behavior, University of Minnesota, 1987 Upper Buford Circle, St Paul, Minnesota 55108, USA. <sup>3</sup>Zoology Department, University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia, Canada, V6T 1Z4.

**Box 1 | Group-dependent functional responses**

If lions forage solitarily, the expected type II functional response<sup>1</sup> is

$$\Psi(N) = \frac{aN}{1 + a(h_1 + h_2)N} \quad (1)$$

where  $a$  is the area of effective search per unit time,  $h_1$  is the expected time to attack and subdue each prey item,  $h_2$  is the expected time to consume and digest each prey item,  $N$  is prey density per km<sup>2</sup>, and  $\Psi(N)$  is prey intake per predator per day.

Group formation by predators changes the handling time of prey (see Methods), leading to the functional response

$$\Psi(N, G) = \frac{aN}{G + a(Gh_1 + h_2)N} \quad (2)$$

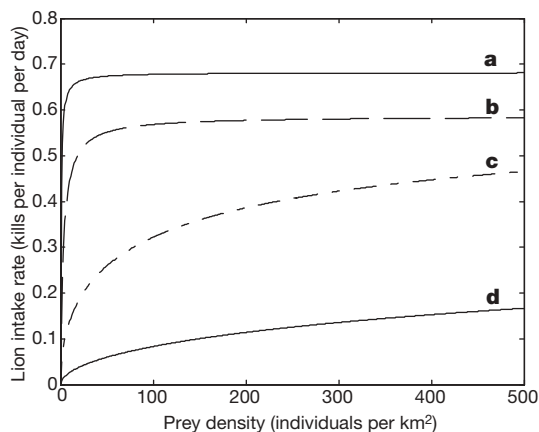
where  $G$  is the predator group size. We can evaluate the effect of prey group formation by inserting a modified encounter rate ( $acN^b$ ) into the standard type II functional response (equation (1)), where  $c = \exp(\text{intercept})$  and  $b$  is the slope of the linear regression of  $\ln(\text{prey group density})$  versus  $\ln(\text{prey density}, N)$ . This alters the functional response to

$$\Psi(N) = \frac{acN^b}{1 + a(h_1 + h_2)cN^b} \quad (3)$$

Equations (2) and (3) can be combined to calculate the functional response when both predators and their prey form groups:

$$\Psi(N, G) = \frac{acN^b}{G + a(Gh_1 + h_2)cN^b} \quad (4)$$

Herd formation reduces search efficiency by predators by creating 'holes' across the landscape that would otherwise be occupied by asocial prey, analogous to the effects of weak diffusive movement by predators and/or prey<sup>7–14</sup>. Sociality accordingly has important dynamical implications because of the reduced frequency with which predators encounter prey<sup>3,13</sup>. In contrast, group formation by predators limits search efficiency to a level similar to a solitary predator because of overlapping perceptual ranges. Although cooperation may compensate, at least to some degree, for the reduced capture rates implicit in the group-dependent functional response, the available evidence does not convincingly demonstrate such an effect<sup>15</sup>. Most individual lions refrain from contributing to group hunts except when pursuing Cape buffalo (*Synserus caffer*), which are inaccessible to solitary individuals or small groups<sup>16</sup>. The fact that natural selection has favoured sociality in lions despite the sizeable cost in terms of prey capture suggests that the compensating benefits must be profound. Lion sociality derives from the greater reproductive success of mothers that defend their cubs cooperatively against infanticidal males<sup>17</sup> and the advantages of group territoriality against neighbouring prides<sup>18,19</sup>.



