

Episodic outbreaks of small mammals influence predator community dynamics in an east African savanna ecosystem

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Little is known about the dynamics of small mammals in tropical savanna: a critical gap in our understanding of Africa's best known ecosystems. Historical evidence suggested small mammals peak in abundance (outbreak) in Serengeti National Park (SNP), as in agricultural systems. We asked 1) what are bottom-up drivers of small mammals and 2) do predators have top-down effects? We documented dynamics of small mammals, birds of prey, and mammalian carnivores in SNP and agricultural areas. We used climatic fluctuations and differences between unmodified and agricultural systems as perturbations to examine trophic processes, key to understanding responses to climate change and increasing human pressures. Data were derived from intermittent measures of abundance collected 1968–1999, combined with systematic sampling 2000–2010 to construct a 42-year time series. Data on abundance of black-shouldered kites (1968–2010), eight other species of rodent-eating birds (1997–2010), and 10 carnivore species (1993–2010) were also collated. Outbreaks occurred every 3–5 years in SNP, with low or zero abundance between peaks. There was a positive relationship between rainfall in the wet season and 1) small mammal abundance and 2) the probability of an outbreak, both of which increased with negative Southern Oscillation Index values. Rodent-eating birds and carnivores peaked 6–12 months after small mammals. In agricultural areas, abundance remained higher than in natural habitats. Abundances of birds of prey and mammalian carnivores were extremely low in these areas and not related to small mammal abundance. Small mammals are an important food resource for higher trophic levels in the Serengeti ecosystem. Changes in climate and land use may alter their future dynamics, with cascading consequences for higher trophic levels, including threatened carnivores. Although outbreaks cause substantial damage to crops in agricultural areas, small mammals also play a vital role in maintaining some of the diversity and complexity found in African savanna ecosystems.

The population dynamics and migratory behavior of large herbivores and predators have been extensively studied for more than 50 years in the greater Serengeti ecosystem (Sinclair et al. 2003, Fryxell et al. 2004, Packer et al. 2005). By comparison, relatively little attention has focused on the role of small mammals in this ecosystem, even though they are a food source for predators elsewhere in Africa (Poulet 1974, Sliwa 2006, Granjon and Traore 2007, Roberts et al. 2007), including for some carnivores that are threatened (TAWIRI 2009). Small mammal abundance and community structure are known to fluctuate in subtropical African grasslands (Monadjem and Perrin 2003) and respond to the abundance of ungulate herbivores (Senzota 1983, Keesing 1998), but

little is known about their dynamics in tropical savanna. This presents a critical gap in our understanding of one of Africa's best known ecosystems.

In agricultural areas throughout east Africa, small mammal populations, particularly of the multimammate rat *Mastomys natalensis* and the African grass rat *Arvicanthis niloticus*, are known to fluctuate with large peaks in abundance (outbreak) (Leirs et al. 1996, 1997, Crespin et al. 2008). Outbreaks are generally triggered by increased food availability during the dry season in response to the amount of rain in the preceding wet season (Leirs et al. 1996, 1997, Julliard et al. 1999, Stenseth et al. 2001, Lima et al. 2003). When outbreaks occur, small mammals cause substantial economic

damage in crop-growing and storage areas throughout Africa (Davis et al. 2004, Arlet and Molleman 2007). Outbreaks have been linked to emerging infectious diseases of humans (Gratz 1997, Morens et al. 2004, Elmore et al. 2010) when land use change or human encroachment on natural ecosystems increase contact with wildlife (Jones et al. 2008). Hence the population dynamics of small mammals are linked to two substantive drivers of environmental change in Africa: land use intensification (Blaum et al. 2006, Mohr et al. 2007) and climate change (Sinclair et al. 2013). Predicted long-term changes in both the frequency and intensity of rainfall postulated for east Africa (Hulme et al. 2001, Ritchie 2008), high growth rates in the human population, and rapid land use change to the west of Serengeti National Park (SNP) (Estes et al. 2012) are likely to have substantial impacts on small mammal communities. Quantifying the underlying relationships among small mammals, predators and climate is therefore an essential precursor to developing management and policy responses to mitigate the impacts of small mammal populations in response to increasing environmental change.

Early unpublished field notes and a few published studies (Senzota 1982, 1984, Packer 1983, Magige and Senzota 2006) suggested that outbreaks of small mammals occurred in SNP. Anecdotal evidence further indicated that the population dynamics of raptors were linked to small mammal abundance (Sinclair unpubl.). We address two questions: 1) what are the bottom-up drivers of food chain dynamics in this group of species; and 2) do predators have top-down effects? We use climatic fluctuations and differences between unmodified and agricultural systems as perturbations to examine these trophic processes. We predicted first that bottom-up processes would be reflected in responses to periodic rainfall events cascading up through small mammal outbreaks to the predator trophic level in SNP. Second we predicted that a

more constant food supply from cereal crops in agricultural areas to the west of the park would result in higher small mammal and predator abundances in those areas. Third we predicted that top-down effects of predators on small mammals would be observed during the decline phase and that predators would drive small mammal abundances to similar low levels in agricultural areas and unmodified savanna.

We use the term 'small mammal' to refer to both rodents (order Rodentia) and shrews (order Soricomorpha), and 'carnivores' to refer to the mammalian order Carnivora. Serengeti National Park (SNP) refers to the protected area within the park boundary, whereas we use the term 'greater Serengeti ecosystem' to refer to SNP and surrounding cultivated lands, game reserves, and conservation areas.

