



the  
**abdus salam**  
international centre for theoretical physics



H4.SMR/1202-19

"Fifth Course on Mathematical Ecology  
including and introduction to Ecological Economics"

28 February - 24 March 2000

**CONSPECIFIC AGGREGATION AND  
CONSERVATION BIOLOGY**



*Andy Dobson*

Princeton University  
Dept. of Ecology and Evolutionary Biology  
Princeton, U.S.A.

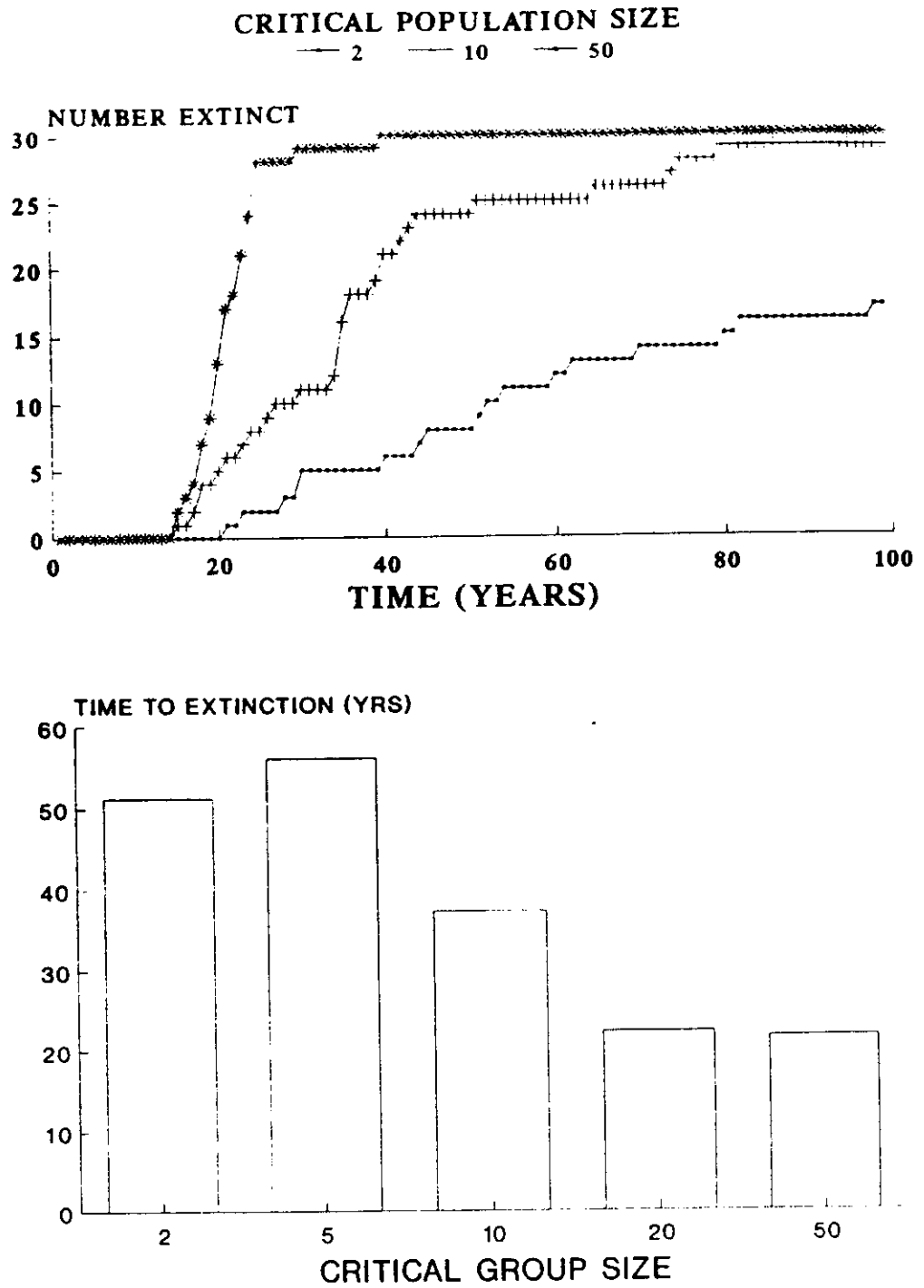


Figure 8-2 (A) The relationship between critical group size,  $G$ , and the proportion of populations that decline to extinction in one year. (B) The average time taken for populations of initial size 50 to decline to extinction for five different values of  $G$ .

exceed 70%; otherwise they were likely to decline in numbers. Harcourt (1995) showed that this was a useful approximation for the mountain gorillas in Rwanda. Such allometric approaches could be more widely used in conservation biology (Peters, 1983; Charnov, 1993).

### Grouping and Pathogen Transmission

The ability of parasites and disease to become established in host populations and the impact they have when accidentally introduced is crucially determined by the spatial distribution of the host population. For most species, this spatial distribution is determined by the social organization of the species, which is in turn a consequence of the underlying distribution of food and other vital resources (Rubenstein and Wrangham, 1986). There have recently been a number of dramatic examples of disease outbreaks in wild populations of large vertebrates (rabies or distemper in wild dogs: Gascoyne et al., 1993; morbilliviruses in lions: Roelke-Parker et al., 1996, in Atlantic white-sided dolphins *Lagenorhynchus acutus* and in harbor seals *Phoca vitulina*: Kennedy, 1990). In each case the social system of the hosts determined their spatial distribution and the impact of the disease. In the Serengeti lions and wild dogs, individual prides and packs were infected, but the rate of spread between packs was slow. In contrast, in the North Sea seal colonies, large numbers of individuals died as a result of living in large groups.

The consequence of social aggregation can be fairly easily added to the classic SIR model for an infectious disease where the host population is divided into susceptible, infectious, and recovered individuals:

$$dS/dt = (a - b) S - f(S, I) S. \quad (2)$$

$$dI/dt = f(S, I) S - bI - \alpha I - \gamma I \quad (3)$$

$$dR/dt = \gamma I - bR \quad (4)$$

Here  $S$ ,  $I$ , and  $R$  are the densities of susceptible, infected, and resistant individuals, respectively,  $a$  and  $b$  are the birth and death rates of the host in the absence of the pathogen,  $\alpha$  is the parasite-induced host mortality rate, and  $\gamma$  is the rate at which infected individuals recover. The transmission term,  $f(S, I)$ , can take a number of alternate forms. Unfortunately, the behavior of many epidemiological models is sensitive to the assumptions made about whether transmission proceeds as a simple pseudomass action function,  $IS$ , or a true mass action function,  $IS/H$ , where  $H = S + R$ . (In some publications these are designated density-dependent and frequency-dependent transmission). Here we will consider a simple modification to the pseudomass action formulation which gives rise to an expression for the basic reproductive ratio of the pathogen,  $R_0$ , that contains an expression for the numbers of susceptible individuals in the population. When the expression for  $R_0$  is rearranged at unity to obtain an estimate of the threshold number of hosts which are required to just sustain an infection of the pathogen,  $H_T$ , this can only be obtained for the pseudomass action transmission model.

$$H_T = (\alpha + b + \gamma)/\beta. \quad (5)$$

We can now add an additional degree of complexity into the transmission term that considers the spatial distribution of the host population. Here we generalize this approach by using a mixture of terms based on Lloyd's mean crowding (Lloyd, 1967) and Taylor's power

100

pop-  
tions

law (Taylor, 1961; Taylor and Taylor, 1977). Lloyd's index of mean crowding was derived to provide an estimate of the number of individuals likely to co-occur in a quadrat centered on a randomly chosen individual. In its simplest form, mean-crowding is measured as

$$\hat{x} = \bar{x} + \frac{s^2}{\bar{x}} - 1. \quad (6)$$

Here  $\bar{x}$  is the mean number of individuals found in a quadrat,  $s^2$  is the variance of the numbers of individuals found in the quadrat, and  $\hat{x}$  is Lloyd's mean crowding. As the population becomes more aggregated in its spatial distribution, the variance increases faster than the mean, and each individual is likely to be surrounded by a greater number of other individuals. The index has interesting epidemiological applications; if we consider the randomly chosen individual to be an infected individual, then  $\hat{x}$  will be the number of susceptible individuals in its vicinity. As the host population becomes more aggregated, any infected individual is likely to transmit the infection to more susceptible individuals.

If we are to include information about the spatial distribution of the host population into simple epidemiological models, it is also important to consider how spatial aggregation will change with changes in population density. An important empirical property of most biological populations is the variance in their spatial density is usually a simple power function of their mean density (Taylor, 1961; Taylor and Taylor, 1977). It allows us to replace the expression for the variance in eq. 6 with one that describes the variance as a function of the mean density:

$$\hat{x} = \bar{x} + \frac{c\bar{x}^d}{\bar{x}} - 1. \quad (7)$$

This allows us to obtain an expression for the transmission of a pathogen that captures phenomenologically some of the details of the spatial aggregation of the host population. Hence the transmission term in eqs. 2-4 becomes

$$f(S, I) = \beta I (\bar{s} + c\bar{s}^{d-1} - 1). \quad (8)$$

Taylor and colleagues (Taylor and Taylor, 1977; Taylor et al., 1978) provide evidence that the slope of the power law relationship for most species is between 1 and 3, with unity corresponding to a randomly distributed population and 3 to a species that is highly aggregated in its spatial distribution.

As the host population becomes more aggregated in its distribution, a significant increase occurs in the number of susceptible hosts that come into contact with any infected individual. This will lead to a significant decline in the threshold for establishment of the pathogen into the host population (fig. 8-3). Obviously, this approach to understanding the role of host spatial distribution on epidemic outbreaks and pathogen establishment ignores many details. In particular, it disregards the explicit spatial distribution of the individuals in the host population, but to examine this would require detailed case-specific computer models. However, the approach provides an intermediate step that uses information that can be quite readily quantified empirically on the spatial distribution of hosts. Most importantly, the results suggest that the spatial distribution of the host population is important in determining the critical community density for pathogen establishment. More detailed spatial models can then be developed to examine the importance of where the parasite is introduced.

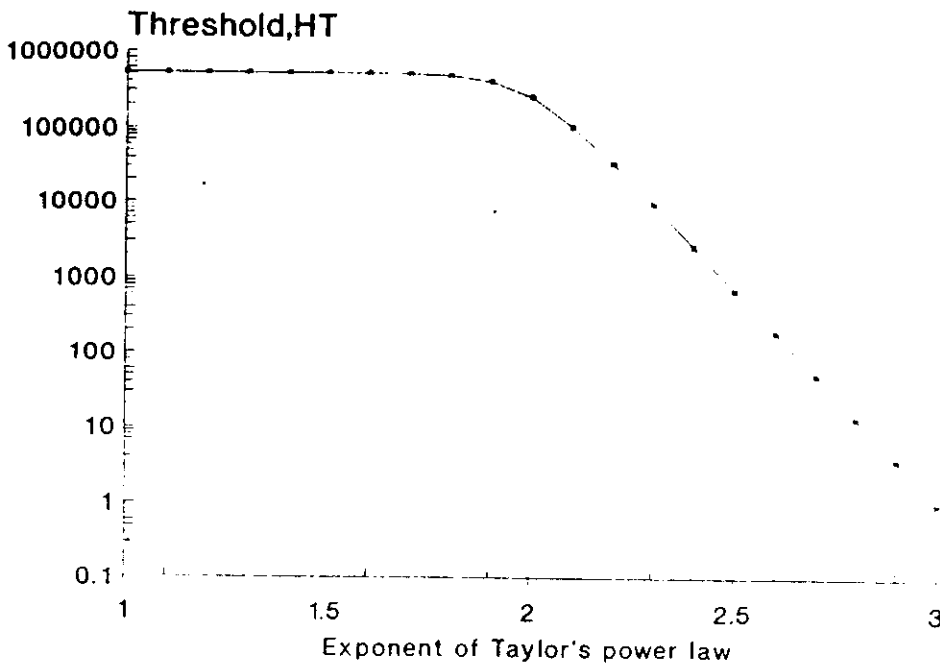
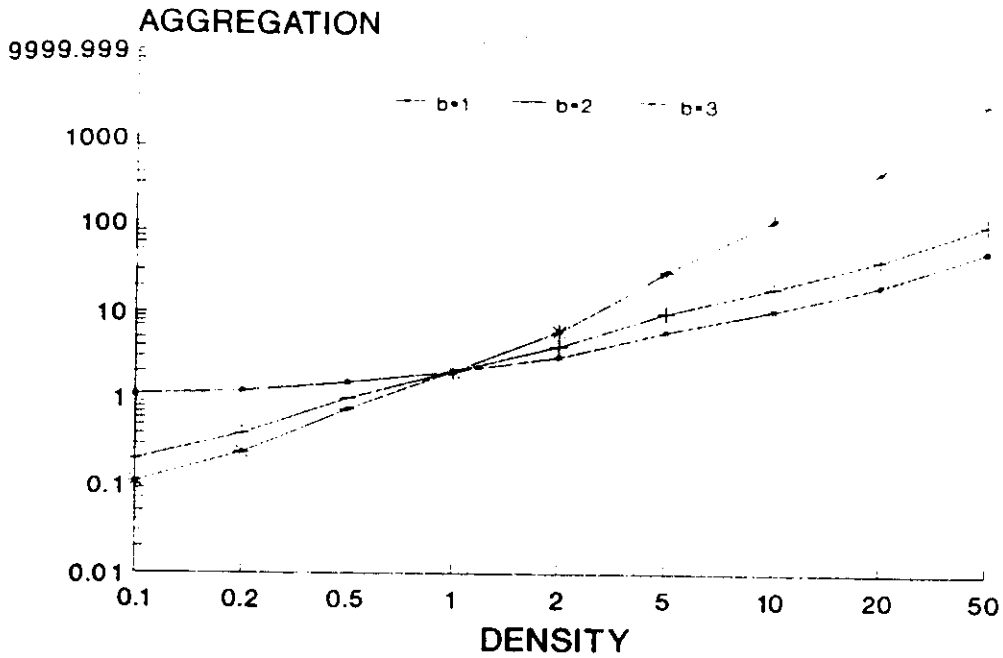


Figure 8-3 (A) The relationship between population density and aggregation, the number of individuals surrounding a single infective individual. Changes in aggregation with population density are determined by the exponent of the power function in Taylor's power law; this is then substituted into the modified expression for Lloyd's mean crowding in the main text (eq. 6). In this figure the exponent  $b$  has been set to 1 (dots), 2 (crosses), or 3 (stars). (B) The relationship between threshold for establishment of a pathogen and degree of aggregation of the host population. The degree of host aggregation is quantified using the slope of Taylor's power law for the relationship between the variance of conspecifics in a transmission circle surrounding an infected host and the mean number of susceptibles within the transmission circle. The area of the circle is assumed to increase with the magnitude of  $\beta_A$ .

### Exploitation of Species

The harvesting of natural resources in particular populations of fish, whales, elephants, and other vertebrates has as an underlying assumption that there is a surplus of individuals in the population. In many long-lived vertebrates, certain individuals often play a crucial role in maintaining recruitment levels, particularly by feeding and protecting young and immature relatives. There are numerous anecdotal examples: old female elephants lead groups to food sources (Moss and Poole, 1983); wildebeest *Connochaetes taurinus* may require a minimum group size to defend their offspring against wild dog attack (Creel and Creel, 1995); and nonbreeding black-backed jackals *Canis mesomelas* increase the reproductive success of their parents (Moehlman, 1979). In short, the excess of individuals is often more apparent than real. While these observations are in urgent need of more systematic study, the idea that wildlife can only be protected by harvesting it remains prevalent in the game departments of many countries and international wildlife organizations.

Our work on African elephants provides a clear example of this problem. Rapid exploitation of elephant populations has led to a continental decline of more than 95% in the last 200 years (Douglas-Hamilton, 1987; Milner-Gulland and Beddington, 1993). Available data show that poachers selectively remove elephants with tusks larger than a minimum size, and this results in a more complex relationship between ivory yield and population size than if poachers removed elephants at random. The reason is that tusk size is dependent on both the age and sex of an elephant (fig. 8-4a). Initially, the larger tusked adult males will be selected in preference to females and younger males. Later, selective poaching at lower tusk weights rapidly produces populations with distorted sex ratios and age structures (fig. 8-4b). Surveys conducted on East African elephant populations confirm these highly skewed sex ratios: in some areas mature females outnumber mature males by a factor of > 50:1 (Poole, 1989a). Furthermore, the proportion of females showing signs of pregnancy or accompanied by recent offspring was diminished in these populations. Because females preferentially mate with older males (Poole, 1989b), there is a danger of reducing the population's growth rate. To examine how these changes in social structure affect the ability of populations to recover, we have extended the model to ascertain the conditions when a paucity of mature males limits conception rates.

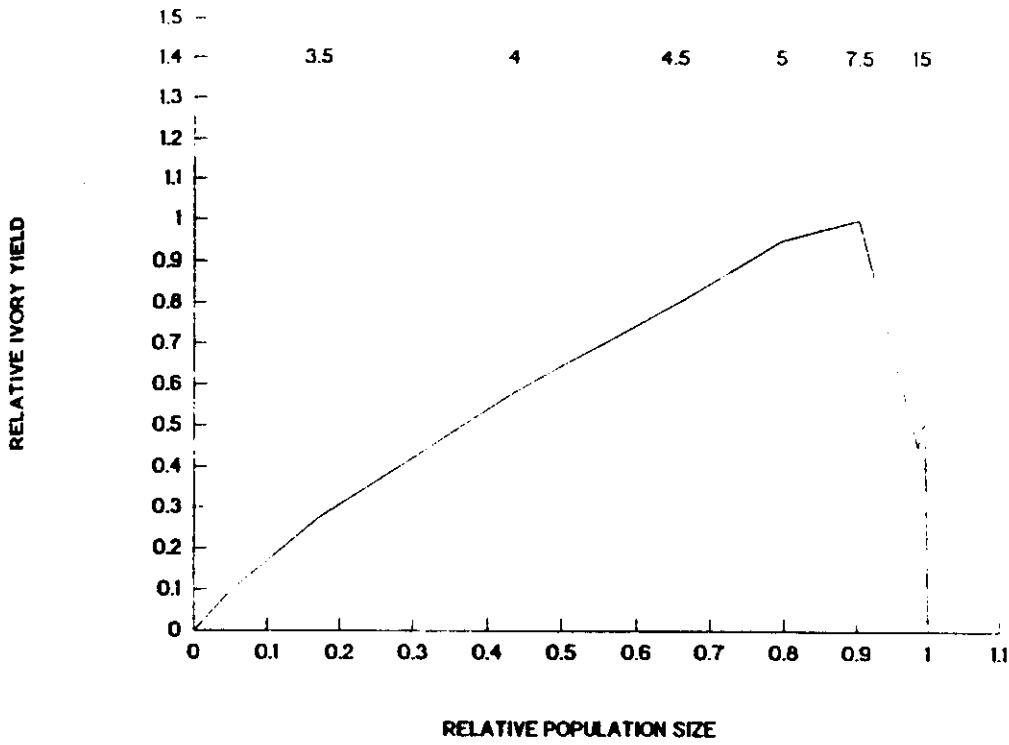
### Recovery from Exploitation

We can model the social system of elephants by assuming that males searching for females have the dynamics of a simple predator-prey system. We assume that  $M$  males search at a

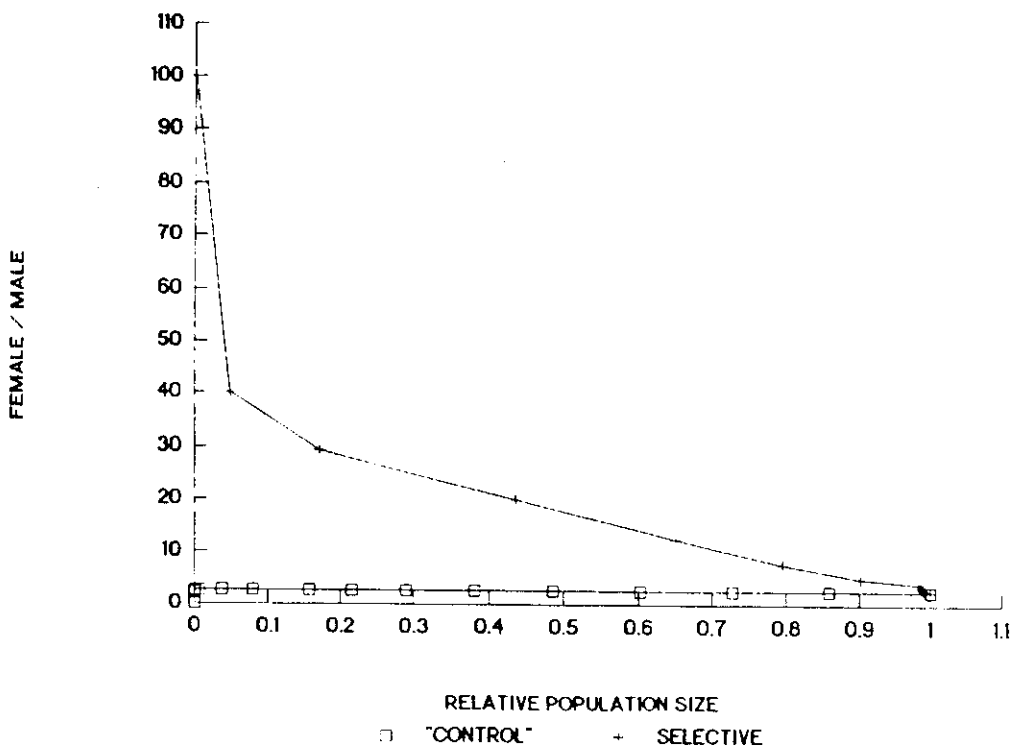
---

Figure 8-4 The effect of selective poaching for large tusks on ivory yield and elephant population size. Here we assume that poachers select elephants with tusks larger than a certain size. As males have substantially larger tusks than females, they will be more heavily exploited in the early years. As mature males become rare, poachers include females and immature males in the harvest, producing a more complex relationship between yield and population size. It is particularly important to note that once females have been included in the harvest, small decreases in average tusk weight produce large decreases in population size. The irregularity that occurs in the recruitment function close to carrying capacity reflects the switching point when poachers begin to include females in their harvest. (B) The effect of selective poaching on the sex ratio of elephants in the population (mature females per mature male).

## MINIMUM TUSK SIZE POACHED



## SEX-RATIO IN EXPLOITED POPULATIONS



rate,  $\alpha$ , in a population of  $F$  females, divided into  $G$  groups (the rate at which males find females in estrus is thus  $\alpha \epsilon F/G$ , where  $\epsilon$  is the proportion of time for which a female is receptive). Each male takes a constant period of time,  $h$ , to consort with each estrus female. The number of females that any male successfully consorts with in a period of time  $T$ , equal to one estrus cycle, is given by the following equation:

$$\frac{N_c}{M_t} = \frac{\alpha T \epsilon F/G}{1 + \alpha h \epsilon F/G} \quad (9)$$

This expression for the instantaneous rate at which males encounter females may be used to estimate the probability that any individual female is not located by the available males during any one estrous period. This probability is given by substituting eq. 1 into the zero-th term of a Poisson distribution:

$$p_0 = e^{-(N_c/F)} \quad (10)$$

The proportion of females who eventually conceive during the time equal to one interbirth period is a function of the probability that a female is not mated,  $p_0$ , the probability,  $c$ , that she conceives if mated, and the number of times a female would come into estrus every 4 years if not successfully mated. Thus the proportion of females who are pregnant or produce offspring in any 4-year interval is given by

$$f(F,M) = 1 - [(1 - c)(1 - p_0) + p_0]^T \quad (11)$$

Substitution of eq. 2 into eq. 3 allows us to obtain an expression for the proportion of females producing young in any 4-year interbirth interval:

$$f(F,M) = 1 - [1 - c(1 - e^{-N_c/F})]^T \quad (12)$$

This expression is a modification of one described by Dobson and Lyles (1989) and adds important biological detail (if we assume that females who do not conceive will continue cycling). Here we assume that males attain sexual maturity at age 20 and are sexually active for a proportion of time,  $\epsilon$ , each year; they are promiscuous and will mate with several females during this period. The mating function suggests that the probability of a female conceiving during any one reproductive cycle is strongly dependent on the numbers of males available and the number of groups into which the female population is divided (fig. 8-5). As the sex ratio becomes more distorted toward females (as is the case in heavily poached elephant populations), or as the females become divided into many small groups, the proportion of females producing offspring declines (fig. 8-6).

The mating function (eq. 11) is most sensitive to estimates of male search rate and the number of times a female enters estrus. We assume that a female enters estrus three times a year; the actual incidence may be lower than this, as females will fail to cycle if resources are limiting. Data collected from studies of bull elephants at Amboseli (Poole, 1989b) were used to quantify the rates at which males locate females. Because females find mature males more attractive than younger, inexperienced males (Poole, 1989b), these data may overestimate the success rate of males in populations where poaching will have reduced the numbers of older males. Both of these effects may cause the model to overestimate expected conception rates in heavily exploited populations.

Inclusion of the mating function (eq. 11) into the fecundity terms of a demographic viability model considerably increases the susceptibility of exploited elephant populations to extinction. Essentially, the elephant's social behavior determines a threshold population size where successful mating becomes limiting and below which the population always col-



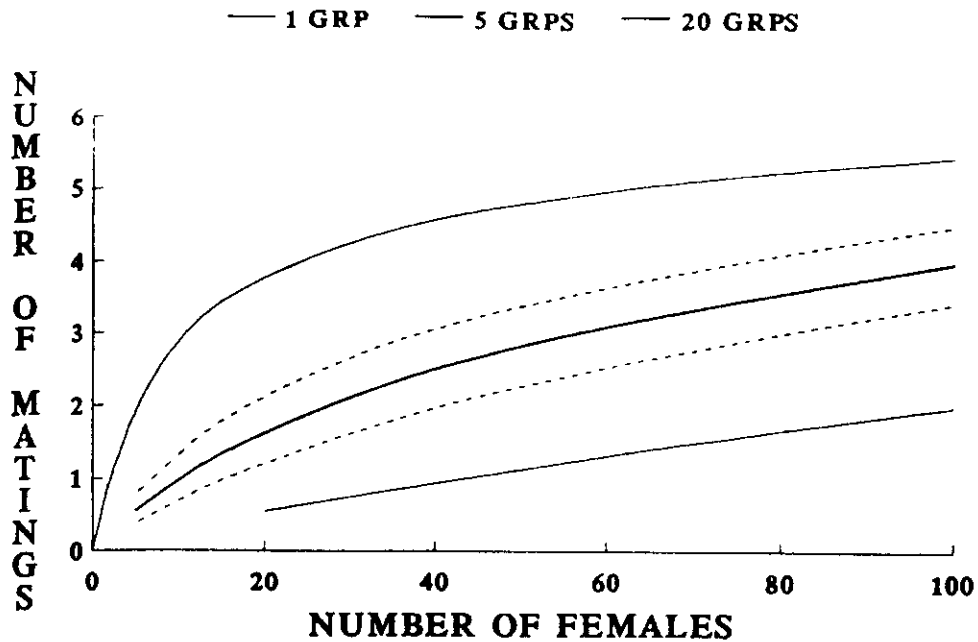


Figure 8-5 The effect of population size and grouping pattern on the rate at which estrous female elephants are located by mature males. The probability that an estrous female will be mated is assumed to have the dynamics of a simple predator-prey system; the numbers of females located depends on encounter rate,  $\alpha$ , female group size,  $F/G$ , and the proportion of females in estrus,  $\epsilon$ . Each estrous female is fertile for 2 days, and if she does not conceive, she will cycle three times a year (thus  $\epsilon = 6/360$ ). The duration of estrus also determines the period of time,  $h$ , that a male spends consorting with any individual female and is unavailable to others. The observed pregnancy rates at Amboseli may be used to obtain a conservative estimate for encounter rate  $\alpha$  ( $\alpha = 3$ ). The dotted lines on either side of the line for five groups illustrate the sensitivity of the mating function to this parameter (upper line  $\alpha = 2$ , lower line  $\alpha = 4.5$ ). When either sex is limiting, encounter rate is likely to be a function of habitat size. We have therefore estimated  $\alpha$  for other parks by modifying the Amboseli estimate by the relative area of each park (we assume  $\alpha$  is a function of distance traveled and that this will scale with the square root of habitat area, thus  $\alpha \approx 1.2$  for Queen Elizabeth and  $\alpha \approx 1.8$  for Mikumi).

lapses to extinction. The presence of such a threshold means that the viability of elephant populations is dependent not only on past and present levels of poaching, but also on the sex ratio and group structure of the exploited populations.

Empirical data from surveys of East African elephant populations provide support for this model of mate limitation (Poole, 1989a). In Mikumi National park, Tanzania, where the surveyed elephants were widely dispersed in many small groups, only 39% of the adult females had developed breasts (and were, therefore, either pregnant or lactating). In contrast, in Queen Elizabeth National Park, Uganda, most of the elephants had grouped together to form a single permanent large aggregation, and 87% of the adult females had developed breasts. The number of mature females to mature males in the two parks was 74:1 and 26:1, respectively. Using the observed numbers of males of breeding age and female group-size structures in these populations (the mean number of females per group for Mikumi is 3, while mean number of females per group in Queen Elizabeth is 67), our model predicts 40%

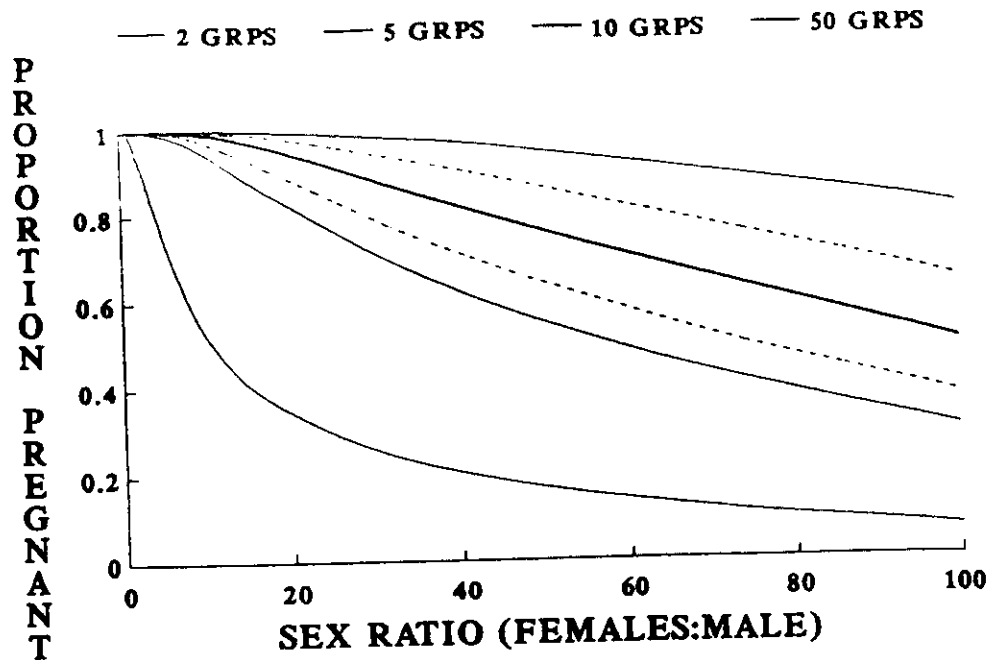


Figure 8-6 The effect of variation in sex ratio on expected proportion of females pregnant or lactating in a population containing 200 sexually mature female elephants. The figure assumes that males search for females with a success rate determined by the functional response depicted in fig. 8-4. Successfully mated females have only a 50% chance of conceiving. The expected proportions of pregnant or lactating females are drawn for populations split into 2, 5, 10, and 50 groups. The lines are discontinued below densities where it would be impossible to subdivide the population to the given extent. The dashed lines on either side of the five-group contour illustrate the sensitivity of the function to  $\alpha$ ; it is again allowed to vary by a factor of 2. Included in the figure are the data from surveys of pregnant or lactating females in Queen Elizabeth National Park, Uganda; Mikumi National Park, Tanzania; and the relatively unpoached population at Amboseli National Park, Kenya.

and 95% of females pregnant or lactating for Mikumi and Queen Elizabeth Parks, respectively.

#### Patch Recolonization and Conspecific Attraction

Although it is possible that some species use food abundance, or perhaps the density of tree snags greater than 3.5 cm in diameter, or the young/mature ratio of secondary successional deciduous tree species as cues to determine potential breeding habitat, most species probably follow simpler rules when attempting to locate suitable nest sites. In particular, "attempt to breed where you were born or where you bred successfully last year" and "attempt to breed as close as possible to someone else who is already defending a potential site" appear to be rules that apply to a range of species (Reed and Dobson, 1993). In both cases, species use conspecific cues to recognize suitable habitat; the presence of appropriate resources (nest sites, food, and protection from natural enemies) will eventually ensure that

individuals in the best sites will survive, reproduce, and be present as cues for subsequent colonists. However, should the residents in a patch of suitable habitat go extinct, then potential immigrants may not recognize the habitat as suitable. Thus patches of habitat classified as ideal by habitat quality indices may remain completely unoccupied when animals require songs or scent marks from conspecifics to initiate territorial defense and other behavioral patterns that attract mates.

The importance of recognizing that animals may use conspecific cues to locate suitable habitat can be quickly perceived from work on *Anolis* lizards. Stamps (1987) observed lizards breeding at natural densities at a number of sites. The boundaries of each male's territories were delineated by fights with the male from the adjoining territory. However, when Stamps removed all the *Anolis* from an area and reintroduced a solitary male who had previously held a territory, he wandered through the previously occupied habitat and failed to establish a territory. The absence of other males with whom to fight meant that the lizard had no means of determining the boundary of its territory and was therefore unable to establish a territory with which to attract a mate. These observations have ramifications for patch recolonization in metapopulations and in initial reintroductions because conspecifics will be absent in both situations.

### Strengths and Weaknesses of Conspecific Aggregation

Information about the size and type of aggregations and the circumstances under which they occur give models of population growth added realism. In addition, parameters of models can be changed quite simply to incorporate different patterns of grouping in different populations or species (see Durant, chapter 5, this volume). Information about aggregations can also be useful for management programs that seek to bolster populations in the wild or to reintroduce individuals. Fortunately, information on conspecific aggregations is relatively easy to tabulate because it simply involves collecting an adequate sample of group sizes and their composition.

Unfortunately, such data are difficult to gather for aquatic, fossorial, or secretive species; for example, we know little about grouping patterns of most fish species that are heavily exploited (Vincent and Sadovy, chapter 9, this volume). Further, little information is available on changes in aggregation patterns in response to exploitation or to environmental disturbance such as disease. Sustained changes in group size or composition in the face of perturbation will alter models' predictions and management programs in ways that we do not yet understand.

### Recommendations

There are a number of recommendations that emerge from considering the phenomenon of conspecific aggregation in conservation biology. We will mention just three.

Game managers have known for centuries that conspecific attraction to decoys is a useful tool for trapping some bird and mammal species when hunting. Conspecific cues are also known to attract birds to breeding sites, either for colonization or to bolster local populations. This suggests that a better understanding of conspecific attraction could provide an important tool for conservation biologists and wildlife managers. In areas where populations have gone locally extinct, conspecific attraction has been used experimentally to

start new colonies of seabirds. For these species, the presence of conspecifics, even painted decoys in the guise of seabirds, was an indicator of acceptable settling sites, particularly for juveniles (Fisher, 1954). In other studies, wildlife managers have often commented on the absence of a species from patches of habitat they regard to be adequate to support small populations (Wilcove, 1994). If the absence of the species is due to failure of the species to recognize the habitat, then artificial cues could be provided that might attract potential colonists. For example, taped recordings of territorial defense calls might attract birds to colonize patches of deserted woodland.

Conspecific cues can also be an important consideration when designing reserves. Verner (1992) points out that large blocks of habitat can attract disproportionate number of birds because of synergistic action in singing rates. Song attracts conspecifics, and song rates are higher in the presence of singing neighbors, so sites rich in birds might become richer. This suggests that larger reserves might contain proportionally more individuals than smaller reserves because of conspecific attraction and interaction. Given the current population fragmentation of many species, decoys and playback might be useful tools for attracting animals to newly recovered or recently abandoned sites. One concern for repopulating sites is that artificial means might attract potential breeders, but adequate social interactions might be required to retain them. Only testing in the field can determine the potential utility of these methods for different species. Social facilitation is an important aspect of biology, and conservation biologists have a good opportunity to make it work for species recovery and maintenance.

In regard to using big game hunting as a management tool (see Greene et al., chapter 11, this volume), our models indicate the importance of maintaining large, old males in the elephant populations. Until recently these individuals were thought to be reproductively senile: young males were originally thought to do all the mating, old males were regarded as dead wood and could be culled (Parker, 1979). This opinion prevails today in some isolated bureaucracies; for example, as recently as 1995, the U.S. Fish and Wildlife Service passed a nondetriment finding to support the culling of older male elephants by sports hunters in Northern Tanzania. Both modeling and empirical data now suggest that old males are important players in rapid recovery of exploited elephant populations. The degree to which this phenomenon may operate in other exploited game populations needs study.

### Summary

Although individuals of some species live together permanently, others form temporary aggregations for at least portions of their lives. If population growth rate depends on a critical group size (the Allee effect), then conspecific aggregations will have conservation consequences. Modeling indicates, for example, that viability thresholds are higher for monogamous primate species than polygamous ones. Modeling also shows that as a host population becomes more aggregated, infection is more likely to be transmitted to susceptible individuals. Aggregation also changes the effect of harvesting for population growth rates. Among elephant populations, modeling shows that the proportion of females producing offspring declines as females become divided into small groups.

Behavioral observations suggest that individuals use conspecifics as cues for where to settle and may avoid uninhabited areas. This will affect habitat patch recolonization and reintroductions. In practical terms, conspecifics can be used to attract individuals to particular areas, and in designing reserves.

Information about aggregations can make models more realistic, but such data can be difficult to collect; in addition, grouping patterns may change in response to exploitation.

**Acknowledgments** We thank Scott Carroll, Dan Rubenstein, Cathy Toft, and an anonymous reviewer for constructive comments. We are particularly grateful to Tim Caro for help in redrafting and reorganizing this chapter.

#### References

- Allee WC, 1931. Animal aggregations. Chicago: University of Chicago Press.
- Allee WC, 1938. The social life of animals. Norton.
- Birkhead TR, 1977. The effect of habitat and density on breeding success in the common guillemot (*Uria ualge*). *J Anim Ecol* 46:751-764.
- Blockstein DE, Tordoff HB, 1985. Gone forever—a contemporary look at the extinction of the Passenger pigeon. *Am Birds* 39:845-851.
- Charnov EL, 1993. Life history invariants. Some explorations of symmetry in evolutionary ecology. Oxford: Oxford University Press.
- Creel SR, Creel NM, 1995. Communal hunting and pack size in African wild dogs *Lycaon pictus*. *Anim Behav* 50:1325-1339.
- Darling FF, 1952. Social behavior and survival. *Auk* 69:183-191.
- De Groot P, 1980. Information transfer in a socially roosting weaver bird (*Quelea quelea*: Ploceinae): an experimental study. *Anim Behav* 28:1249-1254.
- Dobson AP, AM Lyles, 1989. The population dynamics and conservation of primate populations. *Conserv Biol* 3:362-380.
- Douglas-Hamilton I, 1987. African elephant population trends and their causes. *Oryx* 21:11-34.
- Fisher J, 1954. Evolution and bird sociality. In: Evolution as a process (Huxley J, Hardy AC, Ford EB, eds). London: Allen and Unwin: 71-83.
- FitzGibbon CD, 1990. Why do hunting cheetahs prefer male gazelles? *Anim Behav* 40:837-845.
- Gascoyne SC, Laurenson MK, