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Umbrella species: critique and lessons from East Africa

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Abstract

Umbrella species are 'species with large area requirements, which if given sufficient protected habitat area, will bring many other species under protection'. Historically, umbrella species were employed to delineate specific reserve boundaries but are now used in two senses: (1) as aids to identifying areas of species richness at a large geographic scale; (2) as a means of encompassing populations of co-occuring species at a local scale. In the second sense, there is a dilemma as to whether to maximize the number or viability of background populations; the umbrella population itself needs to be viable as well. Determining population viability is sufficiently onerous that it could damage the use of umbrella species as a conservation shortcut. The effectiveness of using the umbrella-species concept at a local scale was investigated in the real world by examining reserves in East Africa that were gazetted some 50 years ago using large mammals as umbrella species. Populations of these species are still numerous in most protected areas although a few have declined. Populations of other, background species have in general been well protected inside reserves; for those populations that have declined, the causes are unlikely to have been averted if reserves had been set up using other conservation tools. Outside one reserve, Katavi National Park in Tanzania, background populations of edible ungulates and small carnivores are lower than inside the reserve but small rodent and insectivore abundance is higher. While we cannot compare East African reserves to others not gazetted using umbrella species, the historical record in this region suggests that umbrella species have been an effective conservation shortcut perhaps because most reserves were initially large and could encompass substantial populations of background species. It is therefore premature to discard the local-scale umbrella-species concept despite its conceptual difficulties.

INTRODUCTION

The design of nature reserves has been placed on a secure scientific footing with the advent of numerous analytic methods for delineating the size and boundaries of proposed reserves on grounds other than availability (Margules & Pressey, 2000; Sanderson *et al.*, 2002*b*). To determine where to place reserves, computational algorithms are applied to data sets on the distribution of different taxa across a large area in order to determine where the greatest number of species' geographic ranges overlap (e.g. Williams *et al.*, 1996; Peterson & Navarro-Siguenza, 1999; Virolainen *et al.*, 1999; Myers *et al.*, 2000). Time and funding are often limited, however, so conservation biologists employ surrogate species (Simberloff, 1998; Caro & O'Doherty, 1999) to select protected sites where distributional data on one well-known taxonomic group are used to predict the distribution of other, lesser-known taxa (Ricketts *et al.*, 1999). The efficacy of this biodiversity-indicator approach depends on scale. Across continents, species richness of different taxa coincides (Pearson & Cassola, 1992; Lawton, 1994) as, for the most part, do species richness and endemism within taxa (Kerr, 1997). At smaller scales, however, such as 10 × 10 km grid squares in the UK (Prendergast *et al.*, 1993), hotspots of species richness in one taxonomic group (e.g. butterflies) are usually weak predictors of hotspots of other groups (e.g. mammals or liverworts) (see also Flather *et al.*, 1997). The general consensus is that places where one taxonomic group is concentrated are unlikely to coincide with species-rich sites in other taxa at the scale of delineating reserve boundaries (Reid, 1998; but see Howard *et al.*, 1998).

At a local scale, the exact site and location of reserve boundaries can be selected using species (either one, or

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several: Lambeck, 1997) that are most demanding on resources. By maintaining these species in the landscape, it should be possible to preserve other 'background' species as well. (Background species are defined here as species that live in the same geographic area as species that have been used to identify an area of conservation concern.) This then is the umbrella-species concept, originally defined by Noss (1990) as 'species with large area requirements, which if given sufficient protected habitat area, will bring many other species under protection'. Umbrella species are generally used at a relatively local scale whereas indicators of biodiversity constitute a biogeographic or community-structure concept employed at larger scales; although both are used to target conservation of other species, many of their biological attributes are dissimilar (Caro & O'Doherty, 1999). Despite these differences, researchers are increasingly using the term umbrella species synonymously with indicators of biodiversity (Andelman & Fagan, 2000; Fleishman, Murphy & Brussard, 2000) and it may be helpful to clarify and critique the umbrella-species concept before it becomes incorporated into the biodiversity literature (see also J. M. Roberge & P. Angelstam, unpubl. data). Here, I discuss the history of the umbrella species concept, identify some problems in choosing appropriate umbrella species, and examine the long-term strengths and weaknesses of umbrella species in a real-life situation by focusing on reserves in East Africa that were inadvertently delineated some 50 years ago using species that we could consider today as umbrella species (Owen-Smith, 1983).

HISTORY

The umbrella-species concept originated as a practical solution to protecting species in the wild through its informal use as a field conservation tool throughout the twentieth century. The idea was only formalized in the 1980s and 1990s when fieldworkers, managers and conservation biologists working independently on different continents explicitly argued that protection of species with large area requirements or with specific habitat preferences would protect other species in specific ecosystems (Table 1). The large area requirement constituted the total area of home ranges of individuals within a viable population (here used informally as a population that appears unlikely to go into rapid decline), and specific habitat requirements referred to the need for individuals to visit particular areas within a home range usually for foraging but also for activities such as hibernating or nesting. From the start, the idea referred to protecting a population of individuals of a particular (umbrella) species and, as a consequence, populations of other species. The term umbrella species is therefore unfortunate since it actually refers to a population. Aside from large area requirements, the concept has, for the most part, been agnostic as to the mechanism by which umbrella species might be successful so it is difficult to predict which background species might be protected. None the less, background species that rely on the same resources as the umbrella species are, a priori, likely to be those that benefit most (Martikainen, Kaila & Haila, 1998; Suter, Graf & Hess, 2002).