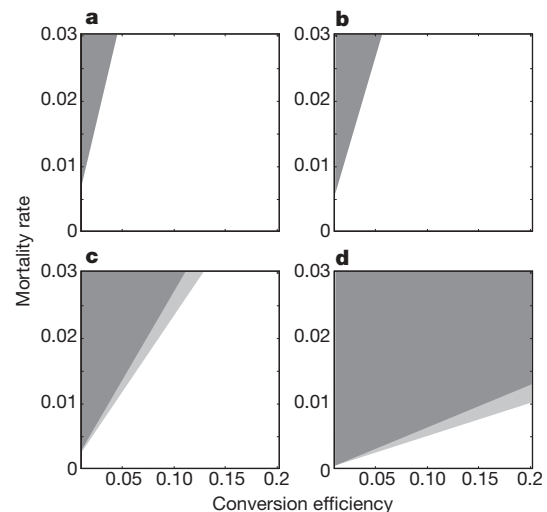
**Figure 2 | Predicted effects of group formation by Serengeti lions and/or their prey on the functional response of individual lions.** **a**, Both predators and prey are solitary; **b**, only predators are gregarious; **c**, only prey are gregarious; **d**, both predators and prey are gregarious.

Previous Serengeti models have shown that herbivore migration provides a seasonal escape from lion predation<sup>20</sup>. Several important prey species (wildebeest, zebra (*Equus burchelli*), Thomson's gazelles (*Gazella thomsoni*) and Grant's gazelles (*Gazella granti*)) spend most of the year in areas far out of reach of a given lion pride. As a result of migratory movements, wildebeest densities varied considerably across the monthly censuses (see Supplementary Information). We assessed the impact of wildebeest movement on lion foraging by comparing average prey intake during censuses that were above the median group density of 0.205 wildebeest groups per km<sup>2</sup> and those that were below the median. In periods when wildebeest were abundant, lion feeding rates averaged  $0.074 \pm 0.038$  wildebeest per day (mean  $\pm$  s.d.;  $n = 15$ ), whereas when wildebeest were scarce, lion feeding rates averaged  $0.013 \pm 0.0092$  wildebeest per day ( $n = 15$ ), a reduction of 82%.

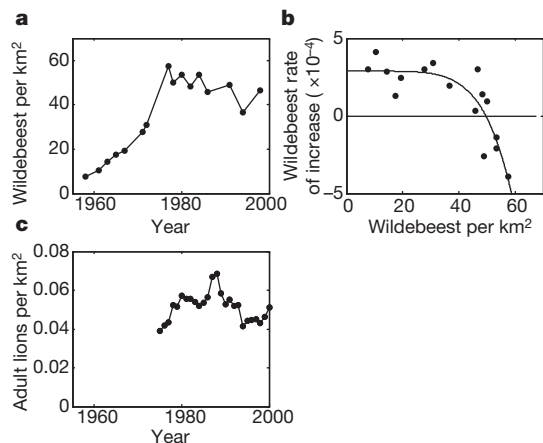
Using wildebeest densities at carrying capacity ( $N = 49.6 \text{ km}^{-2}$ ) as a point of reference, the group-dependent functional response (equation (4)) yields a kill rate of 0.064 wildebeest per lion per day, whereas the non-group-dependent functional response (equation (1)) predicts a kill rate of 0.674 wildebeest per lion per day, a reduction of 90%. The reduction in kill rates as a result of group formation (90%) is therefore similar to the effect of migration (82%). Group formation and migration are complementary processes, reducing the rate of wildebeest predation by lions by nearly two orders of magnitude when acting in tandem.

Previous demographic analyses of the Serengeti wildebeest suggested that starvation inflicted a greater magnitude of mortality than predation and that food limitation was density-dependent<sup>21</sup>. The time-series data show little indication of appreciable covariation in wildebeest and lion densities (Fig. 4), despite the fact that wildebeest contribute strongly to the diet of Serengeti lions; the lion data also do not show autocorrelation functions with significant lags, the fundamental statistical signature of cyclic population dynamics<sup>22</sup>. These results are most consistent with the hypothesis that Serengeti wildebeest are indeed regulated primarily by food abundance rather than by predation, and that the interaction between lions and wildebeest is relatively stable.

