

Natural population die-offs: causes and consequences for terrestrial mammals

Eric I. Ameca y Juárez^{1,2}, Georgina M. Mace², Guy Cowlshaw¹ and Nathalie Pettorelli¹

¹ Institute of Zoology, Zoological Society of London, Regent's Park, London, NW1 4RY, UK

² Centre for Population Biology and Division of Biology, Imperial College London, Silwood Park, Ascot, SL5 7PY, UK

Extreme changes in the environment can generate high mortalities in wildlife populations. When these mortalities are attributable to extreme natural events, they are referred to as natural population die-offs. Despite growing reports of such die-offs, a consensus on how to define them has not emerged. Furthermore, although anthropogenically caused extreme events are predicted to occur at a higher frequency and intensity compared with natural events, an integrative synthesis assessing their significance for wildlife population viability is lacking. These issues hamper the ability to identify populations most at risk. Here, we propose a functional definition of natural population die-offs, an assessment of extrinsic and intrinsic processes shaping these die-offs, and a framework for assessing the vulnerability of terrestrial mammals to natural and anthropogenically caused extreme events.

Extreme natural events and biodiversity loss

Although there is no strict consensus on how to measure biodiversity and biodiversity loss, most conservation decisions are taken at the species level on both global and regional scales [1–4]. Species-focused conservation strategies alone, however, may overlook threats operating at other levels of biological organisation, such as the population level. Processes operating at the population scale can generate significant bottom-up impacts on biodiversity and so compromise the optimal provision of goods and services to human society [2]. To improve the efficacy of conservation efforts, it is necessary to better understand these underlying population processes and how they relate to patterns in species extinctions [2,5–7].

Fluctuations in the size of a population are the reflection of the birth, death and migration dynamics of its individual components [8]. Such dynamics are shaped by density-dependent mechanisms, variation in individual characteristics and environmental variability [8–10]. Extreme natural events, such as droughts, wildfires, hurricanes, insect infestations or epidemics, are one such component of variability in environmental conditions, to the extent that they are classified as a subtype of natural hazards by the United Nations International Strategy for Disaster Reduction (UNISDR; <http://www.preventionweb.net>; Table 1). These events can result in the loss of numerous individuals, which in turn is expected to affect directly and indirectly

the dynamics and overall viability of wildlife populations [11]. This is especially true when extreme events are coupled with other mechanisms, such as density dependence or increased anthropogenic pressure. Drastic population size reductions can leave populations more susceptible to additional threat processes (such as Allee effects, increased demographic stochasticity, higher risk of genetic bottleneck, and habitat loss or habitat fragmentation) that can ultimately lead to population extinction [12,13]. Abnormally high population losses can also have consequences that reach far beyond the population scale, with a sharp reduction in the size of the population of one species potentially leading to an extinction cascade [14]. In ecological networks with strong species interactions, major changes in the population dynamics of one species may alter the entire stability of the network [15]. If, in addition, the species experiencing the drastic loss of individuals is a keystone component of an ecosystem, its decline could reshape the entire structure and function of that ecosystem [16].

There is currently a substantial lack of knowledge on the mechanisms through which extreme natural events affect biodiversity in the form of populations, species and ecosystems [17–20]. In particular, little is known about how wildlife populations inhabiting areas already impacted by anthropogenic disturbances might respond to extreme natural events. This is unfortunate, as global and regional climate change models predict an increase in both the frequency and intensity of climatic anomalies [21–24] and, thus, of anthropogenic extreme events that resemble extreme ‘natural’ events. The International Union for Conservation of Nature (IUCN) recently assessed the susceptibility of species to climate change impacts [25], based on the identification of traits (e.g. dispersal ability or habitat specialisation) associated with enhanced susceptibility to climate change. Here, we introduce a framework for such an initiative, aiming at identifying species whose populations are particularly susceptible to abnormally high losses under natural disturbances. We believe that such information could be used to infer how the extinction risk of species might increase as anthropogenic extreme events become more frequent and more severe. Before introducing our framework, we propose a workable definition of abnormally high population losses, and explore the links between the biology of species and the incidence of these population losses.

