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# Natural Die-Offs of Large Mammals: Implications for Conservation

TRUMAN P. YOUNG

Louis Calder Center  
Fordham University  
Box K  
Armonk, NY 10504, U.S.A.

**Abstract:** *The viability of populations is a central concern of biological conservation. The occurrence of catastrophic die-offs may greatly reduce the long-term viability of populations. Theoretical extinction models and viability analyses require information on the frequency of die-offs and on the distribution of die-off severities. A review of literature identified 96 natural die-offs in large mammal populations, with a die-off being defined as a peak-to-trough decline in estimated population numbers of at least 25%. If such die-offs are common, population viability analyses that ignore them may be overly optimistic. The severities of the natural die-offs of large mammals presented here are not uniformly distributed. There is a relative overabundance of die-offs in the 70–90% range, and an underabundance of die-offs greater than 90%. This may indicate the presence of buffers against population extinction. The reported causes of large mammal die-offs were significantly related to trophic level: herbivore die-offs were more often attributed to starvation, while carnivore die-offs were more often attributed to disease. Populations subject to large-scale phenomena such as drought and severe winters may not be protected from die-offs by population subdivision. On the other hand, populations subject to catastrophic disease epidemics may be protected by subdivision, and threatened by corridors between conservation areas and by translocation efforts.*

## Introduction and Methods

A central task of biological conservation is estimating the viability of populations, and how various factors may

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Declinaciones naturales repentinas y pronunciadas en mamíferos grandes: implicaciones para la conservación

**Resumen:** *La viabilidad de las poblaciones es una preocupación central en la biología de conservación. La ocurrencia de "die-offs" (declinaciones repentinas y pronunciadas) catastróficas reducen en gran medida la viabilidad a largo plazo de las poblaciones. Modelos teóricos de extinción y análisis de viabilidad requieren de información sobre de la frecuencia de los "die-off" y sobre la distribución de la seriedad de los mismos. Una revisión de la literatura identificó 96 "die-offs" naturales en poblaciones de mamíferos grandes, definiéndose al "die-off" como una declinación de por lo menos un 25% en el tamaño poblacional. Si tales "die-offs" son comunes, los análisis de viabilidad poblacional que los ignoran serían sumamente optimistas. La severidad de los "die-offs" naturales de mamíferos grandes aquí presentados no está distribuida uniformemente. Existe una sobreabundancia relativa de "die-offs" en el nivel del 70 al 90%, y una superabundancia de "die-offs" mayores que 90%. Esto último podría indicar la presencia de "buffers" contra las extinciones poblacionales. Las causas reportadas para los "die-offs" de grandes mamíferos estuvieron significativamente relacionadas con el nivel trófico; los "die-offs" de herbívoros se atribuyeron más frecuentemente a la inanición, mientras que los "die-offs" de carnívoros se atribuyeron mas frecuentemente a enfermedades. Las poblaciones sujetas a fenómenos a una escala espacial grande, tales como sequías e inviernos severos no podrían ser protegidas de los "die-offs" mediante la subdivision poblacional. Por otro lado, las poblaciones sujetas a epidemias catastróficas de enfermedades podrían ser protegidas mediante la subdivisión, y puestas en peligro por medio de corredores entre áreas de conservación y por medio de esfuerzos de translocación.*

be manipulated to ensure some (high) probability of long-term population survival (Soule 1987). Limits on the viability of populations are hypothesized to be set by various factors (Lande 1988; Simberloff 1988), including inbreeding, loss of genetic variation (Lande 1988; Simberloff 1988), demographic stochasticity (Richter-

Table 1. Natural die-offs of large mammals.

<i>Species</i>	<i>% Die-off</i>	<i>Primary Cause</i>	<i>Reference</i>	<i>Biome</i>
Gray Kangaroo	55	starvation (drought)	Caughley et al. 1985	temperate
Red Kangaroo	59	starvation (drought)	Caughley et al. 1985	temperate
Red Kangaroo	≥50	starvation (drought)	Newsome 1975	temperate
Red Kangaroo	85	starvation (drought)	Corbet & Newsome 1987	temperate
Warthog	>90	starvation (drought)	Scholes 1985	tropical arid
Warthog	>90?	starvation (drought)	Walker et al. 1987	tropical arid
Warthog	38	starvation (drought)	Walker et al. 1987	tropical arid
Collared Peccary	64	?	Glanz 1982	tropical forest
Mule Deer	42	starvation (winter)	Robinette et al. 1952	temperate
Moose	50–87	starvation (winter)	Mech 1966	temperate
Caribou	89	starvation (winter)	Miller et al. 1977	arctic
Caribou	60	starvation	Davis 1978	arctic
Caribou	78	starvation	Davis 1978	arctic
Caribou	44	starvation	Davis 1978	arctic
Caribou	69	starvation	Davis 1978	arctic
Caribou	71	starvation (winter)	Gates et al. 1986	arctic
Grant's Gazelle	46	starvation (drought)	Stewart & Zaphiro 1963	tropical arid
Thomson's Gazelle	65	predation (competition)	Borner et al. 1987	tropical arid
Springbok	>85	starvation (drought)	Viljoen & Bothma 1990	tropical arid
Gemsbok	>85	starvation (drought)	Viljoen & Bothma 1990	tropical arid
Impala	75	starvation (drought)	Scholes 1985	tropical arid
Impala	72	starvation (drought)	Walker et al. 1987	tropical arid
Impala	36	starvation (drought)	Walker et al. 1987	tropical arid
Impala	87	disease (anthrax)	Prins & Weyerhauser 1987	tropical arid
Impala	90	disease	Prins & Douglas-Hamilton 1990	tropical arid
Impala	49	predation (starvation)	Hirst 1969	tropical arid
Waterbuck	80	starvation (drought)	Walker et al. 1987	tropical arid
Waterbuck	30	starvation (drought)	Walker et al. 1987	tropical arid
Waterbuck	93	disease (brown ear tick)	Melton 1987	tropical arid
Reedbuck	90	starvation (multiple)	Ferrar & Kerr 1971	tropical arid
Reedbuck	91	disease	Prins & Douglas-Hamilton 1990	tropical arid
Kongoni	81	starvation (drought)	Hillman & Hillman 1977	tropical arid
Kongoni	69	starvation (drought)	Stewart & Zaphiro 1963	tropical arid
Wildebeast	88	starvation (drought)	Scholes 1985	tropical arid
Wildebeast	90	starvation (drought)	Walker et al. 1987	tropical arid
Wildebeast	62	starvation (drought)	Walker et al. 1987	tropical arid
Wildebeast	32	starvation (drought)	Hillman & Hillman 1977	tropical arid
Wildebeast	46	starvation (drought)	Stewart & Zaphiro 1963	tropical arid
Wildebeast	31	predation	Hirst 1969	tropical arid
Wildebeast	100	predation (drought)	Prins & Douglas-Hamilton 1990	tropical arid
Kudu	50	starvation (drought)	Walker et al. 1987	tropical arid
Kudu	40	starvation (drought)	Walker et al. 1987	tropical arid
Kudu	51	starvation	Hirst 1969	tropical arid
Eland	50	starvation (drought)	Stewart & Zaphiro 1963	tropical arid
Giraffe	27	starvation	Hirst 1969	tropical arid
Bighorn Sheep	76	disease	Anonymous 1987	temperate
Bighorn Sheep	>50	disease (scabies)	Lange et al. 1980	temperate
Bighorn Sheep	88	starvation (disease)	Uhazy et al. 1973	temperate
Bighorn Sheep	>75	?	Stelfox 1971	temperate
Bighorn Sheep	85	disease (starvation)	Stelfox 1971	temperate
Bighorn Sheep	52	?	Stelfox 1971	temperate
Bighorn Sheep	85	starvation (winter)	Stelfox 1971	temperate
Dall Sheep	70–90	starvation (winter)	Murie 1944	arctic
Dall Sheep	56	starvation (winter)	Walters et al. 1981	arctic
Musk Oxen	86	starvation (winter)	Miller et al. 1977	arctic
Bison	43	?	Meagher 1973	temperate
Bison	63	?	Meagher 1973	temperate
Bison	74	?	Meagher 1973	temperate
African Buffalo	87	starvation (drought)	Walker et al. 1987	tropical arid
African Buffalo	34	starvation (drought)	Walker et al. 1987	tropical arid
Pronghorn	62	starvation (winter)	Martinka 1967	temperate
Burchell's Zebra	90	starvation (drought)	Walker et al. 1987	tropical arid
Burchell's Zebra	73	starvation (drought)	Walker et al. 1987	tropical arid

Table 1. Continued.

Species	% Die-off <sup>a</sup>	Primary Cause <sup>b</sup>	Reference	Biome
Burchell's Zebra	80	starvation (drought)	Scholes 1985	tropical arid
Burchell's Zebra	28	starvation (drought)	Stewart & Zaphiro 1963	tropical arid
Burchell's Zebra	50	starvation (drought)	Hillman & Hillman 1977	tropical arid
African Elephant	29	starvation (drought)	Corfield 1973	tropical arid
African Elephant	29	disease (drought)	Prins & Douglas-Hamilton 1990	tropical arid
Vervet Monkey	72	habitat change (predation)	Isbell et al. 1990	tropical arid
Baboon	95	habitat change	Altmann et al. 1985	tropical arid
Siamong	67	disease	Palombit, personal communication	tropical forest
Tamarin	84	habitat change (?)	Glanz 1982	tropical forest
Cebus Monkey	85	?	Glanz 1982	tropical forest
Howler Monkey	48	disease (yellow fever?)	Collias & Southwick 1952	tropical forest
Langur	"massive"	disease (viral)	Work et al. 1957	tropical forest
Bonnet Macaque	"massive"	disease (viral)	Work et al. 1957	tropical forest
Three-Toed Sloth	76	?	Glanz 1982	tropical forest
Bottlenose Dolphin	50	disease	Harwood & Hall 1990	marine
Coyote	50	disease (parvivirus)	Pence et al. 1983	temperate
Coyote	87	starvation (hare cycle)	Clark 1972	temperate
Wild Dog	84	disease (distemper)	Borner et al. 1987	tropical arid
Wild Dog	72	disease (competition)	Frame et al. 1979	tropical arid
Wild Dog	>63	disease (?)	J. Malcolm, personal communication	tropical arid
African Lion	75	disease (fly outbreak)	Fosbrooke 1963	tropical arid
Northern Sea Lion	39	?	Merrick et al. 1987	marine
Crabeater Seal	85	disease (crowding, starvation)	Laws & Taylor 1957	marine
Harbour Seal	85	disease (?)	Pitcher 1990	marine
Harbour Seal	75	disease (distemper)	Bjorge 1991	marine
Caspian Seal	80	disease	Lauckner 1985	marine
Fur Seal	62	starvation ( <i>El Nino</i> )	Trillmich & Limberger 1985	marine
Fur Seal	33	starvation	Glynn 1988	marine
Sea Otter	33	?	Lubina & Levin 1988	marine
Sea Otter	68	starvation	Kenyon 1969	marine
Sea Otter	68	starvation	Kenyon 1969	marine
Sea Otter	52	starvation	Kenyon 1969	marine
Coati	59	starvation (?)	Kaufmann 1962	tropical forest

<sup>a</sup>Estimates of "percentage die-off" were made on samples of various sizes and methodologies. <sup>b</sup>"Primary cause" was taken from the original investigators' reports. Parenthetical causes are secondary or associated causes.

Dyn & Goel 1972), environmental variability (Leigh 1981; Goodman, 1987a, 1987b; Dennis et al. 1991), and "catastrophes." Catastrophes can be defined as local extinctions of a metapopulation (Ewens et al. 1987) or as rare, severe environmental events (Hanson & Tuckwell 1978) such as drought, disease, or habitat change. There is growing understanding that nongenetic factors, and particularly catastrophic events, may be more likely to limit the viability of populations than genetic factors (Lande 1988).

Catastrophic die-offs have the potential for putting great constraints on minimum viable population size (Hanson & Tuckwell 1978; Mangel & Tier 1993). But how common and how severe are such die-offs in nature? Theoretical models require information on the frequency of die-offs and on the distribution of die-off severity (Mangel & Tier 1993). It is also important that we identify the natural factors that put populations at occasional risk. Populations that are subject to catastrophic disease epidemics are likely to be managed differently than populations subject to catastrophic starvation. It

would therefore be useful to examine the literature on natural die-offs.

Large population fluctuations have been documented in many populations of invertebrates (Williamson 1972; Wolda 1982, 1992), birds (Stout & Cornwell 1976), and small mammals (Williamson 1972; Hanski 1987). I have limited this survey to large mammals for several reasons. First, because of their ecological impact, hunting potential, and conservation attention, there are numerous repeated population estimates of many populations of large mammals. Second, large long-lived animals exhibit less severe population fluctuations than do smaller, shorter-lived species (Williamson 1972; Pimm 1991) and so serve as conservative samples of population die-offs in nature. Third, justifiably or not, large mammals receive a disproportionate share of attention in conservation activity and research.

I identified 96 natural die-offs of large mammals in a survey of the literature (Table 1). Large mammals are defined here as those from all mammalian orders except rodents, shrews, bats, and lagomorphs. A die-off is de-

defined as a monotonic drop in population numbers that occurs between two or among more than two population surveys. In long-term data sets, these die-offs are peak-to-trough population changes. I have included only die-offs in which there was at least a 25% reduction in population size.

I have not included in the analysis any die-offs that were clearly related to human activities (over-exploitation, habitat destruction), nor have I included introduced populations. I attempted to differentiate between natural epizootics and diseases introduced by man. For example, I have not included die-offs associated with rinderpest in African ungulates or *Pasteurella* in bighorn sheep, which are almost certainly recently introduced diseases, but I have included die-offs associated with scabies in bighorn sheep and distemper in wild dogs, even though the origin of these is not completely clear.

Berger (1990) documented extinctions of isolated populations of bighorn sheep, with a greater extinction rates among smaller populations. The large number of local bighorn extinctions strongly implies that the global population was not in equilibrium. Either extinction rates have recently increased dramatically compared to earlier times (perhaps through reduction of population sizes below critical limits), or recolonization rates have lowered. In either case, die-offs in these populations may be related to human activity.

Even though I have included all of the natural die-offs that have come to my attention, it is reasonable to assume that the die-offs reported in Table 1 represent only a small fraction of the severe mammalian die-offs that have occurred in nature in recent decades. Marine mammals are difficult to census unless they come periodically to limited terrestrial breeding and calving sites (Thompson & Harwood 1990). Censusing of forest animals is especially difficult (Glanz 1982; Milton 1990). Even in open terrestrial habitats, detailed population censuses have only recently been carried out, and only for a limited number of species and sites.

Not included here are numerous nonquantitative reports of catastrophic die-offs (such as Longhurs et al. 1952; Simmonds 1992). For example, Longhurs et al. (1952) report 180 local die-offs of deer in California between the late nineteenth century and the mid twentieth century. Over a third of these were attributed to disease and over half to starvation, usually during severe winters. Interestingly, these proportions are similar to those of die-offs attributed to starvation and disease for all herbivores in my survey (see Table 2). Examples:

“The winter of 1889 killed most of the deer and antelope” (Longhurs et al. 1952:14);

“[In 1921] a severe epizootic nearly wiped out a heavy population of black-tails along the McCloud River” (Longhurs 1952:21);

**Table 2.** Numbers of large mammal species whose die-offs were attributed to various causes for herbivores, carnivores, and primates.

Group	Suggested Cause				
	Starvation	Disease	Predation	Habitat Change	Unknown
Herbivores	22 (48)	5 (7)	3 (4)	—	4 (7)
Carnivores	4 (7)	7 (8)	—	—	2 (2)
Primates	—	4 (4)	1 (1)	3 (3)	1 (1)

Numbers in parentheses are the numbers of populations.

“Periodic die-offs of deer on densely populated ranges became commonplace—some caused by parasites or disease, others by outright starvation, but all manifestations of local over-population” (Longhurs et al. 1952:22–23).

## Results and Discussion

These die-offs were widely diverse etiologically (Table 2), ecologically (Table 3), and taxonomically (Table 4). Virtually all types of large mammals are represented. Ungulates and carnivores account for most of the records, but primates, marsupials, edentates, and proboscids are also represented. The seven different mammalian orders did not differ significantly in the mean severity of their die-offs ( $F = 1.04$ , d.f. = 7,  $p = 0.41$ ).

Die-offs in the five different habitat types did not differ significantly in their mean severity ( $F = 0.33$ , d.f. = 4,  $p = 0.86$ ). Semiarid (savanna) regions are numerically strongly represented. There are several possible reasons for this. First, these regions harbor large populations of large mammals. Second, these habitats may be more prone to lethally dry years than are more mesic ecosystems. Third, animals in these open habitats are relatively easy to count. Tropical forests are sometimes considered relatively constant environments. However, several mammal species in tropical forests have experienced documented die-offs.

Die-offs attributed to different causes did not differ significantly in their mean severity ( $F = 1.40$ , d.f. = 4,  $p = 0.24$ ). The most commonly reported sources of mortality were disease and starvation due to drought or severe winter. Although the mean severities of die-offs were independent of guild (herbivores, carnivores, pri-

**Table 3.** Numbers of populations with reported die-offs for different habitat types.

Habitat	Frequency
Tropical Arid	46
Temperate	15
Arctic	9
Marine	12
Tropical forest	8

**Table 4.** Numbers of populations with reported die-offs for different mammalian groups (mostly orders).

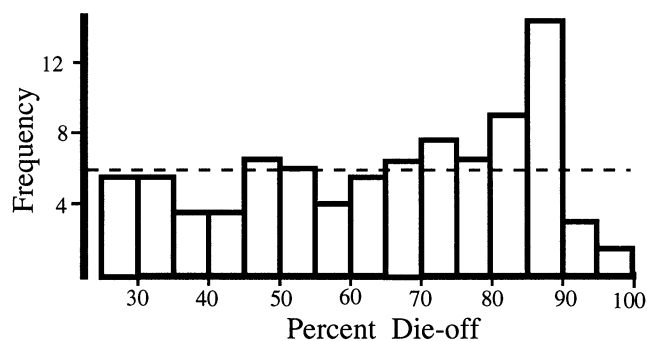
Group	# Species	# Populations
Marsupialia	2	4
Ungulata	24	62
Artiodactyla	23	57
Perissodactyla	1	5
Carnivora	10	17
Primates	7	7
Proboscidae	1	2
Edentata	1	1
Cetacea	1	1

mates;  $F = 0.09$ , d.f. = 2,  $p = 0.92$ ), the frequencies of reported probable causes of die-offs were significantly different between herbivores and carnivores (Table 2). Herbivore die-offs were more often attributed to starvation, and carnivore die-offs were more often attributed to disease, when analyzed either at the species level ( $X^2 = 7.36$ , d.f. = 1,  $p < 0.001$ ) or at the population level ( $X^2 = 11.54$ , d.f. = 1,  $P < 0.001$ ).

There are several possible reasons for this difference in the reported causes of die-offs of predators and herbivores. First, most of the carnivores in Table 1 are highly social and live in more intimate contact than do most social herbivores, which may promote the transmission of disease. Second, the diets of carnivores may facilitate the acquisition and transmission of disease. Third, herbivores as a trophic level may be more often food-limited than are carnivores. Fourth, the food resources of carnivores may be less subject to environmental fluctuations. Herbivores (food for predators) decline more slowly than food plants during a drought or over a severe winter. Finally, these differences could be due to the biases of observers if those studying carnivores were more likely to attribute die-offs of mixed etiology to disease.

Although most studies reported only a single likely cause of the die-off, multiple causes are likely. Overpopulation may manifest itself both in starvation and in disease susceptibility (Longhurs et al. 1952), and habitat loss can increase food limitation and predation (Isbell et al. 1990). Although multiple factors may be common, only a minority of the studies directly addressed contributing factors (see Table 1).

The distribution of die-off intensities was not random. Die-offs of 70–90% were over-abundant, and die-offs greater than 90% were under-abundant (Fig. 1;  $X^2 = 19.1$ , d.f. = 6,  $p < 0.005$ ; among die-offs more than 30%, in 10% intervals). The paucity of natural die-offs greater than 90% may indicate a demographic “boundary effect” that tends to protect populations from local extinction. Of course, these populations are the survivors of long-term, large-scale processes that can be expected to have already eliminated populations susceptible to extinction. Human-caused reductions in



**Figure 1.** The distribution of 92 reported natural die-offs in large mammal populations (From Table 1). The dotted line represents a uniform distribution.

population size may have more profound effects on extinction probabilities than suggested by these data.

The number of die-offs smaller than 70% is also less than those 70–90%. If this is real, it may be a threshold effect, where populations tend to withstand intermediate levels of environmental stress but respond dramatically to extreme events. I believed that it more likely represents the relative under-reporting of less severe die-offs.

A similar pattern also occurs among die-offs in cyclic populations. Figure 2 shows the distribution of carnivore die-offs from the well-known lynx/hare cycle (Keith 1963; Williamson 1972). These data come from trapping data and may underestimate minimum numbers and therefore overestimate population reductions. These data show an abundance of die-off intensities in the range of 78–92%. Strong density dependence is thought to protect these cyclic populations from extinction. The similarity between the large mammal die-offs in Figure 1 and the carnivore crashes in Figure 2 imply that catastrophic die-offs of large mammals may also have a density-dependent component. Those die-offs that were due to density-dependent factors could be the results of either overcompensation (Grenfell et al. 1992) or of changes in carrying capacity due to external factors (such as drought or severe winters; Western 1975; Caughley & Gunn 1993). Unfortunately, it is difficult to demonstrate density dependence from time-series data of natural populations (Vickery & Nudds 1991; Caughley & Gunn 1993).

These data do not allow calculation of the frequency of die-offs for individual populations. However, severe droughts of the kind associated with the recorded die-offs in eastern and southern Africa have occurred several times this century. Longhurs et al. (1952) reported numerous die-offs of deer in California during the late 1800s and early 1900s. Harwood and Hall (1990) concluded that “marine mammal populations are occasionally subject to events that may remove 50% or more of the individuals. In the case of seals in the United Kingdom, such events seem to occur with a periodicity of

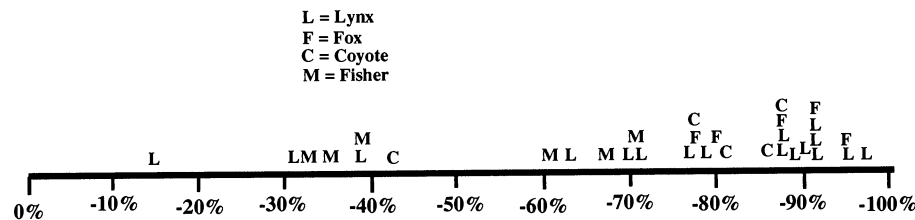


Figure 2. Distribution of cyclic carnivore population crashes from the lynx-hare cycle. These data come from trapping and may underestimate minimum numbers and therefore overestimate population reductions.

about 50 years." Similarly, three major die-offs of Alaskan caribou have occurred in the past hundred years (Miller et al. 1977; Davis 1978). It appears that major die-offs are not uncommon among some large mammal species.

The data are even less able to demonstrate whether such die-offs occur regularly or sporadically. Current models of environmental variation and catastrophic die-offs consider their effects to be temporally random (Hanson & Tuckwell 1978; Goodman 1987a, 1987b; Mangel & Tier 1993). It is likely that if die-offs were more regularly spaced, they would represent less of a threat to population viability because they would allow populations time to recover between die-offs. However, the existence of density dependence as a cause of die-offs does not guarantee their regularity if carrying capacity itself fluctuates randomly and strongly (Caughley & Gunn 1993).

### Implications for Conservation

The patterns reported here have several implications for biological conservation. First, severe population crashes in populations of large mammals are apparently widespread and not uncommon in nature. The frequency and severity of such die-offs may put severe restrictions on the viability of populations of large mammals, which already require large areas per individual. Population viability analyses should incorporate the kinds of population variation indicated by these die-offs (see Mangel & Tier 1993).

Second, there may be limits to the severity of natural die-offs among extant populations. The rarity of extreme die-offs represents a form of density dependence that may help buffer populations against extinction. It appears that the factor(s) that cause severe die-offs are not effective in eliminating individuals when population sizes are greatly reduced. Possible explanations include refuges, immigration, the decreased efficiency of disease transmission at low population density, or the recovery of food resources.

Therefore, these results will affect population viability analysis in conflicting ways. Viability analyses that incorporate occasional catastrophic die-offs will tend to pre-

dict less long-term viability than analyses that do not. On the other hand, viability analyses that incorporate limits to the severity of die-offs will tend to predict greater long-term viability than analyses that do not.

More problematic is that these die-offs may occur so rarely that they are statistically unpredictable. Other stochastic sources of variation ("demographic," "environmental") can be modelled if the variation occurs over time periods that are short relative to the predictive range of the viability analysis. Severe and relatively unpredictable die-offs may limit the usefulness of population viability analysis.

While these die-offs may not often themselves drive natural populations to extinction, such demographic bottlenecks may put large populations regularly at risk from the factors that affect small populations (Keith 1963; Simberloff 1988; Berger 1990), including genetic and demographic effects; in addition, they are likely to be negatively affected by human interference. As human influences in nature increase, major population crashes are likely to become more threatening to species survival, even if they are natural in origin.

Third, different sources of mass mortality are likely to affect subdivided populations in different ways. Population subdivision (metapopulation structure) and the existence and quality of corridors among populations have become important considerations in the study of reserve design (Simberloff 1988). Populations subject to large-scale phenomena such as drought and severe winters may not be protected from die-offs by population subdivision (Quinn & Hastings 1987). On the other hand, populations subject to catastrophic disease epidemics may be protected by subdivision (Simberloff & Cox 1987) and threatened by corridors between conservation areas and by translocation efforts. It is important for managers to consider the relative likelihood of these different potential sources of catastrophic die-offs before making decisions about habitat or population manipulations.

The list of die-offs in Table 1 is undoubtedly incomplete. It is hoped that this preliminary review will serve as a basis for further survey work on catastrophic die-offs in nature. Uncommon events are more likely to be recorded (Weatherhead 1986) and understood (Young

& Isbell, 1994) when studies are conducted over the long term. The patterns revealed in this review are further evidence for the value of long-term field research.

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