



# MINIMUM GROUP SIZE AND OTHER CONSERVATION LESSONS EXEMPLIFIED BY A DECLINING PRIMATE POPULATION

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## Abstract

*Examining the dynamics of naturally declining populations can be useful in understanding some of the problems encountered by endangered populations. A study of a declining population of vervet monkeys *Cercopithecus aethiops* provides a unique opportunity to examine factors associated with minimum social group size, a potentially key variable in population viability analysis. The minimum group size in vervets ranged from three to six individuals, but always with a minimum of two adults. Groups appeared to be stable as long as there were at least two adults, but ceased to exist as independent groups within days of losing their penultimate adult. For species with discrete group structure, population extinction could occur if all individual groups fall below a minimum social group size, even if the overall population is above a 'minimum' size. However, group fusions may minimize population losses. Group fusion in vervets is rare, and appears to occur only as a behavioural response to minimum group size. We also review evidence of the costs vervets incur through movement into unfamiliar places or groups (analogous to translocation and re-introduction), and the benefits they can receive from living in proximity to humans.*

**Keywords:** Kenya, vervet monkeys, conservation, population decline, predation, viability.

## INTRODUCTION

One of the central tasks of conservation biology is population viability analysis, and one of its main tenets is that smaller populations are more likely to go extinct than large ones. Limits on the viabilities of populations are thought to be set mainly by ecological (demographic), and to a lesser degree genetic, constraints

(Lande, 1988; Simberloff, 1988). Although social dysfunction has been suggested as an additional limiting factor (Simberloff, 1988), examples are hard to find. Most often mentioned is the Allee effect, when densities are so low that populations can no longer sustain themselves (e.g. because of failure to find mates).

In addition, for species that live in discrete, well-defined groups, there may be lower limits to social group size. If population size declines so low that many individual groups fall below a minimum viable size, the entire population may be at risk. This could happen independently of either genetic or demographic constraints on overall population size.

Solitary breeding pairs of southern sea lions *Otaria byronia* had much lower reproductive success than individuals breeding in larger groups (Campagna *et al.*, 1992). Greatly reduced fitnesses of individuals in smaller groups have been shown in captive squirrel monkeys *Saimiri sciureus*, due to reduced reproduction (Mendoza *et al.*, 1991) and wild guillemots *Uria aalge*, due to increased predation (Birkhead, 1977). There may be a minimum number of musk-oxen *Ovibos moschatus* necessary for effective anti-predator defense; most known predation events have been on lone individuals (Tener, 1965). It has been suggested that passenger pigeons *Ectopistes migratorius* went extinct after individual flock sizes fell below critical social group size for effective foraging, breeding, or nesting (Schorger, 1955).

Populations of many species are currently declining due to human activity, and these declines are a major threat to species survival (Ehrlich & Ehrlich, 1982). Human-caused declines in population size may be due either to direct over-exploitation of species or to habitat destruction. In addition, many animal populations undergo large natural fluctuations in size (Young, *in press*). Examining the dynamics of naturally declining populations can be useful in understanding some of the problems encountered by endangered populations.

Here we describe a population of vervet monkeys *Cercopithecus aethiops* in a national park in Kenya that underwent a large reduction in size associated with changes in habitat, providing one of the first quantitative examples of the effects of a minimum group size.