The observed patterns suggest that group formation and seasonal migration by wildebeest are potent behavioural mechanisms that contribute substantially to the stability of lion-wildebeest interactions in Serengeti. Lion densities remained constant for decade-long intervals owing to a relatively constant number of prides in each habitat; they then suddenly jumped to new 'equilibria' after major changes in prey abundance or availability (and an associated change



**Figure 3 | Locally stable parameter combinations ( $\epsilon$  versus  $d$ ) for lion-wildebeest models.** **a**, Both predators and prey are solitary; **b**, only predators are gregarious; **c**, only prey are gregarious; **d**, both predators and prey are gregarious. Locally stable combinations are lightly shaded, and locally unstable combinations are unshaded; heavily shaded combinations cannot sustain predators.



**Figure 4 | Time-series data for Serengeti wildebeest and lions.**

**a**, Population densities of wildebeest over time; **b**, the theta-logistic model of daily per capita rate of increase by wildebeest; **c**, population densities of lions over time. Time-series analysis (Akaike's Information Criteria scores calculated with the Levinson–Durbin algorithm for a Yule–Walker autoregressive process) showed no significant evidence of periodic variation in the abundance of either adult lions or the total lion population (order 1 favoured in each case).

in pride density)<sup>6</sup>. Our models clearly predict long periods of population stability for sedentary social predators that primarily feed on mobile herds of prey. Rather than stability being the exception, as predicted by classical theoretical studies of predator–prey interactions, stability may characterize most ecological communities owing to the almost universal tendency for prey species to form flocks, herds, swarms and schools and for so many predators to form packs, pods, prides and clans.

## METHODS SUMMARY

Our general approach involved four linked steps. We first derived an a priori set of feeding rates (functional responses), based on four different assumptions: first, both predators and prey are solitary; second, predators are gregarious, whereas prey are solitary; third, prey are gregarious, whereas predators are solitary; and last, both predators and prey are gregarious. These functional response models were derived as variants of the type II functional response<sup>1</sup> that is most commonly applied in predator–prey models.

Parameters for the new functional response models were estimated for the Serengeti ecosystem by using field data for lions and the predominant eight species of herbivores preyed on by lions. These data include estimates of the amount of meat consumed by each lion, the time expenditure per hunt, the number of hunts required for each kill, the time expenditure per kill, the time expenditure for consumption of prey, the effective search radius for hunting lions, and the digestive pause in lions<sup>16,23,24</sup>. We also estimated the relationship between group density (groups per km<sup>2</sup>) and individual density (individuals per km<sup>2</sup>) for herbivores, based on 33 vehicle transects, each of 391 km, driven across the lion study area<sup>6</sup>. Herbivore transects were replicated at roughly monthly intervals during 2004–2007 to assess seasonal variation in prey abundance.

The alternative functional responses were incorporated into interactive predator–prey models<sup>25,26</sup>. These models were based on a theta-logistic model for the Serengeti wildebeest population<sup>27</sup> that best approximates the curvilinear density-dependent response (Fig. 4). We then used local stability analysis<sup>28,29</sup> to compare the range of stable versus unstable parameter combinations for each functional response form to evaluate the ecological impact of group formation on the population stability of predators and their prey.

**Full Methods** and any associated references are available in the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

Received 9 July; accepted 17 August 2007.

- Holling, C. S. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can. Entomol.* **91**, 293–320 (1959).