Methods

Study sites

Data were collected in the greater Serengeti ecosystem, Tanzania, east Africa (2°20'S, 34°50'E). SNP protects 1.4 million km² of tropical savanna ecosystem and is one of the best-studied savanna ecosystems in the world (Sinclair et al. 2008). Small mammals were surveyed in five vegetation types inside SNP: *Acacia* woodland, *Terminalia* woodland, riverine floodplain, riverine forest and riverine grassland (Anderson et al. 2008, Reed et al. 2009) and one outside the park (cropland around two villages, used for growing maize and millet cereal crops). The climate is warm (mean monthly maximum 27–28°C) and rainfall is typically bimodal; the wet season lasts from October to May with short rains falling between October and December and long rains between February and May (Norton-Griffiths et al. 1975) (Fig. 1). While this

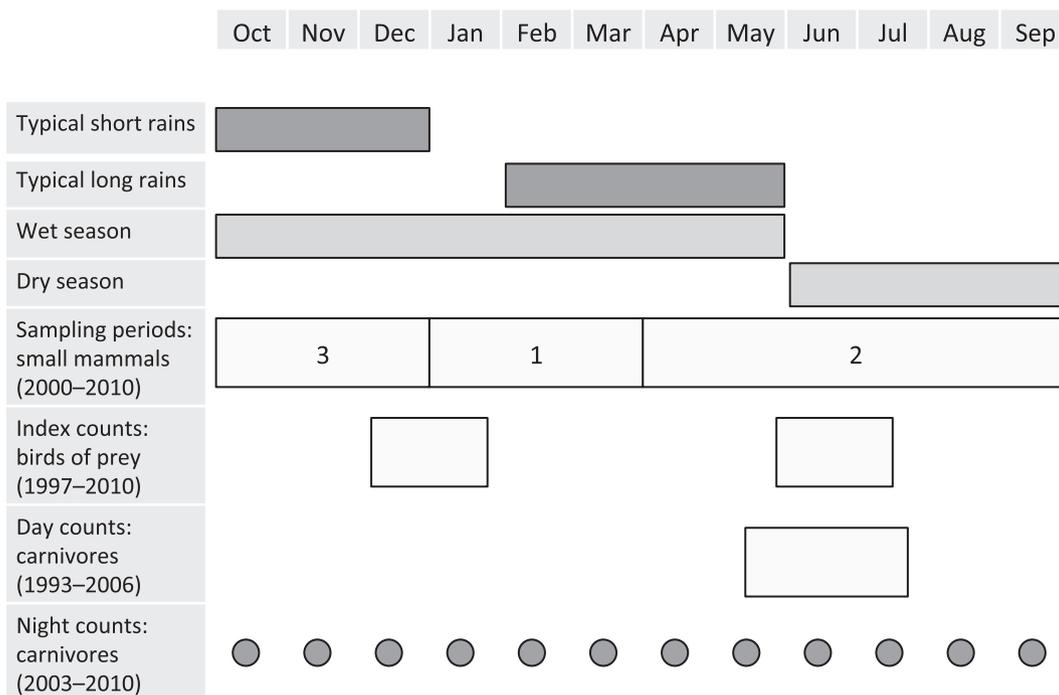


Figure 1. Schematic diagram of phases of data collection for small mammals, medium-sized carnivores and birds of prey in the greater Serengeti ecosystem in relation to a typical annual pattern of bimodal rainfall.

bimodal pattern is predictable annually, the intensity and duration of rainfall is variable (Ritchie 2008). In addition, a rainfall gradient exists across SNP with annual rainfall typically 500 mm year⁻¹ on the dry southeastern plains, increasing to 1200 mm year⁻¹ in the northwest near the Kenyan border (Sinclair et al. 2008).

Data sources: rainfall and small mammals

Historical data on small mammal abundance were collected from Senzota (1978, 1982, 1984), Packer (1983), and unpublished data from D. Reed and A. R. E. Sinclair (1968, 1972–1973, and occasionally thereafter; Sinclair 1975). No data were available from 1978 to 1985 (Sinclair 1995). Data collected from 1968 to 1999 (hereafter termed ‘historical’ data) were obtained mainly in *Acacia* woodland. From 2000 to 2010 (‘recent’ data), small mammals were surveyed in the five vegetation types above as part of the Serengeti Biodiversity Programme (Sinclair et al. 2014). From 2004 to 2010, surveys were extended to include agricultural areas northwest of SNP. Monthly rainfall has been recorded in weather stations in SNP since 1938. Rainfall data from two sites in the Western Corridor (hereafter the ‘west’) and at Seronera in the center of SNP (hereafter the ‘center’) (Sinclair et al. 2014) were used for analyses. Small mammal surveys were conducted within 30 km of a weather station in either the west or center.

Field methods: small mammals

Methods of data collection were similar for historical and recent data. In most studies, small mammals were captured in Sherman live-traps on lines or grids with trap spacing varying from 10 to 50 m, for 3 to 10 nights. Data on shrew abundance (from Sherman traps and pitfall traps comprising a 500-ml plastic container dug into the ground) were available only from the recent period. Bait types included peanut butter, small dried fish, rolled oats, roasted coconut, rice or maize flour. Live-traps and pitfall traps were checked morning and evening to catch both diurnal and nocturnal species. Animals were field-identified and sexed. Samples of ear tissue were taken occasionally for species identification by genetic methods when specimens could not be identified in the field.

For the historical data, when trapping occurred it was done annually at the end of the wet season. For the recent data, trapping was carried out at least three times per year in each habitat type. The recent data were allocated to three time periods in a calendar year (Fig. 1). Period 1 (January–March) was used to estimate small mammal abundance prior to the breeding season. Period 2 (April–September) was used to estimate maximum abundance during the peak breeding phase after the wet season. Period 3 (October–December) was used to estimate dry-season abundance. The timing of each trapping session varied within each period, so the average trap catch of rodents in period 1 and 3, and the highest recorded trap catch in period 2 (to capture peaks in abundance), were used for analysis.