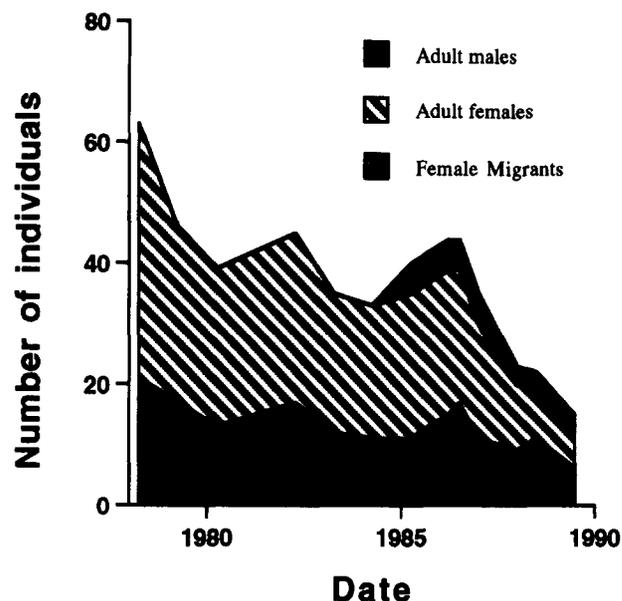
### STUDY SPECIES AND SITE

Vervet monkeys live in multi-male, multi-female social groups that are generally territorial, i.e. they defend their home ranges against incursions by neighboring groups through aggressive interactions (Cheney, 1981). Normally, female vervets are philopatric, remaining in their natal groups on their natal home ranges throughout their lives, whereas male vervets emigrate to neighboring groups and home ranges for the first time around sexual maturity (Cheney & Seyfarth, 1983).

Six vervet groups were studied continuously from 1977 until 1989 by D. Cheney, R. Seyfarth, and their colleagues in Amboseli National Park, Kenya (Hauser, 1987; Cheney, *et al.*, 1988; Isbell, 1990a). Amboseli is part of a semi-arid savannah ecosystem in southern Kenya (2°41'S, 37°10'E) that is characterized by dry seasons occurring in July through October and January through February. Its vegetation includes open plains and two types of woodlands, dominated by either fever trees *Acacia xanthophloea*, or *A. tortilis*. The main study area was located in the southwestern portion of Amboseli (Kitirua), and included both kinds of woodlands. Fever trees now occur mostly along waterways, swamps, and tourist lodges (where they may be planted and irrigated) whereas *A. tortilis* woodlands occur in drier areas. Although vervets in Amboseli historically occurred mainly in fever tree woodlands, in the main study area they are also found in *A. tortilis* woodlands. Within the fever tree woodlands, vervets at the tourist lodges live closer to people and have greater access to food through garbage piles and provisioning by tourists than vervets living at Kitirua (Lee *et al.*, 1986). Within the *A. tortilis* woodland, some vervet groups lived closer than others to non-provisioning humans because of the proximity of their home ranges to a ranger station.

Fever tree woodlands once covered large areas of Amboseli Park. In the mid-1950s the fever tree population began to decline and this continued until at least 1992 when the last fever trees died. This was correlated with an initial decline in the size of existing vervet groups (Struhsaker, 1973, 1976; Cheney *et al.*, 1988), a subsequent decline in the number of vervet groups (Hauser *et al.*, 1986; Isbell *et al.*, 1991), and a shifting of the home ranges of remaining groups away from dying fever tree woodlands and farther into *A. tortilis* woodlands (Isbell *et al.*, 1990). Associated with this movement into unfamiliar areas was an increase in rates of vervet disappearance and a period of severe leopard *Panthera pardus* predation (Isbell, 1990b; Isbell *et al.*, 1990). The number of adults in the study population declined 76% from 63 to 15 between 1978 and 1989 (Fig. 1).

Before the decline of the fever tree population,



**Figure 1.** The decline in the numbers of adult males (solid) and females (cross hatched) in six monitored groups of Amboseli vervet monkeys, from 1978 to 1989. The dotted area represents five adult females that joined these groups from outside in 1985. Data from before 1986 are from Cheney and Seyfarth (1987). The number of males in 1989 may have been underestimated because recent immigrants were unhabituated to human presence and more difficult to census.

vervets living in fever tree woodlands fed throughout the year on fever tree parts, including young leaves, flowers, seeds, and during the long dry season when little else was available, the sap. These groups had higher reproductive rates than groups that lived in *A. tortilis* woodlands, which suggests that fever trees are a significant resource for vervets (Cheney *et al.*, 1988).

The underlying cause of the decline of the vervet population was probably the die-off of fever trees (Struhsaker, 1973, 1976; Cheney *et al.*, 1988). The decline of the fever tree population has been attributed to a number of factors that may have interactive effects, including elephant *Loxodonta africana* browsing, a rising saline water table, and the senescence of even-aged fever tree stands (Western & van Praet, 1973; Young & Lindsay, 1988).

### CONSERVATION IMPLICATIONS

#### Minimum group size in vervets

In many vertebrate species, populations are subdivided into social groups that are discrete, cohesive subunits. In these species, there may be lower limits to social group size that are independent of lower limits to overall population size. Minimum social group size can be defined as the minimum number of individuals in a group necessary for continued functioning of the group. Its lower limit is likely to be set by factors inherent to groups such as shared offspring care, group foraging, or group defense (and vigilance) against predators or competing groups of conspecifics. In vervet monkeys, this minimum group size appears to be

two adults, independent of the number of juveniles and infants also in the group.