Table 1. Examples of umbrella species that have been proposed in relation to specific ecosystems listed in chronological order

Species	Purpose	Reference
Wildebeest	Delineating boundaries of Serengeti National Park, Tanzania	Pearsall, 1957
Jaguar	Setting up Cockscomb Jaguar Reserve in Belize	Rabinowitz, 1986
Grizzly bear	Protecting the Greater Yellowstone Ecosystem, USA	Glick, Carr & Harting, 1991
Spotted owl	Saving areas of old-growth forest from logging in Pacific Northwest, USA	Wilcove, 1994
Large herbivores	Nature reserves in western Europe	Wallis de Fries, 1995

At about the same time, some scientists were putting forward other species that might be good candidates as umbrella species anywhere in their geographic range but without having a specific ecosystem in mind (e.g. tiger, *Panthera tigris*, Tilson & Seal, 1987; red-cockaded woodpecker, *Aicoides borealis*, Walters, 1991; cougar, *Felis concolor*, Beier, 1993; rhinoceros, *Diceros* sp., Foose, 1993). Yet other scientists were attempting to determine whether species that others, or that they themselves, had put forward as umbrella candidates really did protect other species. As an example of the former, Berger (1997) found that individual ranges of black rhinoceroses (*Diceros bicornis*) in Namibia were sufficiently inflexible that they failed to encompass the seasonal movements of enough individuals of other, sympatric herbivores that would constitute viable populations. He concluded that delineating a reserve that only circumscribed movements of rhinoceroses would fail to protect viable populations of other large desert mammals. As an example of the latter, Launer & Murphy (1994) found that if bay checkerspot butterfly (*Euphydryas editha*) populations were protected throughout their restricted geographic range in California, most native spring-flowering non-grass plant species would be protected too, but that the number of these species would drop off rapidly if butterflies were offered protection in only some areas. A key difference between the rhinoceros and butterfly studies is that the former tried to discover whether individual home ranges of a population of one species would encompass a sufficient number of ranges of individuals of other species for their populations to be viable, whereas the latter study counted how many species were covered by the range of the putative umbrella population (presence/absence data) but did not determine whether these (forb) species had viable populations. Investigations of the latter kind continue to appear every year (e.g. Martikainen *et al.*, 1998; Swengel & Swengel, 1999; Chase *et al.*, 2000; Rubinoff, 2001; J. M. Roberge & A. Angelstam, unpubl. data). Berger's study differs because it tried to see whether an umbrella species might protect other species in the long term (by addressing population viability in a coarse way) rather than simply protecting other species now (presence data) and it thus adhered more closely to the origins of the umbrella-species concept.

More recently, some studies of umbrella species have dispensed with measuring population sizes altogether and have become virtually synonymous with studies of biodiversity indicators. Here, the presence of a species in a relatively small area such as a canyon (Fleishman *et al.*, 2000), or a 25 km^2 grid square or county (Andelman & Fagan, 2000), is noted and the presence of other species in the same area is reported. The extent to which the presence of one or a suite of umbrella species, chosen on the basis of rarity or trophic level or degree of specialization, occurs with other background species is then analyzed in order to see how many species might be protected if the umbrella species were to be conserved. These studies do not attempt to discriminate among large or small, viable or extinction-prone populations of background species, nor are they targeted at a particular geographic area that might be protected, except in so far as the database is derived from a particular study area or portion of, say, a state. These newer studies resemble those examining cross-taxonomic overlap in species richness. As a result of all these lines of enquiry, the use of umbrella species has grown in the literature over the last 16 years (Fig. 1).

CHOOSING AN APPROPRIATE UMBRELLA SPECIES AT A LOCAL SCALE

Consider a viable population (of umbrella species *A*) whose individuals have home ranges that together cover x km^2 (Fig. 2(a)). Living in area x might be individuals of ten other species, the population of which each has a range of y km^2 whose ranges just overlap (each by 10%) the range covered by the umbrella species ($10 \times 0.1y = y$ in total). Now consider another umbrella species (*B*) population covering x km^2 elsewhere; *B* is overlapped by only two species, each with a range of y km^2, but here 50% of their ranges are each under x ($2 \times 0.5y = y$ in total) (Fig. 2(b)). Is *A* or *B* the better umbrella species? The answer hinges on the way that individuals of each background species are spaced within their population's

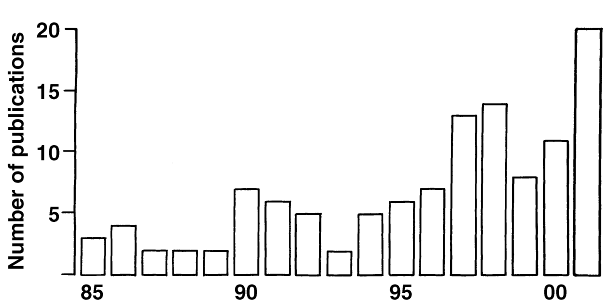

Fig. 1. Number of publications using the keywords 'umbrella species' plotted from 1985 to 2001 based on BIOSIS