Field methods: birds of prey

Black-shouldered kites *Elanus caeruleus* were recorded in field notes whenever they were numerous from 1968 to

1996 along a 50 km transect from Seronera in the center to Naabi in the south of SNP (Sinclair unpubl.). This was one of the transects used in formal counts from 1997–2010: kites and other known rodent-eating birds of prey (black-chested snake eagle *Circaetus pectoralis*, brown snake eagle *Circaetus cinereus*, long-crested hawk eagle *Lophaetus occipitalis*, martial eagle *Polemaetus bellicosus*, and tawny eagle *Aquila rapax*), as well as the black-headed heron *Ardea melanocephala*, marsh owl *Asio capensis*, spotted eagle owl *Bubo africanus*, and secretary bird *Sagittarius serpentarius* were also counted twice a year, once in the wet season and once at the beginning of the dry season (Fig. 1) on transects inside SNP (total transect length 250 km), and in agricultural areas outside the park (transect length 75 km), from 1997 to 2010 (Jankowski et al. in press). For both the earlier (1968–1996) and later data (1997–2010), two observers counted these large, easily identifiable species up to 0.5 km either side of a vehicle, with a recorder noting the observations. Further details on transect surveys for birds of prey are contained in the Supplementary material Appendix 1, Fig. A1).

Field methods: carnivores

Data on the abundance of small- to medium-sized carnivores (defined as body mass 1–18 kg) were available from 1993 to 2010, a period spanning the four most recent small mammal outbreaks. Daytime sightings of carnivores were collected (1993–2006) as part of the Serengeti Cheetah Project (Durant et al. 2007, 2011). Carnivores were also counted monthly (2003–2010) on transects at night (Craft et al. 2013), both inside SNP and in adjacent agricultural areas to the northwest. These two data sets were combined to form a single time-series of abundance (1993–2010). Only species that 1) had a known murid preference (Kingdon 1977, Geertsma 1985, Moehlman 1986) and 2) were recorded in both data sets were included in the carnivore time series. They included: black-backed jackal *Canis mesomelas*, golden jackal *Canis aureus*, side-striped jackal *Canis adustus*, caracal *Caracal caracal*, wildcat *Felis silvestris*, serval *Leptailurus serval*, common and large-spotted genet *Genetta genetta* and *Genetta maculata*, honey badger *Mellivora capensis*, and white-tailed mongoose *Ichneumia albicauda*. In addition to the above species, the abundance of domestic dogs *Canis lupis* and cats *Felis catus* was recorded in agricultural areas (Craft et al. 2013). Further details on transect surveys for carnivores are contained in the Supplementary material Appendix 1, Fig. A1).

Statistical analyses

Small mammals

We standardized measures of small mammal abundance by calculating trap catch (proportion of traps containing an animal, corrected for non-functional traps; Nelson and Clark 1973). Peaks in abundance occurred simultaneously in all five vegetation types inside SNP (Byrom et al. in press), so we combined data from vegetation types for analysis. Analyses of abundance in agricultural areas outside the park were conducted separately.

Trap catch of rodents (see Supplementary material Appendix 1 Table A1 for a list of genera) and shrews, *Crocodyra*,

Suncus and *Elephantulus* spp., were analyzed separately, but species were combined within these two groupings. This was because there were too few data on the abundance of each species individually, and no data were available for demographic variables such as breeding status or survival. This approach is justified because 1) we expected similar mechanisms to be driving the dynamics of many of the species; 2) we expected changes in abundance during outbreaks to overwhelm all other population changes, and 3) our aim was to infer general spatial and temporal patterns in groups of small mammals rather than make inferences about individual species. Such approaches have been used elsewhere (Jaksic et al. 1992, Krebs et al. 2003).

Data were analysed using R ver. 2.15.2. As there was no evidence of regular periodicity (cycles) in the time series (autocorrelation function; no lags reaching $p = 0.05$) we focus here on extrinsic drivers. For analyses of dynamics, we restrict our focus to rodents; shrews were not included. The only available explanatory variable for the 42-year time series of rodent abundance was rainfall. We used linear regression to analyze the relationship between rodent abundance inside SNP and rainfall. To quantify the probability of an outbreak in a given year (1 = outbreak; 0 = no outbreak), we used a logistic regression model. All combinations of rainfall (short rains, total wet season (short + long rains) dry season, and total annual), direct or lagged relationships between rodents and rainfall (12-month lag; there were too few data to explore a 6-month lag), and location of weather stations (west or center) were explored. We used model selection (Burnham and Anderson 2002) to determine which models had the strongest support. Because rainfall in east Africa is related to the Southern Oscillation Index (SOI) (Plisnier et al. 2000, Sinclair et al. 2013), we also analyzed the relationship between rodent abundance and annual SOI values, using linear regression, and quantified the probability of an outbreak for each annual SOI value using logistic regression.

Using recent data (three data points on rodent abundance available in each calendar year) we also sought evidence of density-dependence in rodent populations and the effects of short rains. Regression models were fitted to the abundance of rodents in period 2 (April–September) using 1) abundance in the previous two periods (October–December and January–March) and short rains as explanatory variables, and 2) by dropping rainfall from the model altogether and using only the abundance of rodents in the previous two time periods as explanatory variables.

The shrew time series was too short to determine possible drivers of abundance, but we used data from 1999 to 2010 (period 1 and 2) to quantify the relationship between rodent and shrew abundance using a two-parameter asymptotic non-linear regression, with 100 simulated confidence envelopes constructed using the model estimates and their variances and covariances (mvrnorm function in MASS package in R; Venables and Ripley 2002).

Rodent-eating birds

To analyze the relationship between black-shouldered kite and rodent abundances, historical records of kite abundance inside SNP (1968–1997) were standardized against the maximum number of black-shouldered kites recorded (in 1997) and scaled between 0 and 1. Recent records (1998–2010)

were standardized against the maximum number of kites recorded (in 2008) and also scaled between 0 and 1, resulting in a 42-year index of kite abundance from 1968 to 2010. Data on black-shouldered kite abundance were split into the same three time periods as rodents within each calendar year in order to improve statistical inference on the relationship between kites and small mammals. We used linear regression models to explore direct and lagged relationships between rodent abundance and the kite index. Scaling the data did not influence the outcome of these analyses.