Between 1984 and 1989, six different groups of vervet monkeys declined in size to the point where they abandoned their territories and fused with neighboring groups (Isbell *et al.*, 1991). This invariably happened soon after the group lost its penultimate adult. For the three groups closely monitored at the time of fusion, fusion occurred within five days of this event. In contrast, groups appeared to be essentially stable as long as they consisted of at least two adults and a variable number of juveniles, independent of the sexes of the adults. Minimum group sizes, including juveniles and infants, ranged from three to six. Because these groups were all declining in size, it was not possible to assess the long-term viability of very small groups, but one group consisting of two adult females and two juveniles remained stable for six months (Hauser *et al.*, 1986).

The relative stability of groups in which all adults are of one sex may appear maladaptive. However, small groups of vervet monkeys consisting of adults of only one sex can be viable in the long run. All-female groups can obtain males through normal male immigration, and groups in which all adults are male can obtain adult females through the maturation of juvenile females. In addition, natural selection in vervet monkeys may put a premium on long-term survival, sometimes at the expense of short-term reproductive opportunities.

The presence of juveniles did not appear to influence the timing of group fusions. Juvenile vervets are active participants in predator detection, but not in intergroup encounters. Therefore, Isbell *et al.* (1991) suggested that minimum group size in vervets was more likely a limitation set by successful intergroup competition than by predator detection or avoidance.

Because of the behaviour of group fusion in these declining groups (see below), it was not possible to measure the long-term success of vervets in groups with less than two adults. However, southern sea lions *Otaria byronia* breeding in isolated pairs had much lower infant survivorship (40%) than individuals breeding in larger groups consisting of a male and several females (99%), even if those groups had as few as two adult females and a male (Campagna *et al.*, 1992), indicating a minimum group size similar to that in vervets. In the sea lion study, mortality of young was due to infanticide by outside males and starvation after separation of mothers and offspring.

#### **Fusion as a behavioural mechanism to avoid being in groups of less than minimum size**

Although vervet groups smaller than the critical size ceased to exist as separate social units by fusing with other groups, many of the individuals survived. Minimum group size in vervet monkeys was determined by the behaviour of the monkeys themselves, through group fusions (Isbell *et al.*, 1991). Group fusion may avoid the consequences of falling below the minimum social group size of two adults plus accompanying

immatures. We do not know what the fate of these animals would have been had they not fused with other groups; however, group fusion was itself costly and resulted in lower social ranking (Hauser *et al.*, 1986) and greater mortality of the immigrants (Isbell *et al.*, 1993, see below). The occurrence of group fusion implies that living in a group with less than two adults is more costly than group fusion. The continual coalescing of vervet groups during this period of population decline may have minimized individual losses, and reduced the likelihood of population extinction.

#### **Forced movement into unfamiliar areas and new social settings can put animals at increased risk of death**

Human-induced habitat change is a major source of population extinction (Ehrlich & Ehrlich, 1982). In addition to the direct loss of species and lowering of carrying capacities, the movement of animals into unfamiliar habitats often follows habitat destruction. These habitats may be unsuitable for long-term population survival. Even if these new habitats are suitable, unfamiliarity with the habitat may increase individual animals' risks of mortality. In vervet monkeys, movement into unfamiliar areas was associated with increased mortality. This was expressed in two ways.

First, the movement of entire intact groups into areas they had not previously used was associated with increased mortality through predation (Isbell *et al.*, 1990). This predation was apparently related to the unfamiliarity of these new areas, and not to other characteristics of the habitat or vervet behaviour. Similarly, in India a group of commensal rhesus monkeys *Macaca mulatta* forced by humans to shift its home range suffered an increase in mortality that lasted several years (Siddiqi & Southwick, 1988).