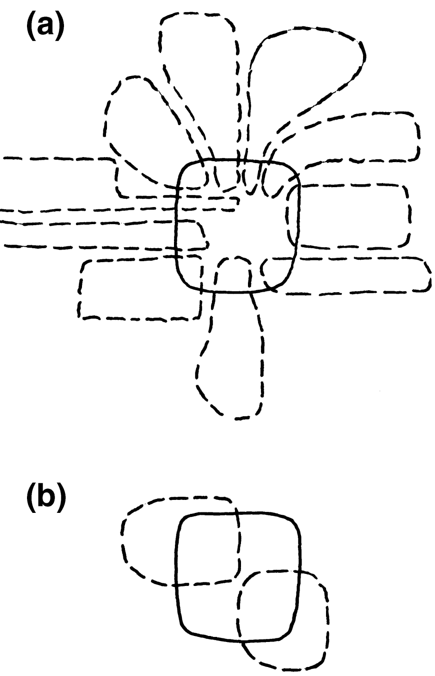

Fig 2. Two hypothetical umbrella populations. In the top panel, umbrella species *A* (solid line) is overlapped by ten background species (dashed lines). In the bottom panel umbrella species *B* is overlapped by two species. The total area of overlap is the same in both panels.

total range. If these individuals are wide ranging or migratory and each moves outside the umbrella population's area, x, they may be subject to mortality or suffer low reproduction (Fig. 3(a)). If, however, they have small ranges, some of which are completely circumscribed by the umbrella population's movements, then these individuals will be completely protected (Fig. 3(b)). Thus, the question reverts to whether there are sufficient individuals that are completely protected to constitute a viable population (Woodroffe & Ginsberg, 2000). A related issue is the extent to which individuals of the background species require complete protection under the umbrella, i.e. the severity of threat outside the protected area since this will affect the probability of survival of wide-ranging individuals. This is particularly pertinent to situation (a) in Fig. 3 where individuals range widely, but in both (a) and (b) it would be helpful to conduct population viability analyses on background populations.

The impact of individual ranging patterns on the ability of reserves to protect species is known to be important in the real world. Woodroffe & Ginsberg (1998, 2000) found that the critical reserve size for large carnivores was significantly correlated with female range size. They argued that this was due to very high levels of human-induced mortality (an average of 74% from 16 studies) that occur on reserve borders. Similarly, with intense fishing pressure around a marine reserve, the umbrella population may retain utility only for populations found entirely within the reserve (Botsford, Hastings & Gaines, 2001). Thus, as soon as we allow the umbrella-species concept to embrace the idea of protecting background

(a)

(b)

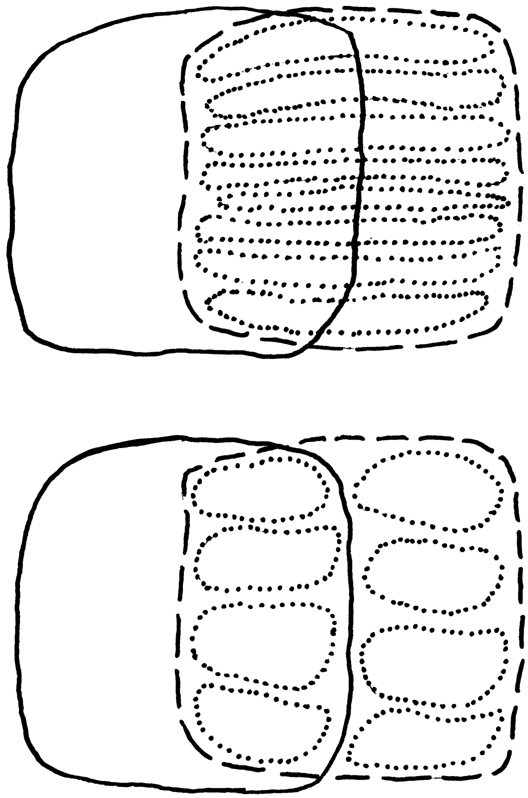

Fig. 3. Two hypothetical umbrella populations. In the top panel, individuals' movements (dotted lines) in the background population's total range (dashed line) take them outside the area covered by umbrella species a's population (solid line). In the bottom panel, some individuals in the background population are found inside the area covered by umbrella species b but others receive no protection. Total area covered by the umbrella-species population, and by the background-species population, and the overlap between population ranges, are the same in both panels.

species in the long term, and this is the key idea setting it apart from surrogates of species richness, the concept becomes onerous because it necessitates consideration of multiple demographic and environmental factors operating inside and outside the protected area.