Corresponding author: Pettorelli, N. (Nathalie.Pettorelli@ioz.ac.uk).

Table 1. Examples of extreme natural events reported in the literature as related to, or being drivers of, recent natural population die-offs

Natural hazards ^a	Extreme natural events ^b	Refs
Hydrometeorological: process or phenomenon of atmospheric, hydrological or oceanographic nature that may cause loss of life, injury or other health impacts, property damage, loss of livelihoods and services, social and economic disruption, or environmental damage	Cold wave: extreme weather, extreme temperature or cold temperatures	[29,58]
	Cyclone: hurricane, tropical storm, tropical depression or typhoon	[39,59]
	Drought: deficiency of precipitation, desertification or pronounced absence of rainfall	[50]
	Flood: inundation; includes flash floods	[60]
	Wildfire: bush fire, forest fire, uncontrolled fire or wild land fire	[61]
Biological: process or phenomenon of organic origin or conveyed by biological vectors, including exposure to pathogenic microorganisms, toxins and bioactive substances, that may cause loss of life, injury, illness or other health impacts, property damage, loss of livelihoods and services, social and economic disruption, or environmental damage	Epidemic: a disease affecting, or tending to affect, a disproportionately large number of individuals within a population, community, or region at the same time	[62]
	Insect infestation: spreading or swarming in of various kinds of insect over or in a troublesome manner	[63]

^aCategories and definitions following the terminology of the UNISDR [57].

^bBasic definitions of extreme natural events were collated from the web-based project of the UNISDR (<http://www.preventionweb.net>).

Defining abnormally high population losses

'Population die-offs' generally refer to the loss of a large number of individuals in a population over a short time interval. When die-offs are attributable to one or more extreme natural events (Table 1), they are referred to as 'natural' population die-offs. A growing number of studies report natural population die-offs in terrestrial mammals (Table 1), yet few of them provide a quantitative definition of what a 'natural population die-off' actually is. Without a clear definition that can be used across taxa, the usefulness of the 'natural population die-off' concept might be limited for conservation purposes.

The first attempt to provide an across-species, quantitative definition of natural population die-off was provided by Young [26], who defined them as 'a monotonic drop in population numbers that occurs between two or among more than two population surveys with at least a 25% reduction in population size'. Later, Reed and collaborators [27] proposed another definition, namely, 'any 1-year decrease in population size of 50% or greater'. As illustrated by these definitions, there are various challenges associated with defining natural population die-offs. The first issue concerns the setting of a temporal span threshold, because a population loss of sufficient magnitude could occur over a range of potential timescales. In the context of the ecology and dynamics of the population, setting such thresholds should allow natural population die-offs to be differentiated from other patterns of mortality. The second problem involves defining a mortality threshold beyond which a population loss is considered to be a die-off. Choosing a fixed mortality threshold to identify die-offs (as proposed by Young and Reed) overlooks the fact that the same population loss can be more severe for some species than for others owing to differences in their life histories [28–30]. In the context of long-term persistence, populations of long-lived species with late sexual maturity and low reproductive rates may have less chance to recover than might species with fast life-history strategies [31].

A workable definition of natural population die-off should thus ideally take into account the variability in average mortality rates for a given population and time interval. The importance of taking into account differences in life histories while comparing susceptibility to die-offs

across species was previously acknowledged by Reed and collaborators [27], who compared the frequency of natural population die-offs in vertebrates by dividing the number of die-offs ($\geq 50\%$ population decrease) observed during a census period by the approximate number of generations elapsed for that same period, for each species considered. We therefore propose to reformulate the definition of natural population die-off as: a 1-year decline in the number of individuals within a population derived from one or more extreme natural events, where individual losses increase by at least 25% in comparison to that expected from the annual average mortality rate reported for the species. We aim here to formulate a definition that could help assess the vulnerability of populations to natural population die-offs, as well as making it possible to consider such vulnerability as a component of the current risk for a species when estimating its potential to become extinct. This quantitative definition attempts to differentiate drastic population size reduction from background population variability, while taking into account the fact that the same population loss associated with the impact of an extreme natural event can be more harmful for some species than for others. In accordance with Reed and colleagues, it moreover supports the decision to exclude die-offs reported over just 1 year. This exclusion is based on the assumption that a population could experience a further decline and recover, or vice versa, owing to: (i) processes normally shaping population size variation (e.g. immigration or emigration of individuals); (ii) human intervention (e.g. harvesting); or (iii) the combined effect of natural and anthropogenic disturbance (e.g. habitat change and food shortage; drought and hunting).