To determine relationships between rodent abundance and other species of rodent-eating birds, we grouped the five raptor species monitored (black-chested snake eagle, long-crested hawk eagle, martial eagle and tawny eagle) and scaled their abundance between 0 and 1 to generate a ‘raptor index’. Relationships between abundance of rodents and absolute numbers of secretary birds and black-headed herons were analyzed separately. There were too few data on numbers of marsh owls and spotted eagle owls to carry out meaningful statistical analyses. Linear regression was used to explore both direct and lagged relationships between rodent abundance and either indices (kites and raptors) or numbers (secretary birds and herons) of rodent-eating birds.

Carnivores

Each data set of aggregated carnivores was standardized by scaling to 1 relative to maximum counts in 1996 (day counts) and 2004 (night counts). Where available, data on carnivore abundance were split into the same three time periods as for rodents within each calendar year. With the exception of the honey badger, which has a gestation period of 153–162 days (Hancox 1992), most of the carnivore species have gestation periods of 55–70 days (Kingdon 1977), so we expected lags of 6–12 months in the numerical response of rodent-eating carnivores to rodent outbreaks, taking into account the breeding response and subsequent growth of juveniles to ‘sightable’ age. Linear regression was used to explore both direct and lagged 12-month relationships between rodent abundance and the index of carnivores. There were too few data to explore a 6-month time lag.

Results

Small mammals

Some 37 genera of rodents and shrews were recorded over more than four decades in the greater Serengeti ecosystem (Supplementary material Appendix 1 Table A1, Byrom et al. in press). There were at least six major peaks in abundance (defined as trap catch > 50%) from 1968 to 1999 (1968, 1977, 1986, 1987, 1992 and 1998), with another moderate peak in 1978 (48% trap catch; Senzota 1982). For intervening years, there were either no records, or field notes recorded no or few rodents present. The magnitude of the peaks varied from 48% trap catch to ‘very high rodent abundance’ from field notes (all peaks in historical data except 1998; assigned 80% trap catch) to ‘plague’ (1998; assigned 100% trap catch). Three further peaks in abundance occurred in the recent data: 2001 (49% trap catch), 2002 (62%), and 2007 (80%), with very low (< 5%) or zero rodent

abundance in intervening years. Putting the historical and recent data together we infer that episodic outbreaks of rodents occurred in SNP over more than four decades of recorded data (Fig. 2).

Rodents

There was a significant positive relationship between wet season rains and both rodent abundance (linear regression model; west: $t_{31} = 3.11$; $r^2 = 0.24$; $p < 0.003$; center: $t_{31} = 2.91$; $r^2 = 0.21$; $p < 0.007$) and the probability of a rodent outbreak (logistic regression model; west: $z = 2.32$, $p < 0.02$, 22% deviance explained; center: $z = 2.23$, $p < 0.03$, 17% deviance explained; Fig. 3a). There was also a significant positive effect of short rains in the west of SNP on both abundance (linear regression: $t_{31} = 3.10$; $r^2 = 0.24$; $p < 0.004$) and the probability of an outbreak (logistic regression: $z = 2.23$, $p < 0.03$; 17% deviance explained). There was some evidence that lower rainfall in the year prior to an outbreak resulted in greater rodent abundance in an outbreak year, and that lower dry-season rainfall increased the probability of an outbreak (Supplementary material Appendix 1 Table A2 and A3 show results for the full set of candidate models tested).

We found a significant relationship between SOI and rodent abundance (linear regression: $t_{26} = 3.10$; $r^2 = 0.16$; $p < 0.005$) and the probability of an outbreak (logistic regression: $z = 1.77$; $p < 0.08$; 9% deviance explained), with outbreak probability increasing at large negative SOI values (Fig. 3b). From the 10 years of recent data we found no evidence of a density-dependent effect on rodent abundance: there was no significant interaction between rodent abundance in previous time periods and short rains ($t_{10} = 1.23$, $r^2 = 0.33$, $p = 0.25$), no effect when the interaction was dropped from the model ($t_{11} = 1.73$, $r^2 = 0.23$, $p = 0.11$), and no effect of rodent abundance alone in previous time periods (i.e. when rainfall was dropped from the model) ($t_{14} = 0.67$, $r^2 = 0.03$, $p = 0.51$).

Shrews

Shrew abundance showed fluctuations with moderate peaks in 2001, 2002 and 2007, and was strongly related to rodent abundance from 1999 to 2010 (non-linear regression: shrews = $a(1 - e^{-(b \times \text{rodents})})$ where $a = 0.26 \pm 0.05$, $b = 7.77 \pm 3.63$; $t_{20} = 2.14$, $r^2 = 0.49$, $p = 0.04$; Fig. 4). Unlike rodents, shrews did not exceed 50% trap catch in peak years.

Black-shouldered kites

Black-shouldered kites often peaked simultaneously with rodents, but lagged behind rodent abundance in their decline phase (Fig. 2). The relationship between rodent abundance and black-shouldered kite abundance was highly significant (linear regression model; $t_{31} = 4.12$, $r^2 = 0.35$, $p < 0.001$). We also found a positive relationship between rodent abundance in one year, and kite abundance in the following year (linear regression model, $t_{29} = 2.25$, $r^2 = 0.15$, $p = 0.03$) although the lagged relationship was weaker than the direct relationship.

Other rodent-eating birds

The abundance of other raptors (black-chested snake eagle, brown snake eagle, long-crested hawk-eagle, martial eagle and tawny eagle), secretary birds, and herons also fluctuated coincident with rodent outbreaks (Fig. 5a–c). There was evidence of a one-year lag between raptor and rodent abundance that was marginally significant (linear regression model, $t_{11} = 1.97$, $r^2 = 0.26$, $p = 0.07$); there was also weak evidence of a direct association between secretary birds and rodent abundance ($t_{11} = 2.00$, $r^2 = 0.33$, $p = 0.08$). There was no evidence of a direct or lagged association between black-headed herons and rodent abundance (direct: $t_{12} = 1.23$, $r^2 = 0.11$, $p = 0.24$; lagged: $t_{11} = 1.13$, $r^2 = 0.10$, $p = 0.28$). Abundance of owls showed a peak in 2007, coincident with a rodent outbreak.