In short, to judge the efficacy of an umbrella species in providing long-term protection for populations of background species, one needs to know annual movements of the latter (Berger, 1997); where they breed (inside or outside the umbrella's range) since this will influence population growth rate; and the probability of mortality outside the protected area. This is damning criticism of the umbrella-species concept since it demands extensive ecological information that takes time to collect, yet the justification for using umbrella species is to shortcut data collection on sympatric species. Simply determining the congruence of species' geographic ranges over large areas based on presence/absence data may be a useful heuristic tool in determining areas of species richness at a large scale, but at a local scale it says little about the long-term conservation benefits of using umbrella surrogates to set up protected areas.

Finally, it may be important that the umbrella population remains viable for political reasons (Berger, 1997; Fleishman, Murphy & Blair, 2001) as local extinction could open the door to developers or agricultural concerns casting (unwarranted) aspersions on the importance of the reserve now that the original reason for gazetting the reserve has disappeared. Long-term viability of proposed umbrella species is rarely calculated, however (but see Armbruster & Lande, 1993), and many proposed umbrella species are large (hence wide-ranging) and consequently have low reproductive rates and live at low densities which make them prone to extinction (Meffe & Carroll, 1997). Indeed, some studies have systematically tested whether rare and threatened species co-occur with many other species, arguing that they would be good umbrella species if they did so because they would attract public attention (Andelman & Fagan, 2000; Fleishman *et al*., 2000). Large or threatened species may garner publicity and funding (flagship species, Leader-Williams & Dublin, 2000; Sanderson *et al*., 2002*a*) but, because they are prone to extinction, are unlikely to serve as umbrellas in the long term. As Berger (1997) noted, 'inevitably appropriate umbrellas will be more-common species because of their higher probability of long-term persistence'.

These issues cast doubt on the umbrella-species concept employed at a local scale, but before dismissing it we should examine whether it has worked in the real world. To date, however, it has proved impossible to assess the long-term success of umbrella species as used by managers because there are almost no examples of old reserves that were formally set up using umbrella species. Fortunately, however, reserves in East Africa were designated in the twentieth century using species that we would nowadays consider as umbrella species.

RESERVES IN EAST AFRICA

East Africa has one of the most developed networks of protected areas in the world, including well-known reserves such as Tsavo, Serengeti and Queen Elizabeth National Parks, and the Selous Game Reserve (Siegfried, Benn & Gelderblom, 1998). Many of the reserves were delineated by colonial authorities for sport hunting in the early part of the twentieth century because they attracted professional hunters; high large-mammal abundances made it easy to find and shoot trophy species (Selous, 1908; Roosevelt & Heller, 1922). Subsequently these areas became national parks and game reserves in the 1950s, 1960s and 1970s (Neumann, 1998). This contrasts with North American parks, many of which were designated on grounds of geological interest. East African governments therefore inherited the legacy of sportsmen's choices of where best to hunt large mammals, in particular elephant (*Loxondonata africana*), lion (*Panthera leo*), leopard (*Panthera pardus*) and about a dozen species of large ungulates, most of which have large home ranges (Table 2). Although these areas were formally designated without knowledge of these species' movements, they were unquestionably set up to protect sufficient habitat to maintain large to moderate numbers of these species. Moreover, in one area, now covered by the Serengeti National Park and Masai Mara National Reserve, the population range of migratory wildebeest (*Connochaetes taurinus*) was used to realign the boundaries of these protected areas (Pearsall, 1957; McNaughton & Banyikwa, 1995; Sinclair, 1995). By good fortune, we have an opportunity to examine the long-term effectiveness of umbrella species on a regional scale and in an area where protection has been conscientious. However, there are several problems with such an analysis: we do not know precisely the number of species, umbrella or background, or their population sizes, at the time the reserves were set up; nor do we have a control network of reserves set up for other reasons in the same region. Despite these shortcomings, it seems worthwhile examining how wildlife populations have fared in East African reserves, given that there are so few possibilities of assessing the long-term efficacy of reserves actually set up using the umbrella-species concept, albeit implicitly. Here, using only mammals as a sample of the East African biological community, I examine whether umbrella populations are still faring well and hence immune to arguments about degazetting reserves, whether background populations are robust in umbrella-initiated reserves, and whether background populations are higher inside than outside reserves as might be expected if umbrella species were performing a conservation service.

Umbrella species inside reserves

In general, most umbrella populations appear to be large and still viable, in an informal sense, in East African reserves. For example, in Tanzania, umbrella species such as buffalo (*Syncerus caffer*) are found at significantly higher densities inside legally protected National Parks and Game Reserves that are patrolled by rangers and game scouts, respectively, than in Game Controlled Areas and Open Areas which are given only nominal legal protection and lack on-site enforcement. Although densities of some other umbrella species do not differ between the two sorts of area, none lives at significantly lower densities inside National Parks and Game Reserves (Table 3). Time-series data (C. J. Stoner, T. M. Caro & S. Mduma, unpubl. data) show that over 15 years populations have declined less in heavily protected Tanzania National Parks and Game Reserves than in partially protected Open Areas and particularly Game Controlled Areas (see also Pelkey, Stoner & Caro, 2000). This suggests that the differences in Table 3 cannot simply be attributed to National Parks and Game Reserves being set up in areas of high mammal abundance.