Extreme natural events, the biology of species and the incidence of natural population die-off

Comparative analyses have shown that species extinction risk is shaped by intrinsic and extrinsic factors [32–35]. Applying such reasoning to population extinction risk, the probability for a population to experience a natural die-off is likely to be a function of the nature of the extreme natural event affecting this population, as well as biological differences among species [36,37]. What might be a 'catastrophe' for some species could be a 'bonanza' for

others. For example, with respect to extrinsic changes in key ecological resources associated with natural population die-offs, Widmer and collaborators [38] found that the winter hurricane Lothar that devastated woodlands in northeast France in 1999 did not increase mortality rates of roe deer (*Capreolus capreolus*) but rather increased the availability of one of its principal winter foods. Conversely, a population of black howler monkeys (*Alouatta pigra*) inhabiting a tropical forest of Belize was severely deprived of its primary food items by hurricane Iris [39] resulting in a 42% population loss.

Intrinsic biological characteristics, such as body mass, diet breadth or dispersal capacity, have already been shown to affect species extinction risk [36,37,40–42]. Such traits could also be involved in shaping the probability of a given population experiencing a natural population die-off. During a wild fire, for example, survival should initially depend on the ability of the population to cope with the disturbance: this can be achieved through good dispersal abilities or access to refuges [43]. Species with a specialised diet may then experience malnutrition owing to the local post-fire reduction of key food resources [44–46]. This would lead populations with limited dispersal abilities and habitat specialisation to be more likely to undergo natural population die-offs through a combination of inefficiency in dispersing to undisturbed areas, and potential lack of key resources for near-term persistence.

The social ecology of species could also play a role in shaping the occurrence of natural population die-offs. In highly sociable species, individual survival can rely upon the maintenance of large social units [11,33]. Yet such units can potentially exacerbate disease outbreaks when the successful transmission of a pathogenic agent within a population depends on the frequency of contact between individuals [47]. Conversely, territoriality can also facilitate transmission by increased exposure to pathogens prevailing within defended areas [48,49]. Bearing in mind the above, territorial organisms aggregated in dense populations might be particularly vulnerable to natural population die-offs driven by disease outbreaks.

Leadership and group coordination can also be influential. A recent study by Foley and colleagues [50] showed that African elephant (*Loxodonta africana*) family groups with older matriarchs had fewer calf losses during a severe drought than did groups with young matriarchs. This observation led the authors to hypothesise that older individuals that had acquired behavioural coping strategies from past exposures to drought might have informed the behaviour of their group, increasing its chances of persisting when similar conditions arose.

Predicting vulnerability to natural population die-offs

With increasing risks and challenges posed by climate change, increasing attention has been devoted to assessing and predicting the vulnerability of human societies to extreme natural events [7]. Such knowledge could contribute to the development of an integrated framework for predicting vulnerability to die-offs in wildlife populations mediated by extreme natural events. According to recent work [51], the risk of a wildlife population experiencing a natural population die-off can be considered to be its