- Arditi, R. & Ginzburg, L. R. Coupling in predator–prey dynamics: ratio-dependence. *J. Theor. Biol.* **139**, 311–326 (1989).
- Cosner, C., DeAngelis, D. L., Ault, J. S. & Olson, D. B. Effects of spatial grouping on the functional response of predators. *Theor. Popul. Biol.* **56**, 65–75 (1999).
- Jeschke, J. M., Kopp, M. & Tollrian, R. Predator functional responses: discriminating between handling and digesting prey. *Ecol. Monogr.* **72**, 95–112 (2002).
- Abrams, P. A. & Ginzburg, L. R. The nature of predation: prey dependent, ratio dependent, or neither? *Trends Ecol. Evol.* **15**, 337–341 (2000).
- Packer, C. *et al.* Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science* **307**, 390–393 (2005).
- McCauley, E., Wilson, W. & de Roos, A. M. Dynamics of age-structured and spatially-structured predator–prey interactions: individual-based models and population-level formulations. *Am. Nat.* **142**, 412–442 (1993).
- Nisbet, R. M., de Roos, A. M., Wilson, W. G. & Snyder, R. E. Discrete consumers, small scale resource heterogeneity, and population stability. *Ecol. Lett.* **1**, 34–37 (1998).
- Donalson, D. D. & Nisbet, R. M. Population dynamics and spatial scale: effects of system size on population persistence. *Ecology* **80**, 2492–2507 (1999).
- Keeling, M. J., Wilson, H. B. & Pacala, S. W. Reinterpreting space, time lags, and functional responses in ecological models. *Science* **290**, 1758–1761 (2000).
- Pascual, M., Mazzega, P. & Levin, S. A. Oscillatory dynamics and spatial scale: the role of noise and unresolved pattern. *Ecology* **82**, 2357–2369 (2001).
- Hosseini, P. R. How localized consumption stabilizes predator–prey systems with finite frequency of mixing. *Am. Nat.* **161**, 567–585 (2003).
- Nachman, G. A functional response model of a predator population foraging in a patchy habitat. *J. Anim. Ecol.* **75**, 948–958 (2006).
- Cantrell, R. S. & Cosner, C. The effect of spatial heterogeneity on population dynamics. *J. Math. Biol.* **29**, 315–338 (2001).
- Packer, C. & Rutan, L. M. The evolution of cooperative hunting. *Am. Nat.* **132**, 159–198 (1988).
- Scheel, D. & Packer, C. Group hunting behaviour of lions: a search for cooperation. *Anim. Behav.* **41**, 697–709 (1991).
- Packer, C., Scheel, D. & Pusey, A. E. Why lions form groups: food is not enough. *Am. Nat.* **136**, 1–19 (1990).
- McComb, K. E., Packer, C. & Pusey, A. E. Roaring and numerical assessment in contests between groups of female lions *Panthera leo*. *Anim. Behav.* **47**, 379–387 (1994).
- Grinnell, J., Packer, C. & Pusey, A. E. Cooperation in male lions: kinship, reciprocity or mutualism? *Anim. Behav.* **49**, 95–105 (1995).
- Fryxell, J. M., Greever, J. & Sinclair, A. R. E. Why are migratory ungulates so abundant? *Am. Nat.* **131**, 781–798 (1988).
- Mduma, S. A. R., Sinclair, A. R. E. & Hilborn, R. Food regulates the Serengeti wildebeest population: a 40-year record. *J. Anim. Ecol.* **68**, 1101–1122 (1999).
- Turchin, P. *Complex Population Dynamics* (Princeton Univ. Press, Princeton, NJ, 2003).
- Scheel, D. Profitability, encounter rates, and prey choice of African lions. *Behav. Ecol.* **4**, 90–97 (1993).
- Elliott, J. P., Cowan, I., McT. & Holling, C. S. Prey capture by the African lion. *Can. J. Zool.* **55**, 1811–1828 (1977).
- Rosenzweig, M. L. Paradox of enrichment—destabilization of exploitation ecosystems in ecological time. *Science* **171**, 385–387 (1971).
- Rosenzweig, M. L. & MacArthur, R. H. Graphical representation and stability conditions of predator–prey interactions. *Am. Nat.* **97**, 209–223 (1963).
- Sinclair, A. R. E., Fryxell, J. M. & Caughley, G. *Wildlife Ecology, Conservation, and Management* (Blackwell, Oxford, 2006).
- Yodzis, P. *Introduction to Theoretical Ecology* (Harper & Row, New York, 1989).
- Hastings, A. *Population Biology: Concepts and Models* (Springer, New York, 1997).