None the less, umbrella populations have declined in some reserves. Long-term population data on resident populations of ungulates in the Masai Mara National Reserve, Kenya, show declines of 81% for wildebeest, 82% for buffalo, 76% for eland (*Taurotragus oryx*), 73% for topi (*Damaliscus korrigum*) and 66% for Coke's hartebeest (*Alcephalus buselaphus*) over a 20-year period (Ottichilo *et al*., 2000; Ottichilo, de Leeuw & Prins, 2001; see also Broten & Said, 1995; Runyoro *et al*., 1995). Decline of wildebeest from 119,000 in 1977 to 22,000 in 1997 was attributed to encroachment of wheat farms into former wet-season ranges, subsistence poaching, changes in vegetation and drought. By extension, these factors have probably affected other ungulate populations, too. Moreover, a small number of umbrella-species populations have become extinct in East Africa since time of reserve establishment. Rhinoceroses have been hunted to extinction in nearly all reserves (Western, 1982), lions have been lost from six out of 29 reserves (20.7%, correcting for presence in Amboseli) (Harcourt, Parks & Woodroffe, 2001), and Coke's hartebeest has been lost

Table 2. Examples of large-mammal species favoured and disfavoured by expatriate hunters in East Africa in the twentieth century. Those hunted for sport were the umbrella species used to gazette reserves. (Most have large home ranges except bushbuck which have specific habitat requirements.) All others are background species. Species listed in alphabetical order.

Hunted for sport	Hunted as vermin	Not hunted	Usually ignored
Buffalo	Spotted hyena	Giraffe	Bushpig
Bushbuck	Wild dog		Cheetah
Eland			Duiker sp.
Elephant			Hippopotamus
Hartebeest			Warthog
Impala			
Kudu			
Leopard			
Lion			
Reedbuck			
Rhinoceros			
Roan antelope			
Sable antelope			
Topi			
Waterbuck			
Wildebeest			
Zebra			

Table 3. Umbrella species for which densities were (represented as < or >) and were not (represented as =) significantly different inside National Parks (NPs) and Game Reserves (GRs) (heavily protected) and Game Controlled Areas (GCAs) and Open Areas (OAs) (nominal protection). Species listed in alphabetical order. These species were, and still are, sportsmen's targets of choice and can thus be viewed as umbrella species (from Caro *et al*., 1998; Caro, Rejmanek, & Pelkey, 2000).

NPs & GRs > GCAs & OAs	NPs & GRs = GCAs & OAs	NPs & GRs < GCAs & OAs
Buffalo	Elephant	
Bushbuck	Gazelle sp.[b]	
Hartebeest[a]	Impala	
Eland	Kudu[c]	
Roan antelope	Reedbuck[d]	
Waterbuck	Sable antelope	
Zebra	Topi	
	Wildebeest	

[a]*Alcelaphalus buselaphus* and *A. caama* combined
[b]*Gazella grantii* and *G. thomsoni* combined
[c]*Tragelaphus strepsiceros* and *T. imberbis* combined
[d]*Redunca redunca* and *R. arundinum* combined.

from Lake Manyara National Park, and roan antelope (*Hippotragus equinus*) from Tarangire National Park (Newmark, 1996).

In short, optimistically we can conclude that there still remain viable populations of the vast majority of umbrella species inside reserves in East Africa approximately 50 years after they were formally gazetted, except for rhinoceros species which have suffered severe poaching. A likely principal reason for the persistence of ungulate populations is that they were very numerous to begin with and have been well protected. Reserves in the region are unlikely to be degazetted on the basis of having lost the species which they were set up to protect.

Background mammal species inside reserves

The great majority of populations of background mammals, recorded as being present in colonial hunting areas, are still found at high densities in East African reserves. None the less, some declines have been documented. For example, 20 years of data from the Masai Mara show a 49% and 72% decline in small and medium-sized ungulate species respectively (Ottichilo *et al*., 2000; see also Broten & Said, 1995; Runyoro *et al*., 1995). Some extirpations have occurred as well (e.g. Burrows, 1995). Wild dogs (*Lycaon pictus*) have become extinct in 29 out of 38 reserves since time of establishment (76% loss, scoring them as present in Katavi, T. M. Caro, pers. obs.) and spotted hyena (*Crocuta crocuta*) populations have been lost from seven out of 35 reserves (20%) (Harcourt *et al*., 2001). Also, during the last 35–83 years, four population extinctions have occurred in Tanzania's northern national parks (Newmark, 1996): mountain reedbuck (*Redunca fulvorufula*) from Lake Manyara and Kilimanjaro National Parks, steenbok (*Raphicerus campestris*) from Arusha National Park and klipspringer (*Oreotragus oreotragus*) from Kilimanjaro National Park, although the causes of these extinctions are unclear. Since species loss is inversely related to reserve size (Soulé, Wilcox & Holtby, 1979; Newmark, 1987), other species in small unstudied parks are likely to have been lost as well (Harcourt *et al*., 2001).

Table 4. Examples of causes of declines in background-species populations in East African reserves. Species are those that were not specifically sought after for sport by expatriate hunters.