Translocated animals may also experience reduced survivorship. For example, mule deer *Odocoileus hemionus* translocated to an area with predators, hunters, and vehicular traffic from an area where these were absent suffered substantially greater mortality than residents despite having similar diets and ranging behaviour (O'Bryan & McCullough, 1985). Captive animals introduced into the wild often have difficulty adjusting to new environments (Gipps, 1991). Even human groups whose knowledge of wild food plants is limited to the local flora may suffer from movement into unfamiliar areas (Gadd *et al.*, 1962). Such difficulties may be due to the inability of re-introduced animals to deal with truly novel foods or predators, or to unfamiliarity of particular aspects of the new environment, e.g. the location of food plants and the behaviour of individual predators. The data from Amboseli vervets imply that the latter can occur in natural populations.

Second, immigrant vervets that moved into unfamiliar social and ecological environments when their groups fused with neighboring groups suffered greater mortality than residents (Isbell *et al.*, 1993). Costs of transfer into new areas or groups have been demonstrated in red howling monkeys *Alouatta seniculus*

(Pope, 1989) and toque macaques *Macaca sinica* (Dittus, 1986, 1987). Presumably, these costs may be experienced by translocated animals of other species.

**Animals moving voluntarily may not experience as much dispersal cost**

As in the case of fusion as a response to minimum group size, certain behaviours may minimize the costs of moving into new areas. Although immigrants that transferred as a result of fusion suffered greater mortality than the residents of the groups they joined, vervet monkeys whose transfers were not as sudden showed no greater mortality (Isbell *et al.*, 1993). Individuals who are not forced to move as a result of adverse social or ecological conditions but instead move voluntarily (or slowly) may be able to minimize the risk of mortality by timing their movements appropriately and by learning about residents and habitats on forays into new areas.

Similarly, Stanley-Price (1989) suggested that re-introduced Arabian oryx *Oryx leucoryx* in Oman differed in their ability to deal with unfamiliar territory based on the different ways in which animals encountered new territory. 'Range development and exploration by the two herds were gradual and methodical, and each major move was made in response to readily apparent ecological conditions or changes. In marked contrast, one incident ... demonstrated clearly the low chances of survival of an animal dispersing speedily', which displayed 'panic at being in an unfamiliar area' (Stanley-Price, 1989, pp. 162-4).

**Human presence can be beneficial to species that are commensal by reducing the effects of environmental fluctuations or by reducing predation risk**

Although there has been a general decline of numbers and groups of vervet monkeys with the disappearance of fever tree woodlands in Amboseli (Isbell *et al.*, 1991), exceptions to this trend were the vervet groups that lived near the tourist lodges. Food availability at these sites remained relatively high during a time of continuing resource decline elsewhere in the ecosystem (Lee *et al.*, 1986). Indeed, food was so plentiful for the 'lodge' vervets that births occurred year-round in these groups, in contrast to seasonal birth peaks experienced by vervets in Kitirua (L.A.I., personal observations). Similarly, groups of baboons *Papio cynocephalus* in Amboseli that fed on foods from lodges increased in size while non-provisioned groups remained stable but at lower group sizes than in the past when food resources were more plentiful (Altmann *et al.*, 1985; Samuels & Altmann, 1991). These examples suggest that some commensal wild animals can benefit from human presence, at least in the short term, particularly during periods of resource scarcity, if they are intentionally or inadvertently provided with food. Similar patterns have been shown for several other primate populations (Dittus, 1977; Southwick & Siddiqi, 1988; Fa & Southwick, 1988; Lyles & Dobson, 1988). Goldstein and Richard (1989) believe that anthro-

pogenic forest disturbance favors rhesus macaques *Macaca mulatta*, which feed preferentially on plants found in secondary forest. Richard *et al.* (1989) further suggest a dichotomy among different species of macaque monkeys, with 'weedy' species that thrive in association with humans, and 'non-weedy' species that do not.

Human presence may also discourage predators. Both spatial and temporal variation in human presence were significantly negatively associated with leopard predation of vervet monkeys in Amboseli (Isbell & Young, 1993). In the Kitirua study area, the nearer a vervet group lived to the continuously occupied ranger station, the fewer losses it incurred during a recent bout of increased leopard predation. In addition, over at least one seven-month period, the rate of vervet losses was more than three times greater during periods of researcher absence than during periods of researcher presence (Isbell & Young, 1993). It is possible that the leopards, being wary of humans (Kruuk, 1986), were discouraged from hunting near human habitation and during periods of human presence (Hamilton, 1986).