**Supplementary Information** is linked to the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

**Acknowledgements** We thank the many individuals who have assisted with Serengeti population monitoring over the decades. J.M.F. thanks the Visitor's Programme of the Centre for Population Biology, Imperial College London, for logistic support during the preparation of this work. This work was supported by Discovery Grants to J.M.F. and A.R.E.S. from the Natural Sciences and Engineering Research Council of Canada, and by NSF Grants for Long-Term Research in Environmental Biology and Biocomplexity to C.P.

**Author Contributions** Field data used for this paper came from long-term collaborative studies by J.M.F., C.P. and A.R.E.S., with statistical analysis of the data by J.M.F. and A.M. Models were developed and analysed by J.M.F. All four authors participated in discussion of the results at a workshop and contributed to manuscript preparation.

**Author Information** Reprints and permissions information is available at [www.nature.com/reprints](http://www.nature.com/reprints). Correspondence and requests for materials should be addressed to J.M.F. (jryxell@uoguelph.ca).

## METHODS

**Data sources.** Three sources of data were used to parameterize the group-dependent functional response by lions. First, Scheel<sup>16,23</sup> followed individual Serengeti lions during 96-h watches just before or after full moons, recording all hunting activity as well as counts of prey species in the immediate vicinity of focal individuals. These data provide estimates of the amount of meat consumed by each lion, the time expenditure per hunt, the number of hunts required for each kill, the time expenditure per kill, the time expenditure for consumption of prey, and the effective search radius for hunting lions. We augmented Scheel's data with the field estimate by Elliott *et al.*<sup>24</sup> of the digestive pause in lions, a key component of handling time, to predict the type II functional response (Box 1).

The second source of data was regular monitoring of lion prides in the 2,000-km<sup>2</sup> Serengeti study area since 1966; mean pride size was calculated annually across 27 years of data. Most hunting is conducted by adult females, and beginning in 1984 at least one female in each pride was fitted with a radio collar and relocated every few days. The lions' belly sizes were routinely recorded, and the overnight displacement distance was calculated for animals whose bellies were initially empty (because these individuals were the most motivated to search for prey;  $n = 2,218$  occasions). The maximum overnight displacement (10 km d<sup>-1</sup>) provided an estimate of velocity during prey search. The search path radius of 200 m was based on Scheel's statistical analysis<sup>23</sup> of the determinants of successful versus unsuccessful attacks.

Our third data source was encounter rates with herds in relation to herbivore density. To estimate this relationship, we conducted 33 monthly herbivore censuses during 2004–2007 over the same study area monitored by the lion project. Herbivores were counted from a vehicle travelling at 10–20 km h<sup>-1</sup> along each 391-km path, recording the frequency of encounters as well as herd size and species composition within a 100-m radius of the vehicle.

**Functional response derivation.** Here we consider the effects of group formation by lions and their prey on the rate of prey consumption. For simplicity and notational convenience, we consider only wildebeest, but the general pattern applies to all prey species. As described by Cosner *et al.*<sup>3</sup>, a tight group of predators should experience an overlapping visual range; the area of effective search per unit time ( $a$ ) of a group-hunting predator should therefore be equivalent to that of a solitary predator. We estimated the effective search area for any group size of lions by multiplying the effective search path ( $\alpha = 0.4$  km) by the travel velocity ( $\omega = 10$  km d<sup>-1</sup>) and the probability of success per attack ( $\sigma = 0.29$  for wildebeest). Hence,  $a = \alpha\sigma\omega = 1.16$  km<sup>2</sup> d<sup>-1</sup>. The average time required by lions to capture each prey item ( $h_1$ ) is a critical component of the total handling time and is estimated by multiplying the average time per attack by the expected number of attacks per successful capture<sup>23</sup>. For wildebeest,  $h_1 = 0.045$  days, and Scheel<sup>23</sup> found no evidence that  $h_1$  varied with lion group size. The expected digestive pause ( $h_2$ ) is a direct linear function of meat per carcass. The estimated wildebeest carcass mass (85.2 kg)<sup>23</sup> combined with the digestive time estimates by Elliott *et al.*<sup>24</sup> (0.401 h per kilogram consumed) suggest that  $h_2 = 1.422$  days for each wildebeest killed. The digestive time for each predator depends on predator group size, however, because each individual feeds from the same