Carnivores

Abundances of carnivores inside SNP usually peaked simultaneously with rodents, but showed an extended decline phase (Fig. 5d). There was no evidence of a direct response of carnivores to rodents (linear regression model: $t_{11} = 0.94$, $r^2 = 0.05$, $p = 0.36$) but there was weak evidence for a 12-month time lag ($t_{11} = 1.80$, $r^2 = 0.16$, $p = 0.09$). Data from 2000 onwards showed a better regression with a 12-month lag ($t_{11} = 2.4$, $r^2 = 0.34$, $p = 0.043$).

Cultivated areas outside SNP

Peaks in small mammal abundance occurred in agricultural areas in 2004 (36% trap catch) and 2007 (49%). Trap catch

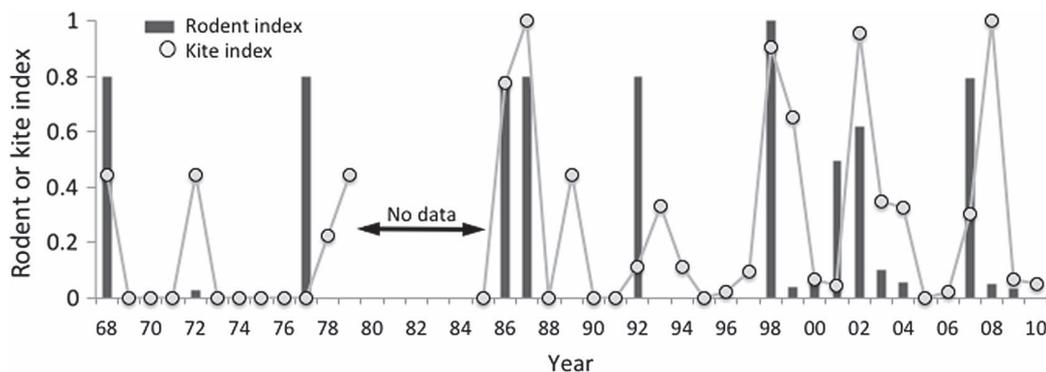


Figure 2. Fluctuations in rodent abundance (proportional trap catch of live-captured rodents in Sherman traps; grey bars) and index of black-shouldered kites (grey line) in Serengeti National Park, 1968–2010. See text for the relationship between rodents and kites.

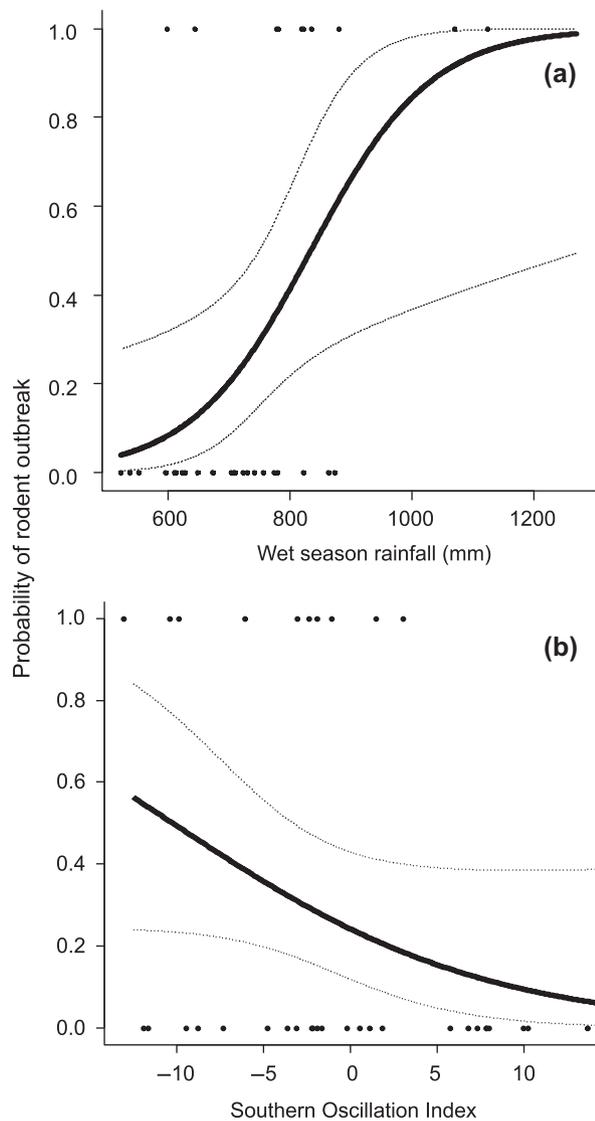


Figure 3. Probability of a rodent outbreak in Serengeti National Park as a function of (a) intensity of wet-season rains and (b) Southern Oscillation Index. Dotted lines are 95% confidence intervals. Outbreaks were defined as >50% trap catch and included all rodent species.

between peak years was ~10% compared with that inside the park boundary where abundance declined to zero or near-zero between outbreaks (Fig. 6a). This time series was too short to characterize the relationship between rodent abundance and rainfall in cultivated areas. Kites were almost completely absent in cultivated areas even when abundance peaked in neighboring SNP (Fig. 6b). There was no response of kites to rodents in cultivated areas even though rodents were at higher average abundance between peaks than in SNP. Few wild carnivores were observed in these areas, and their abundance did not fluctuate in relation to rodent abundance ($t_5 = 0.80$, $r^2 = 0.11$, $p = 0.46$; Fig. 6c). Domestic cats and dogs were present in higher numbers in these areas compared with wild mammalian carnivores (Craft et al. 2013), but abundance of dogs and cats was not correlated with the abundance of rodents ($t_5 = 0.26$, $r^2 = 0.01$, $p = 0.80$; Fig. 6d).