Both white-tailed deer *Odocoileus virginianus* and chital *Axis axis* seem to benefit from moving near human habitation and avoiding predation from wolves *Canis lupus* and tigers *Panthera tigris*, respectively, which avoid humans (Nelson & Mech, 1981; Johnsingh, 1983). An absence of predators can be beneficial to those populations that are predator-limited (Terborgh & Winter 1980), and may for some species help to offset other costs of human presence, such as habitat modification.

**The factors that result in primate die-offs may differ from those of other large mammals**

In a recent review of natural die-offs of large mammals (Young, in press), natural declines of different kinds of mammals were attributed to different causes. Herbivore die-offs were usually (75%) attributed to starvation, with most of the remainder attributed to disease. Carnivore die-offs were attributed to both disease (44%) and starvation (22%). In contrast, none of the eight primate die-offs reviewed was attributed to starvation. Primate die-offs were instead attributed to disease (50%; see also Goodall (1986) and Brain (1992)), predation (25%; see also Chism *et al.* (1984) and Goodall (1986)), and habitat change (38%); infanticide can also be a major source of primate mortality (Hausfater & Hrdy, 1984; Goodall, 1986; Brain, 1992). These effects may interact with each other and with food limitation in complex ways (Isbell *et al.*, 1990), but the absence of primate die-offs clearly associated with starvation is striking. The die-offs of Amboseli vervets and baboons were examples of the effects of habitat change, that in vervets was also mediated by predation. Although several ungulate species in Amboseli suffered from starvation-related mortality during this time (T.P.Y., personal observations), there was little evidence of starvation being a proximate source of mortality for these primates. Vervet monkeys

visibly lost condition during a recent drought, but they continued to survive and even reproduce (Hauser, 1987). Similarly, Southwick and Siddiqi (1988) noted the ability of rhesus monkeys to maintain high birth and survivorship rates in the face of environmental stress, in contrast to other mammal species (but see Hamilton, 1985). A population of toque macaques *Macaca sinica* in Sri Lanka emerged from the worst drought in half a century and a coincident loss of a major food source with no change in the numbers of adults, and only moderate decreases (-28%) in juvenile recruitment (Dittus, 1977). Conversely, some species of primates may rely more heavily than many other mammals on key species for food (Terborgh, 1986) and as sleeping trees (Isbell *et al.*, 1990). This could make them more susceptible than other mammals to human-induced habitat change, particularly deforestation.

Although natural die-offs such as those experienced by the vervets and baboons of Amboseli may not be common, such events are taxonomically and ecologically widespread (Young, *in press*). Populations subject to massive die-offs may be at risk of extinction from these events, and be particularly sensitive to anthropogenic reductions in population size. Theoretical models indicate that the likelihood of large die-offs may put severe restrictions on the viability of populations (Hanson & Tuckwell, 1978).

## CONCLUSION

Field studies of natural populations are essential to conservation efforts for several reasons. First, field studies are necessary to describe ecological and demographic baselines essential to recognizing changes in ecosystems and populations, and identify factors affecting individual and population success, as illustrated above. These are essential in determining appropriate remedial actions for declining populations and for comparison when monitoring translocated and reintroduced animals. Detailed behavioural studies are far more valuable in this regard than simple demographic surveys.

Second, long-term field work is necessary to distinguish between baseline variation and extraordinary events, which can be confused by short-term observations (Trivelpiece *et al.*, 1990). Field workers are often the first to notice potentially critical changes in an environment and its populations, whether these changes are natural or caused by humans. Also, the very presence of researchers can discourage activities detrimental to conservation. It is no coincidence that Amboseli Park has had the fewest losses of elephants over the last 20 years in Kenya; it has had the greatest number of researchers and the only population of constantly studied elephants in East Africa.

Declining populations are at risk from a variety of sources, whether or not the reasons for the decline are due to human activity. Small populations are more at risk of extinction than larger ones (Pimm, 1991). In addition, for species in which populations are divided

into discrete groups, our results suggest that there may be a minimum group size that operates independently from minimum overall population size. Some factors causing declines of groups and populations also result in the movement of individuals into unfamiliar areas, which poses special risks.

Humans are increasingly intervening in natural communities, both for exploitation and for conservation. Human interventions are likely to have myriad positive and negative effects on endangered populations that interact in complex and sometimes unexpected ways.

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