carcass<sup>3</sup>. Hence, the digestive pause for a group of size  $G$  equals  $h_2/G$ . Finally, the capture rate per individual in the group is obtained by dividing the group capture rate by group size.

There are some circumstances in which a type II functional model may not provide an accurate model of consumption rate, even for solitary predators and prey, because of spatial heterogeneities in capture risks for individual prey<sup>30</sup>. Nonetheless, the type II response is commonly used as a 'null' model that captures the essential elements of many ecological interactions. Asymmetries in risk<sup>30</sup> would further reduce the efficiency of predation, although by far less than the order of magnitude caused by group formation.

**Trophic model.** We used a modified Rosenzweig–MacArthur model as our template for considering the effect of group formation on lion–wildebeest interactions<sup>25,26</sup>, a model for which the dynamics has been thoroughly studied<sup>28,29</sup>. The model has the following structure for the rates of change by predators and prey:

$$dN/dt = r_{\max}N[1 - (N/K)^\theta] - \Psi(N, G)P \quad (5)$$

$$dP/dt = \Psi(N, G)\varepsilon P - dP \quad (6)$$

The modelled wildebeest population of density  $N$  has theta-logistic growth, where  $r_{\max}$  is the maximum per capita rate of change of wildebeest,  $\theta$  is a dimensionless parameter influencing the curvature of the relationship between the exponential rate of growth and wildebeest population density, and  $K$  is the equilibrium population density of wildebeest in the absence of predation. The lion population of density  $P$  grows at a per capita rate determined by  $d$  (the lion mortality rate),  $\varepsilon$  (a coefficient converting consumed wildebeest into new lion recruits) and  $\Psi(N, G)$  (the lion functional response, using equations (1)–(4) derived in Box 1). Long-term population data were available (Fig. 4a) to arrive at a first approximation of the parameters for wildebeest logistic growth<sup>27</sup>, suggesting that  $r_{\max} = 2.884 \times 10^{-4}$  per day,  $\theta = 5.946$  and  $K = 49.6$  wildebeest per km<sup>2</sup> (based on the assumption that the more than one million wildebeest occupy the full Serengeti ecosystem, comprising 25,000 km<sup>2</sup>). The fit of this model is shown in Fig. 4b.

For all models of this form, stability properties depend on the magnitude of the elements of the community interaction matrix ( $\alpha_{ij}$ ), evaluated at equilibria for the system ( $N_{\text{eq}}$  and  $P_{\text{eq}}$ ). This is due largely to changes in predator and prey equilibria, which change in a complex manner with predator and prey group size (see Supplementary Information). The predator–prey system will be locally stable if the eigenvalues of the community matrix have a negative real part<sup>28,29</sup>. This will apply only when the combination of community matrix coefficients are such that  $\alpha_{11} + \alpha_{22} < 0$  and  $\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} > 0$ , evaluated at the equilibria  $N_{\text{eq}}$  and  $P_{\text{eq}}$  (refs 28, 29). Expressions for the community matrix coefficients are given in Supplementary Information.

30. Mols, C. M. M. *et al.* Central assumptions of predator–prey models fail in a semi-natural experimental system. *Proc. R. Soc. Lond. B* 271 (Supplement), S85–S87 (2004).