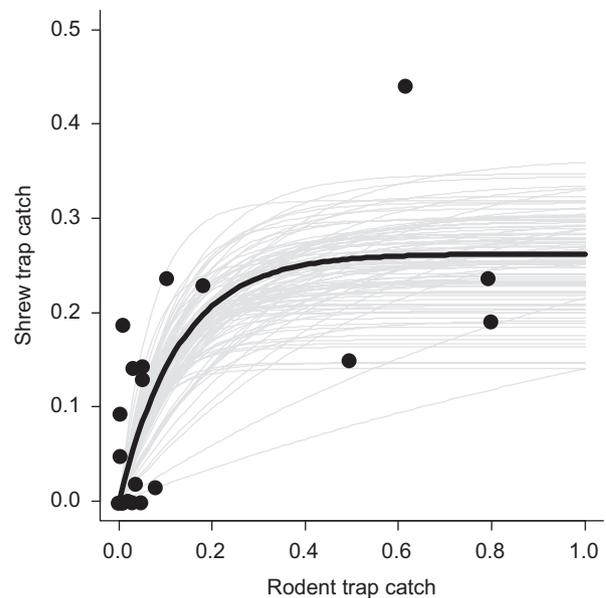


Figure 4. Relationship between rodent abundance (all species grouped) and shrew abundance, 1999–2010. Grey lines represent 100 confidence envelopes.

Discussion

Trophic dynamics of small mammals

Few studies have investigated the long-term dynamics of small mammals in tropical ecosystems (Krebs 2013). This presents a critical gap in our understanding of the ecological role of these species in tropical ecosystems worldwide. Bottom-up drivers predict an upward cascade in a food chain following episodic rainfall events. Our results corroborate this prediction. Other work has shown that higher rainfall increases primary productivity and generates small mammal outbreaks in tropical ecosystems in Africa (Sinclair et al. 2013), Australia (Madsen and Shine 1999), and South America (Jaksic et al. 1992, Lima et al. 1999). Rainfall was also correlated with increased abundance of rodents, birds of prey and carnivores in SNP. Further, there was a higher average abundance of rodents between outbreaks in agricultural areas, consistent with a higher food base there (Mohr et al. 2007) compared with the natural savanna ecosystem. Our data thus support a hypothesis that small mammal dynamics in SNP are driven bottom-up, with higher food availability in years with greater rainfall in the wet season resulting in an increased probability of an outbreak of rodents, and favorable conditions for shrews. To our knowledge these are the first long-term data on outbreaks of rodents in tropical African savanna cf. an agricultural system (Leirs et al. 1996). They provide vital baseline data from which to monitor the future resilience of tropical savanna ecosystems (Woinarski 2000, Woinarski et al. 2001).

The role of top-down regulation of small mammal populations by predators in SNP is less clear. Abundances of carnivores and birds of prey often lagged behind rodent numbers in both their peak and decline phases (Fig. 5). Lagged declines in carnivores have been observed elsewhere (Jaksic et al. 1992, Duncan et al. 2009) and suggest that