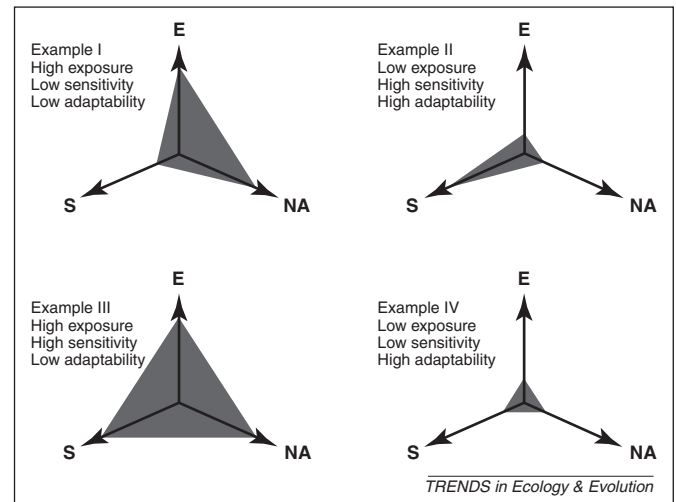


Figure 1. Conceptual model for assessing the vulnerability of species to natural population die-offs. Vulnerability (grey triangle) is assessed by evaluating the degree of exposure (E) of the population of a species to a given extreme natural event, the intrinsic biological sensitivity of a species (S) to this event, and its inability to adapt (i.e. its non-adaptability; NA) to the event. Based on this framework, vulnerability to natural population die-offs can be low (example II and IV), moderate (example I) or high (example III) depending on the relationship between the level of exposure, sensitivity and non-adaptability (displayed as individual arrows).

vulnerability. This can be seen as a function of three main components: sensitivity, adaptability and exposure (Figure 1). Population sensitivity can be expected to be shaped by species traits (e.g. body size, home range area or sociality) and will be determined largely by intrinsic, biological features that have evolved over time. Adaptability (in a non-evolutionary sense) will refer, in this case, to plasticity in traits; that is, whether mechanisms such as behavioural and/or physiological flexibility exist to allow a given population to avoid or withstand the effects of particular extreme natural events [52,53]. The plasticity of many traits varies systematically among species, representing a limit to their tolerance of environmental change, but the plasticity is itself an evolved trait [54]. Finally, exposure is expected to indicate how often a given extreme natural event will affect a given population and is largely a feature of the environment in which the species lives. However, the exposure that a particular population is likely to face depends on prevailing conditions, many of which are exacerbated by human activities and, therefore, can change quite rapidly. For example, the likelihood of a wildfire may be increased by land-use practices. Therefore, even if extreme natural events are hard to predict, being able to identify areas or habitats where the background level of risk is elevated will allow the overlay of high exposure risk areas with species that are sensitive and have low adaptive capacity. A key aspect to this vulnerability framework is the need to take into account any spatial variation in the local attributes of the environment, as populations of a species exposed to similar extreme natural events but occurring in different habitats might display different patterns of vulnerability (Box 1, Figure I). Priority can then be given to develop strategies enhancing the resilience of populations to extreme natural events in these areas. Such strategies might include the creation of a

Box 1. Within-species vulnerability to natural population die-offs: black howler monkeys in the Yucatán Peninsula

Vulnerability to natural population die-offs mediated by extreme natural events can contrast radically across populations of a single species, depending on: (i) the location of a population relative to the source of disturbance; (ii) the intrinsic features of the phenomenon experienced by various populations, such as intensity and duration; and (iii) differences in the exposure of populations as shaped by differences in habitat structure.

For example, populations of the black howler monkey (*Alouatta pigra*) have been reported to occupy areas of evergreen rainforests and mangroves, among other vegetation types, within the Yucatán Peninsula, Mexico [64]. This region in southern Mexico is frequently exposed to hurricanes that, although of short life-span, have the potential to generate substantial ecological disturbance [65]. As with other members of the genus *Alouatta*, black howler monkeys are highly arboreal, making them particularly sensitive to hurricanes in any type of habitat. Yet, an ecological advantage of howler monkeys is their ability to survive on very low-quality diets [66]. Such high ecological adaptability may assist in the fulfilment of their nutritional needs during harsh conditions, including those occasions when hurricanes cause extensive defoliation and tree mortality [39,67].

Mangrove forests are located closer to the shore than are rainforests, and are thereby directly exposed to hurricanes. Howler populations can thus be expected to be better buffered against the impacts of hurricane damages in rainforests than in mangroves, given

their natural inland horizontal zonation. Physical protection for howlers is then substantially lower in mangroves than in rainforests (Figure 1, Case II), with vegetation composition in mangroves being less heterogeneous, the mangrove canopy being less complex than in rainforests and wood density being relatively low, resulting in reduced resistance against strong winds [68,69]. Altogether, howlers in rainforests might thus be less exposed to hurricanes than are howlers in mangroves (Figure 1, Case I).