Cause	Species	Location	Reference
Habitat change	Baboon	Amboseli NP	Altmann, Hausfater & Altmann, 1985
Predation	Vervet monkey	Amboseli NP	Isbell, Cheney & Seyfarth, 1990
Disease	Wild dog	Serengeti NP	Gascoyne *et al*., 1993
Poaching	Giraffe	Serengeti NP	Campbell & Hofer, 1995
Interspecific competition	Cheetah	Serengeti NP	Kelly *et al*., 1998
Wet-season range encroachment	Small antelope	Masai Mara NR	Ottichilo *et al*., 2000

In short, anecdotal records suggest most background mammal populations are viable although limited data indicate that populations of certain background species have experienced declines and even some extinctions since time of reserve establishment. Nevertheless, the causes are very diverse (Table 4). Aside from interspecific competition from lions (*Panthera leo*) affecting cheetahs (*Acinonyx jubatus*) (Laurenson, 1995) and wild dogs (Creel & Creel, 1996), none of these factors is specifically tied to using umbrella-species so it is unlikely that reserves sited elsewhere (using a criterion other than the umbrella species concept) would have been immune from these adverse influences. Tentatively, then, in East Africa there appears to be nothing inherently dangerous in protecting species using umbrella species, at least in regards to mammals.

Background mammal species outside reserves

Whether or not background species are being lost from reserves, at the very least background species should exist at lower abundances outside reserves than inside because the umbrella-species concept dictates that if species with large area requirements are given sufficient protected habitat, they should bring other species under protection (following Noss, 1990). We might therefore expect to see reduced populations and species extinctions outside reserves after a period of time. Four types of data collected outside Katavi National Park in western Tanzania address this issue and are enumerated below.

Katavi National Park and its surrounds consist largely of miombo woodland, dry forest habitat characterized by *Acacia*, *Brachystegia*, *Commifora*, *Kigelia*, *Pterocarpus* and *Terminalia* tree species (Rodgers, 1996; Schwartz *et al*., 2002). The region was gazetted as a Game Reserve by the German authorities in 1912 and perpetuated under the Game Preservation Ordinance passed by the British administration in 1921. The area was regarded as a prime hunting ground in Tanganyika Territory in the 1920s, with wildlife densities second only to Serengeti (Caro *et al*., 1998*b*). The Game Reserve was extended westwards in 1957 and was upgraded to National Park status in 1974, 11 years after independence (Sommerlatte, 1995). Human population density is low outside the Park.

(1) I recorded all individual mammals >1 kg by driving a total of 2953 km in a vehicle at < 10 km/hour along the same established but minor tracks once every month over a period of 14 months; transects ranged in length from 0.7 to 31.1 km (X = 11.5 km, N = 20 transects). For each species, density was calculated from the total number of individuals seen on a given transect divided by visible area that was scored continuously during the course of a transect. For each transect and species, average densities were calculated across 14 months. Mean densities for seven transects in Katavi National Park were then compared to 13 transects outside (for details see Caro,

1999*a*,*b*,*c*; Caro, Rejmanek & Pelkey, 2000). I found that large and middle-sized background species of mammals lived at significantly lower densities, or at similar densities, outside the Park than inside but never at significantly higher densities (Table 5). Large edible species (e.g. giraffe, *Giraffa camelopardalis*, and hippopotamus, *Hippopotamus amphibius*) abundances were low outside, almost certainly as a result of hunting (Caro, 1999*a*); spotted hyena densities were low possibly as a result of reduced prey biomass or perhaps poisoning. Background species, giraffe and warthog (*Phacochoerus aethiopicus*) have declined outside the Park over 14 years, whereas populations have not changed inside (C. J. Stoner, T. M. Caro & S. Mduma, unpubl. data).

(2) I set Sherman small-mammal traps 10 m apart in a 7×7 array in up to 12 sites inside and 12 outside the Park and baited them with banana (2 seasons) or peanuts, fish and maize (1 season). Trap-grids were set in habitat types representative of the two areas, including different types of woodlands and wetter open grasslands inside; bushland, grazing areas, areas under differing cultivation, banana gardens and in villages outside. Traps were set each evening and checked next morning over 3–5 nights depending on the season. Relative abundances were calculated as number of different individuals captured divided by the number of trap-nights × 100, and species richness as the number of different species captured per grid (see Caro, 2001 for details). I found that there were significantly greater relative abundances of small native mammals and more species caught outside the Park than inside for each season of trapping (Table 6) after controlling for vegetation, and even when traps set in houses were excluded from analysis. Preliminary attempts to uncover causes for greater species richness and relative abundance outside the Park suggest that food availability is higher there (Caro, 2002). Thus, contrary to expectations, one guild of mammals, small rodents and insectivores, has a higher population size outside than inside a protected area originally designated using umbrella species.

Table 5. Mean densities of background mammals/km^2 inside and outside Katavi National Park, Tanzania, listed in alphabetical order. *N* refers to number of transects driven each month for 14 months (from Caro *et al*., 2000).