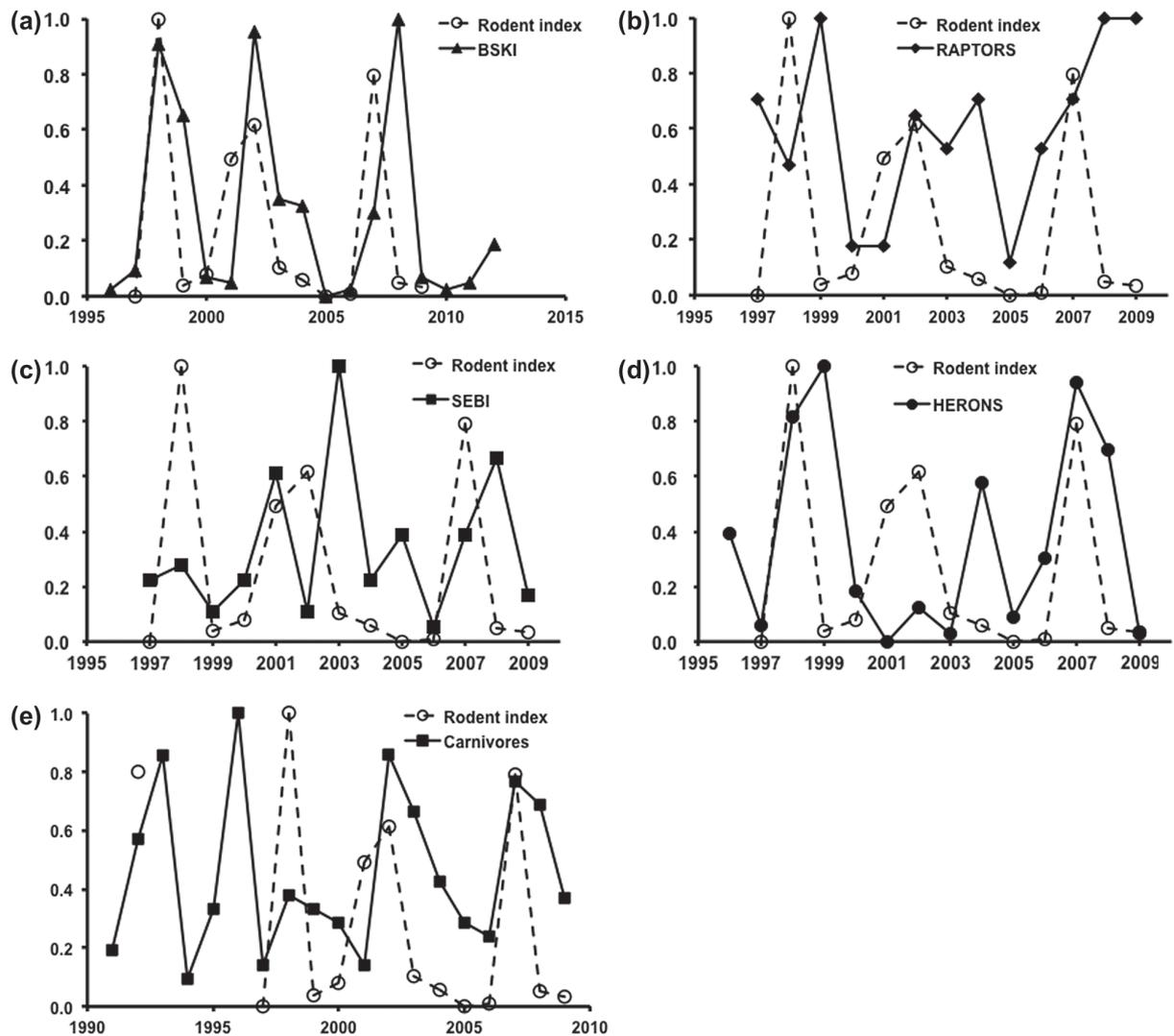


Figure 5. Indices of rodents (broken line, open circles), rodent eating birds (relative to the maximum count) and medium sized carnivores in Serengeti National Park. (a) black-shouldered kites (triangles); (b) five other raptor species (see text for species) (diamonds); (c) secretary birds (SEBI) (squares); (d) black-headed herons (closed circles); (e) medium-sized carnivores (squares).

predators are responding to fluctuations in small mammal abundance, rather than causing them. However, the higher average rodent abundance in agricultural areas relative to the savanna (Fig. 6a) could also come about through reduced abundance of wild carnivores (Mshu et al. 2012) and almost complete absence of rodent-feeding raptors (Fig. 6b–c), implying a top–down effect. The very high number of domestic carnivores (Fig. 6d) does not appear to counterbalance the virtual absence of wild carnivores. Overall we cannot rule out the hypothesis that predators have a role to play in regulating rodents in the greater Serengeti ecosystem.

Worldwide, rainfall and other climatic factors have been postulated to influence system productivity and therefore food supply for rodents, both in agricultural areas (Stenseth et al. 2003, Zhang et al. 2003, Davis et al. 2004) and natural ecosystems (Letnic and Dickman 2010, Letnic et al. 2005). Leirs et al. (1996) found that the short rains explained 69% of the variation in occurrence of *M. natalensis* outbreaks in human-dominated, agricultural Morogoro (eastern Tanzania) between 1925 and 1990. Our data also suggest that

shrews may respond to similar environmental cues (i.e. pulsed increase in food availability after rainfall).

Small mammals are an important food source for both mammalian and avian predators elsewhere in Africa (Poulet 1974, McCauley et al. 2006, Sliwa 2006, Brown et al. 2007, Granjon and Traore 2007, Roberts et al. 2007). Black-shouldered kites are known to travel large distances and aggregate in response to food availability, but they also show a pronounced breeding response to small mammal abundance in good years (Brown et al. 1982). Our data suggest that the response of black-shouldered kites to rodents comprises both an immediate aggregative response of adults to food availability (as with a similar raptor in Australia; Sinclair et al. 1990), followed by a breeding response in the 6–12-month period after the rodent peak. Likewise, we found that secretary birds respond numerically to high abundance of small mammals. The dynamics of several other species of rodent-eating birds – raptors, owls and herons – appear to be influenced by rodent abundance in SNP, and rodent abundance also influenced the dynamics of small- to medium-sized

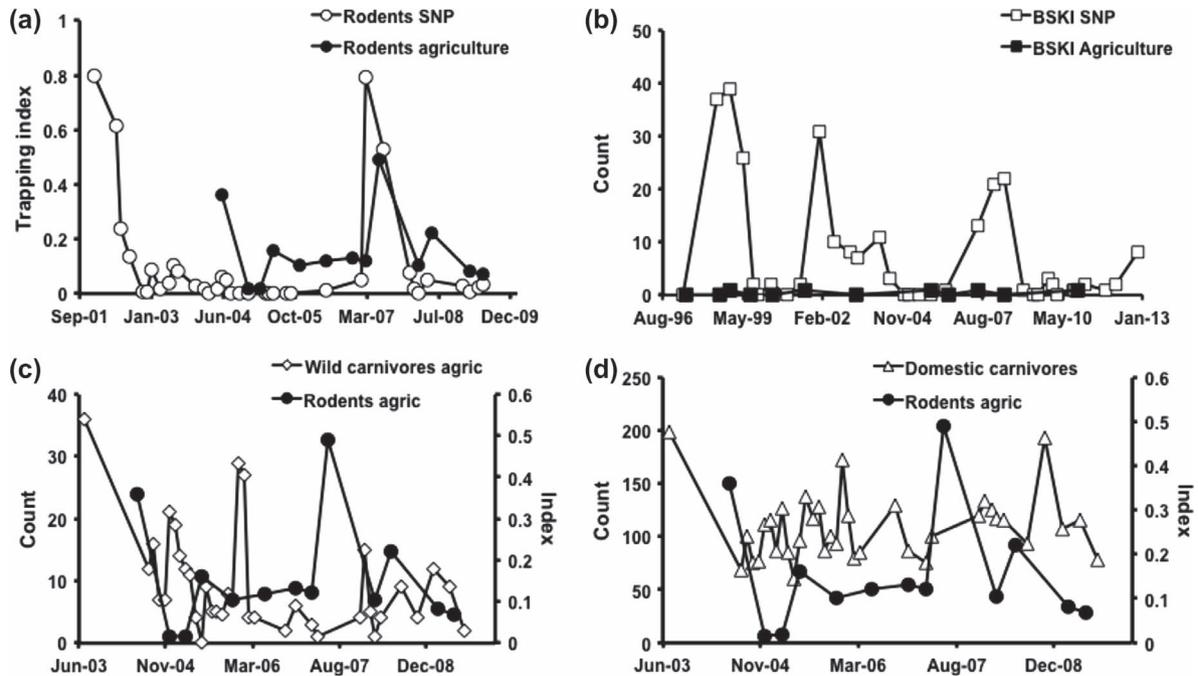


Figure 6. Abundance of rodents, birds of prey and medium-sized carnivores in cultivated agricultural areas adjacent to Serengeti National Park. (a) rodents in SNP (open circles) and agriculture (closed circles); (b) black-shouldered kites in SNP (open squares) and agriculture (closed squares); (c) wild carnivores in agriculture relative to rodents in agriculture (closed circles); (d) domestic carnivores in agriculture relative to rodents in agriculture (closed circles).

felid, canid, and viverrid carnivores. Although consistent time-series data were available for just nine mammalian carnivore species, rodents are known to be an important food source for a much wider variety of mammalian carnivores, as well as birds of prey, in SNP (Brown et al. 1982, Durant et al. 2007).