Anthropogenic pressure on the habitat of a population will also affect the vulnerability of that population to a given extreme natural event. If howlers live in poor habitats; for example, in small fragments of highly degraded habitat (Figure 1, Case III), the impacts of hurricanes on population viability are expected to be more severe. In poor habitats, animals are expected to spend more time foraging on the ground, making them more prone to additional threats, such as predation [39], compared with howlers living in more continuous and richer habitats.

Based on these scenarios, and following our theoretical framework, vulnerability to natural population die-offs would thus be greatest for populations occupying degraded habitats, irrespective of the nature of the habitats (rainforests versus mangroves), because neither the high adaptive capacity of howlers nor their low biological sensitivity would be sufficient to help the population cope with the disturbance generated during or in the aftermath of hurricanes.

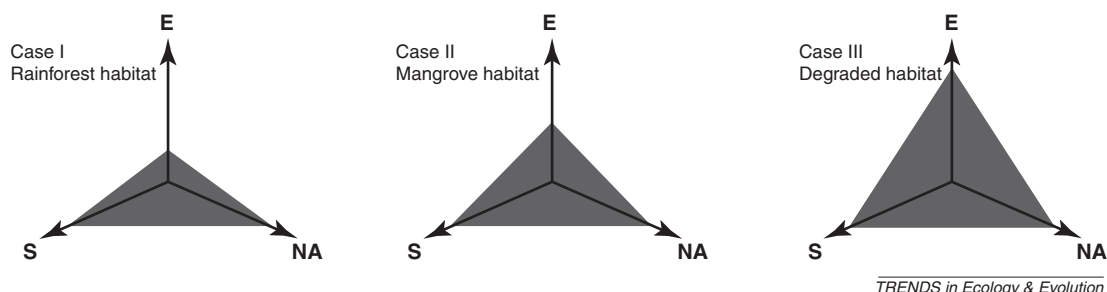


Figure 1. Theoretical example of vulnerability to natural population die-offs of black howler monkeys in the Yucatán Peninsula, Mexico exposed to hurricanes. Vulnerability is assessed for populations inhabiting three contrasting habitat conditions. Overall vulnerability (grey triangle) can be heightened or lessened depending of the interplay between exposure, sensitivity and non-adaptability to particular extreme natural events.

network of waterholes (where droughts are a high risk), vaccinations (where disease is high risk) and fire breaks and/or clearing of undergrowth (where wildfires are a threat). However, there will be particular circumstances where the impacts of extreme natural events will be more difficult to mitigate (e.g. hurricanes [39]). Under such scenarios, options could include the temporary or permanent translocation of individuals from those populations at imminent risk. Admittedly, such an option will not always be viable and caution will be required when it comes to assessing the suitability of the release site and the potential impacts of the translocated individuals on the local ecological dynamics.

Concluding remarks

With extreme natural events of anthropogenic origins expected to occur more frequently and with greater intensity in the coming decades, there is increasing awareness that such events represent a growing threat to biodiversity [55,56]. This might be particularly true for populations currently under pressure owing to human-related processes, such as habitat loss and degradation, overexploitation or spread of invasive species [57]. Despite the increased importance of extreme events as drivers of biodiversity loss

across the globe, current understanding of what processes drive such phenomena is limited and the ability to anticipate population die-offs is low. Yet, determining which sets of factors affect the vulnerability of a population to undergo a natural die-off would enable the important distinction to be drawn between those populations that are experiencing and might continue to experience severe losses (and thus are in need of tailored response strategies) and those that are less vulnerable. This work therefore underlines the critical need to advance the current ability to link climatic and ecological modelling at subglobal scales if researchers are to provide the most appropriate strategies to mitigate the expected negative impacts of climate change on biodiversity at the scale at which prevalent threat processes compromise the provision of goods and services to human society [2].