Species	In (N = 7)	Out (N = 13)	Z-value[a]	P-value[a]
Baboon	0.01	0.07	–0.191	NS
Bushpig	0.07	0	2.947	0.003
Giraffe	2.17	0.68	2.906	0.004
Hippopotamus	5.15	0	3.385	0.001
Mongoose[b]	0.21	0.13	1.524	NS
Small antelope[c]	0.06	0.38	–1.646	NS
Small mammal[d]	0.01	0	1.977	0.048
Smaller carnivore[e]	0.04	0	2.947	0.003
Spotted hyena	0.19	0	4.231	<0.001
Vervet monkey	0.47	0.10	1.348	NS
Warthog	1.34	0.56	2.582	0.010

[a]Z-values and *P*-values using Mann–Whitney *U*-tests.
[b]Banded, black-tipped, dwarf and marsh mongoose combined
cBush duiker, dik-dik, klipspringer and oribi combined
[d]Hare and squirrel combined
[e]Leopard, ratel, serval, side-striped jackal and wild dog combined (leopard, the only umbrella species, was seen only twice throughout the study)

Table 6. Mean values of measures of small-mammal abundance and species richness inside Katavi National Park and outside in the Open Area to the south (from Caro, 2002)

	1998 Aug–Sept Dry season		1999 Feb Wet season		2000 Jul–Oct Dry season	
	In	Out	In	Out	In	Out
Number of trap-nights	1402	1704	1317	1722	2345	2380
Individuals/ 100 trap-nights	0.7	15.8*	1.0	5.8*	0	3.0***
Species per grid	0.6	1.9*	1.0	1.7	0.1	1.6***
Total number of species caught[a]	3	7	5	6	1	8

*< 0.05, ***< 0.001 using Mann–Whitney *U*-tests
[a] Preliminary identification: *Crocidura hirta*, *Dasymys incomtus*, *Graphirus murinus*, *Lemniscomys striatus*, *L. griselda*, *Mastomys natalensis*, *Mus minutoides*, *Myomys fumatus*, *Rattus rattus*, *Saccostomus campestris*, *Tatera leucogaster*, *T. robusta*. *Rattus rattus* is the only non-native species and was only caught in houses.

(3) I used track-plates to obtain an index of small-carnivore species richness and relative abundance outside and inside the Park. I placed four track-plates covered with sand in each of 12 sites inside and 11 outside the Park over 4 consecutive nights. Plates were baited with catfish each evening, and next morning the presence of carnivore tracks was noted. Carnivore prints were identified to the family and often species level from field guides. Conservative data on whether a given species was found at a site showed that the number of sites in which most native carnivore species was noted was lower outside than inside the Park (Table 7), particularly for side-striped jackals (*Canis adustus*), banded mongooses (*Mungos mungo*), civets (*Viverra civetta*) and wildcats (*Felis lybica*). Aside from lion and leopard, all these native species are background species. In contrast, domestic dogs (*Canis familiaris*) and cats (*Felis domesticus*) were found at significantly more sites outside. The causes of lower relative abundances of native species are unknown but it is unlikely to be reduced food supply outside the Park since rodent densities are high there. In short, terrestrial carnivore populations live at lower densities outside than inside the protected area as might be expected if umbrella-initiated reserves are performing an adequate conservation service.

(4) I collected presence/absence data on large and middle-sized mammals outside and inside the Park. Inside, data were obtained from intermittent fieldwork over a 6-year period and from discussions with the late Principal Park Warden and the Park Staff Ecologist; outside, data were obtained from fieldwork and systematic examination of field guides with villagers south of the Park. Findings indicate a high degree of similarity in large and medium-sized mammal species identity outside and inside the Park (Table 8). There were only four background species found inside but not outside. The weakness of these data is that it is unclear whether absent species outside have been lost since the Park was set up

Table 7. Percentage of sites visited by carnivores as determined from footprints inside Katavi National Park and the Open Area outside. At each site (N), four baited track-plates were set over 4 consecutive nights (T. M. Caro, unpubl. data).

Species	Inside (N = 12)	Outside (N = 11)	P-value[a]
Canidae			
Domestic dog	0	54.5+	0.005
Side-striped jackal	75.0	18.2	0.009
Herpestidae			
Banded mongoose	66.7+	0	0.056
Dwarf mongoose	8.3	0	NS
White-tailed mongoose	8.3	9.1	NS
Black-tipped mongoose	8.3	27.3+	NS
Unidentified mongoose	66.7	27.3	NS
Hyaenidae			
Spotted hyena	41.7	18.2	NS
Viverridae			
Common genet	50.0	45.5+	NS
Civet	83.3	9.1	0.001
Felidae			
Domestic cat	0	36.4+	0.037
Wild cat	66.7	0	0.056
Serval	16.7	9.1	NS
Leopard	8.3	0	NS
Lion	8.3+	0	NS
Unidentified small carnivore	41.7	54.5	NS
Unidentified larger carnivore	41.7	54.5	NS

[a]Using Fisher exact probability test for visited/not visited sites inside and outside
+ Additionally trapped or sighted on small-mammal trap-grid

or never existed outside the Park. For example, there are few large rivers where hippopotamus can live in the area south of the Park. Nevertheless, the data do indicate that few background-species mammal populations are extinct outside the Park.

In short, data at a local scale show that certain background species are found at low abundances outside one national park in East Africa. These are large edible mammals and small carnivores. Other species, very small mammals, are found at greater abundances outside (Table 9). At present, however, 28 years after Katavi was established as a National Park, there have been few species extinctions outside Park borders. This single example shows that delineating a reserve using umbrella species and then granting it protection clearly benefits populations of some background taxa but by no means all.

Table 8. Species of mammal found inside Katavi National Park and outside in the Open Area to the south listed in alphabetical order (T. M. Caro, unpubl. data).

	Inside		*Outside*	
	Seen[a]	Reported	Seen[a]	Reported
Umbrella species				
Buffalo	X		X	
Bushbuck	X		X	
Eland	X			X
Elephant	X			X
Hartebeest	X		X	
Impala	X		X	
Leopard	X			X
Lion	X			X
Reedbuck	X			
Roan antelope	X			X
Sable antelope		X		
Topi	X		X	
Waterbuck	X			X
Zebra	X		X	
Background species				
Aardvark		X		X
Banded mongoose	X		X	
Black-tipped mongoose	X		X	
Bush hyrax				X
Bushpig	X			X
Cape clawless otter				X
Cape hare	X			X
Civet	X			X
Common genet		X	X	
Dik-dik		X		X
Dwarf mongoose	X			X
Galago (2 spp.)				X
Giraffe	X		X	
Grimm's duiker	X		X	
Hippopotamus	X			
Marsh mongoose	X			
Molerat		X		X
Oribi	X			
Pangolin		X		X
Porcupine		X		X
Ratel	X			X
Serval	X			X
Side-striped jackal	X			X
Spotted hyena	X		X	
Springhare		X		X
Squirrel	X			X
Vervet monkey	X		X	
Warthog	X			X
Wild cat		X		X
Wild dog	X			
Yellow baboon	X			X

[a]seen by author

CONCLUSION

Informally, the umbrella-species concept was used to delineate specific reserve boundaries at a local scale. Currently, it is being used in different ways according to scale. At a large biogeographic scale, umbrella species are used to identify areas of species richness employing presence/absence data. At a small scale, umbrella species are being used to identify areas that encompass viable populations of background species. In the second arena, there is a potential dilemma of whether to use populations of umbrella species to maximize the number of populations or number of viable populations of background species. The extent to which these goals overlap will depend on ranging patterns of individuals within background populations and level of threat outside the aegis of the umbrella population. Additionally, umbrella species need to have high long-term population viability or adversaries could mount arguments to say that the reasons that the reserve was set up apply no longer.

Using data from reserves in East Africa, most of which were gazetted on the basis of high large-mammal abundance, long-term effectiveness of applying umbrella species to reserve design can be examined in the real world from a management perspective, albeit in a *post hoc* fashion and without proper controls. In this reserve network, few umbrella-species populations have been lost

Table 9. Summary of findings about population sizes of mammals around Katavi National Park.

Taxonomic group	Example	Population size	
		Inside	Outside
Umbrella species			
Trophy species	Rhinoceros	Extinct	Extinct
Large herbivore	Buffalo	High	Low
Large carnivore	Lion	High	Low
Background species			
Large herbivore	Giraffe	High	Low
Small carnivore	Serval	High	Low
Small mammal	Striped grass rat	Low	High

although several have declined. As umbrella populations occasionally disappear, it seems sensible to base site selection on several umbrella species (Lambeck, 1997; Fleishman, Blair & Murphy, 2001) that have large initial-population sizes and hence reduced probability of extinction. In general, background species have been well protected. While certain background-species populations have declined in reserves, causes are varied and include disease and illegal hunting. A third expectation, that background populations might be smaller outside areas protected by umbrella species, was supported at least around one national park, where populations of large edible ungulates and large and small carnivores live at low abundances without protection although few of these species are extinct outside the Park. Small-mammal abundance and diversity are higher in unprotected areas, questioning the use of umbrella species as a conservation tool for these taxa. While it is difficult to separate the effects of protection *per se* from the umbrella-species protection strategy because we lack control reserves (set up for other reasons) with matching protection, it would nevertheless be worrying if background populations consistently fared better outside umbrella-initiated reserves than inside.

How do we reconcile the conceptual difficulties in using umbrella species with their apparent success in East Africa? It is unlikely that there is an absence of threat outside reserves because illegal hunting and population growth are high. More likely, reserves in East Africa are sufficiently large that they maintain viable populations of background species even if some individuals leave reserve boundaries (Harcourt *et al*., 2001). That large mammals with *de facto* large area requirements were chosen as umbrellas is fortuitous because it meant that large areas would be protected.

In summary, we can tentatively conclude that, despite conceptual problems, umbrella species were a useful tool in reserve design in East Africa in part because habitat requirements of umbrella populations were large and thus reserves were big. Not all taxa have benefited equally, however. Before using the umbrella-species concept more widely as a conservation tool at a local scale, we need to predict which background populations are likely to receive long-term protection from umbrella species and why.

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