Causes of small mammal outbreaks

We were not able to determine direct drivers of rodent abundance because long-term data on food availability were not available. Our data suggest that an outbreak of small mammals usually follows wet season rains exceeding ~800 mm in the west of SNP, and short rains exceeding 250 mm. The latter threshold is somewhat lower than the 380 mm predicted by Leirs et al. (1996) to generate *M. natalensis* outbreaks in agricultural areas in central and southern Tanzania. Our rainfall data were collected relatively close (< 30 km) to trapping sites, so there is unlikely to be a spatial discrepancy between rainfall amount and outbreaks in our model. We propose three possible explanations for the difference. First, Leirs et al. (1996) parameterized their model with more than 70 years of time-series data for a single species (*M. natalensis*). Their model had greater predictive ability compared with ours (69% cf. 22%), which combined several small mammal species. Nevertheless, our data were dominated by *M. natalensis* and *A. niloticus*, so the lower predictive ability of our model is unlikely to be explained by the inclusion of more species alone.

Second, we would expect high primary productivity in response to rainfall to be more spatially heterogeneous in a natural ecosystem containing a variety of topographic features, soil types and vegetation types (Anderson et al.

2007, Bonnet et al. 2010). The crop monoculture model (Leirs et al. 1996) showed a much steeper threshold for rodent outbreaks compared with our savanna ecosystem. Greater complexity in a system generates less predictable responses of consumers to primary productivity spatially and temporally (Bonnet et al. 2010), and productivity increases with species richness (Hooper et al. 2005), so in principle, a lower rainfall threshold should be required for a species-rich system to generate an outbreak, which is what we observed. Doubtless this complexity contributed to the low predictive power of our statistical models, a problem also encountered by Krebs et al. (2004) and Singleton et al. (2007) when quantifying house mouse outbreaks in Australian agricultural systems.

Third, it is possible that a higher level of background food available in the form of spilled grains and grain storage units in agricultural areas (Mohr et al. 2007) could result in a higher density of small mammals at the onset of breeding, altering the rapidity of build-up to an outbreak cf. the natural savanna ecosystem.

Environmental change and small mammals in east Africa

Two substantive drivers of environmental change in the greater Serengeti ecosystem are land use modification and intensification outside SNP (Estes et al. 2012, Hampson et al. 2013) and climate change through long-term changes in rainfall (Hulme et al. 2001, Holmgren et al. 2006, Ritchie 2008), both of which can alter the frequency and intensity of rodent outbreaks. Internationally, there is increasing concern about the effects of such drivers on ecosystems (Holmgren et al. 2006, Tylanakis et al. 2008), including their influence

on small mammal outbreaks and the resulting trophic cascades (Lima et al. 1999, Letnic et al. 2005).

Ritchie (2008) observed a decreasing trend in both wet-season rainfall and variability in rainfall for SNP from 1960 to the present day. If our bottom-up hypothesis is correct, we might predict fewer rodent outbreaks in Serengeti with decreased variability in rainfall. A reduced prey base could potentially threaten the long-term persistence of some species of carnivores, with implications for their management and conservation, as has been observed for Ethiopian wolves (Sillero-Zubiri et al. 2008). Long-term climate trends could influence the extent of savanna vegetation (Ritchie 2008), and alter community composition of rodent and predator populations (Blaum et al. 2007, Thiam et al. 2008). Land use change (agricultural intensification) will also bring humans into more frequent contact with wildlife (Estes et al. 2012, Hampson et al. 2013), which is known to exacerbate the problem of emerging infectious diseases (Morens et al. 2004, Jones et al. 2008). Changing land use patterns have been implicated in sudden declines in small mammals in tropical savannas in northern Australia (Woinarski et al. 2001) and Brazil (da Silva and Bates 2002). Collating baseline information ours is a vital first step to understanding the mechanisms behind such declines.

Indirect role of small mammals in the savanna ecosystem

There is increasing evidence that small mammals play a wide range of key indirect roles in the function of savanna ecosystems. For example, small mammals disperse seeds and prey on seeds and seedlings of tree species, thereby influencing tree establishment and woodland dynamics (Keesing 1998, Shaw et al. 2002, Walters et al. 2005, Goheen et al. 2010), and they respond numerically to burning and ungulate grazing (Senzota 1983, Keesing 1998, 2000, da Silva and Bates 2002, Yarnell et al. 2007, Hagenah et al. 2009), sometimes resulting in increased food supply for predators such as snakes (McCauley et al. 2006). Further, the numerical responses of predators to small mammals may indirectly impact other functional groups of invertebrates, amphibians and reptiles. Other than the studies above, the roles of small mammals in nutrient cycling and ecosystem engineering have barely been quantified for African ecosystems.

Our 42-year time series demonstrates that small mammal dynamics are complex with strong cascading effects on predators in African savanna ecosystems. It further demonstrates the value of long-term ecological data as a baseline from which to predict the impact of future environmental changes on the greater Serengeti ecosystem, and highlights the influential role of small mammals in both natural and modified ecosystems in east Africa. Future research could focus on experimental manipulation of the primary agents of disturbance in the greater Serengeti ecosystem, such as fire and land use change, in order to identify the mechanisms underlying the patterns we observed.

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Supplementary material (available as Appendix oik-00962 at <www.oikosjournal.org/readers/appendix>). Appendix 1