We propose a framework for assessing vulnerability to natural population die-offs. Such an exercise could be particularly valuable at the national scale, helping governments to identify populations most at risk (e.g. informing initiatives such as the National Red List). This could also support previous efforts to assess the vulnerability of species to climate change [25], by providing a framework allowing the quantification, for each species, of the

expected changes in IUCN risk categories resulting from the increasing occurrence and severity of anthropogenically caused extreme events that resemble extreme 'natural' events. This could involve, for example, assessing how increased occurrence and severity of extreme events may impact the geographical range size of a species and then translating such changes to changes in individual numbers. Although we have used terrestrial mammals as a focus here, we believe the proposed framework could be used as a tool to generate response strategies for other taxa. For those species whose populations already face such circumstances, there is an urgent need to incorporate their vulnerability to natural population die-offs in the current assessment of their extinction risk.

Acknowledgements

This research was conducted with support from the Mexican Council for Science and Technology (Ref. 209160) and the World Wildlife Fund (Ref. RM60) to E.I.A.J. Many thanks to Alienor Chauvenet, James Duffy, William Cornforth and two anonymous referees for comments on previous drafts of this work.

References

- Pimm, S.L. and Jenkins, C.N. (2009) Extinctions and the practice of preventing them. *Conserv. Biol.* 23, 183–188.
- Ceballos, G. *et al.* (2010) The sixth extinction crisis loss of animal populations and species. *J. Cosmol.* 8, 1821–1831.
- Mace, G.M. (2004) The role of taxonomy in species conservation. *Philos. Trans. R. Soc. B* 1444, 711–719.
- Isaac, N.J.B. *et al.* (2007) Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PLoS ONE* 3, e296.
- Collen, B. *et al.* (2009) Monitoring change in vertebrate abundance: the Living Planet Index. *Conserv. Biol.* 23, 317–327.
- Cowlishaw, G. *et al.* (2009) High variability in patterns of population decline: the importance of local processes in species extinctions. *Proc. R. Soc. B* 276, 63–69.
- IPCC (2007) *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press.
- Benton, T.G. *et al.* (2006) Complex population dynamics and complex causation: devils, details and demography. *Proc. R. Soc. B* 273, 1173–1181.
- Vasseur, D.A. and McCann, K.S., eds (2007) *The Impact of Environmental Variability on Ecological Systems*, Springer.
- Bonenfant, C. *et al.* (2009) Empirical evidence of density dependence in population of large herbivores. *Adv. Ecol. Res.* 41, 313–357.
- Lande, R. *et al.*, eds (2003) *Stochastic Population Dynamics in Ecology and Conservation*, Oxford University Press.
- Fagan, W.F. and Holmes, E.E. (2006) Quantifying the extinction vortex. *Ecol. Lett.* 9, 51–60.
- Courchamp, F. *et al.*, eds (2008) *Allee Effects in Ecology and Conservation*, Oxford University Press.
- Thébaud, E. and Fontaine, C. (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 5993, 853–856.
- Waite, T.A. *et al.* (2007) La Niña's signature: synchronous decline of the mammal community in a protected area in India. *Divers. Distrib.* 13, 752–760.
- Estes, J.A. *et al.* (2011) Trophic downgrading of planet earth. *Science* 333, 301–306.
- Yu, J. *et al.* (2010) Response of tropical cyclone potential to global warming scenario in the IPCC AR4 CGCMs. *J. Clim.* 6, 1354–1373.
- Thomas, C.D. *et al.* (2004) Extinction risk from climate change. *Nature* 427, 145–148.
- Jentsch, A. and Beierkuhnlein, C. (2008) External geophysics, climate and environment: research frontiers in climate change effects of extreme meteorological events on ecosystems. *C.R. Geosci.* 340, 621–628.
- Keith, D.A. *et al.* (2008) Predicting extinction risk under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biol. Lett.* 4, 560–563.
- Krawchuk, M.A. *et al.* (2009) Global pyrogeography: the current and future distribution of wildfire. *PLoS ONE* 4, e5102.
- Grossmann, I. (2009) Atlantic hurricane risks: preparing for the plausible. *Environ. Sci. Technol.* 43, 7604–7608.
- Wang, W. *et al.* (2010) Remote sensing analysis of impacts of extreme drought weather on ecosystems in Southwest Region of China based on Normalized Difference Vegetation Index. *Environ. Sci. Res.* 23, 1447–1455.
- Sienz, F. *et al.* (2010) Extreme value statistics for North Atlantic cyclones. *Tellus* 62A, 347–360.
- Foden, W. *et al.* (2008) Species susceptibility to climate change impacts. In *The 2008 Review of The IUCN Red List of Threatened Species*. (Vié, J.C. *et al.*, eds), pp. 1–11, IUCN.
- Young, T.P. (1994) Natural die-offs of large mammals: implications for conservation. *Conserv. Biol.* 8, 410–418.
- Reed, D.H. *et al.* (2003) The frequency and severity of catastrophic die-offs in vertebrates. *Anim. Conserv.* 6, 109–114.
- Liow, L.H. (2009) Lower extinction risk in sleep-or-hide mammals. *Am. Nat.* 173, 264–272.
- Taylor, W.A. *et al.* (2006) Population dynamics of two sympatric antelope species grey rhebok (*Pelea capreolus*) and mountain reedbuck (*Redunca fulviviflora*) in a high level grassland region of South Africa. *J. Zool.* 268, 369–379.
- Worden, J. *et al.* (2010) *Aerial Census of Wildlife and Livestock in Eastern Kajiado*, Amboseli Conservation Programme.
- Frankham, R. and Brook, B.W. (2004) The importance of time scale in conservation biology and ecology. *Ann. Zool. Fenn.* 41, 459–463.
- Mace, G.M. *et al.* (2008) Quantification of extinction risk: IUCN's system for classifying threatened species. *Conserv. Biol.* 22, 1424–1442.
- Cowlishaw, G. and Dunbar, R., eds (2000) *Primate Conservation Biology*, University of Chicago Press.
- Fisher, D.O. *et al.* (2003) Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. *Proc. R. Soc. B* 270, 1801–1808.
- Collen, B. *et al.* (2006) Extinction risk: a comparative analysis of central Asian vertebrates. *Biodiv. Conserv.* 15, 1859–1871.
- Cardillo, M. *et al.* (2008) The predictability of extinction: biological and external correlates of decline in mammals. *Proc. R. Soc. Lond. B* 275, 1441–1448.
- Price, S.A. and Gittleman, J.L. (2007) Hunting to extinction: biology and regional economy influence extinction risk and the impact of hunting in artiodactyls. *Proc. R. Soc. Lond. B* 274, 1845–1851.
- Widmer, O. *et al.* (2004) The effects of hurricane Lofar on habitat use of roe deer. *For. Ecol. Manage.* 195, 237–242.
- Pavelka, M.S.M. and Behie, A.M. (2005) The effect of hurricane Iris on the food supply of black howlers (*Alouatta pigra*) in southern Belize. *Biotropica* 37, 102–108.
- Davidson, A.D. *et al.* (2009) Multiple ecological pathways to extinction in mammals. *Proc. Natl. Acad. Sci. U.S.A.* 106, 10702–10705.
- Isaac, N.J.B. and Cowlishaw, G. (2004) How species respond to multiple extinction threats. *Proc. R. Soc. Lond. B* 271, 1135–1141.
- Fritz, S.A. *et al.* (2009) Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecol. Lett.* 12, 538–549.
- Lyon, L.J. *et al.* (2000) Direct effects of fire and animal responses. In *Wildland Fire in Ecosystems: Effects of Fire on Fauna* (Smith, J.K., ed.), pp. 17–23, US Department of Agriculture.
- Peres, C.A. *et al.* (2003) Vertebrate responses to surface wildfires in central Amazonian forest. *Oryx* 37, 97–109.
- Lunney, D. *et al.* (2004) Post-fire survival and reproduction of rehabilitated and unburnt koalas. *Biol. Conserv.* 120, 567–575.
- Barlow, J. and Peres, C.A. (2008) Fire-mediated dieback and compositional cascade in an Amazonian forest. *Philos. Trans. R. Soc. B* 363, 1787–1794.
- De Castro, F. and Bolker, B. (2005) Mechanisms of disease-induced extinction. *Ecol. Lett.* 8, 117–126.
- Kuiken, T. *et al.* (2006) The 2000 canine distemper epidemic in Caspian seals (*Phoca caspica*): pathology and analysis of contributory factors. *Vet. Pathol.* 43, 321–338.

- 49 Nunn, C.L. and Tae-Won Dokey, A. (2006) Ranging patterns and parasitism in Primates. *Biol. Lett.* 2, 351–354
- 50 Foley, C. *et al.* (2008) Severe drought and calf survival in elephants. *Biol. Lett.* 5, 541–544
- 51 Birkmann, J. (2005) Risk and vulnerability indicators at different scales: applicability, usefulness and policy implications. *Global Environ. Change B: Environ. Hazards* 7, 20–31
- 52 Geiser, F. and Turbill, C. (2009) Hibernation and daily torpor minimize mammalian extinctions. *Naturwissenschaften* 96, 1235–1240
- 53 Canale, C.I. and Pierre-Yves, H. (2010) Adaptive phenotypic plasticity and resilience of vertebrates to increasing climatic unpredictability. *Clim. Res.* 43, 135–147
- 54 Chevin, L.M. *et al.* (2010) Adaptation, plasticity and extinction in a changing environment: towards a predictive theory. *PLoS Biol.* 8, e10000357
- 55 Lee, T.M. and Jetz, W. (2010) Unravelling the structure of species extinction risk for predictive conservation science. *Proc. R. Soc. Lond. B* 278, 1329–1338
- 56 Brook, B.W. *et al.* (2008) Synergies among extinction drivers under global change. *Trends Ecol. Evol.* 23, 453–460
- 57 United Nations International Strategy for Disaster Reduction UNISDR (2009) *2009 UNISDR Terminology on Disaster Risk Reduction*, United Nations
- 58 Miller, F.L. and Barry, S.J. (2009) Long term control of peary caribou numbers by unpredictable exceptionally severe snow or ice conditions in a non equilibrium grazing system. *Arctic* 62, 175–189
- 59 Scorolli, A.L. *et al.* (2006) Unusual mass mortality of feral horses during a violent rainstorm in Parque Provincial Tornquist Argentina. *Mastozool. Neotrop.* 13, 255–258
- 60 Prins, H.H.T. and Douglas-Hamilton, I. (1990) Stability in a multi-species assemblage of large herbivores in East Africa. *Oecologia* 83, 392–400
- 61 Woolley, L.A. *et al.* (2008) Population and individual elephant response to a catastrophic fire in Pilanesberg National Park. *PLoS ONE* 3, e3233
- 62 Bermejo, M. *et al.* (2006) Ebola outbreak killed 5000 gorillas. *Science* 314, 1564
- 63 Elkan, P.W. *et al.* (2009) A die-off of large ungulates following a *Stomoxys* biting fly out-break in lowland forest, northern Republic of Congo. *Afr. J. Ecol.* 47, 528–536
- 64 Serio-Silva, J.C. *et al.* (2006) Mapping primate populations in the Yucatán peninsula, Mexico: a first assessment. In *New Perspectives in the Study of Mesoamerican Primates: Distribution, Ecology, Behavior and Conservation* (Estrada, A. *et al.*, eds), pp. 489–511, Springer
- 65 Boose, E. and Foster, D. (2006) *Ecological Impacts of Hurricanes across the Yucatán Peninsula*, Harvard Forest Data Archive: HF071
- 66 Pozo-Montuy, G. and Serio-Silva, J.C. (2007) Movement and resource use by a group of *Alouatta pigra* in a forest fragment in Balancán, Mexico. *Primates* 48, 102–107
- 67 Gilman, E.L. *et al.* (2008) Threats to mangroves from climate change and adaptation options: a review. *Aquat. Bot.* 89, 237–250
- 68 Whigham, D.F. *et al.* (2010) Impact of hurricanes on the forest of Quintana Roo, Yucatán Peninsula, Mexico. In *The lowland Maya Area: Three Millennia at the Human–Wildland Interface* (Gómez-Pompa, A. *et al.*, eds), pp. 193–213, CRC Press
- 69 Imbert, D. *et al.* (1996) Hurricane damage and forest structure in Guadalupe, French West Indies. *J. Trop. Ecol.* 12, 663–680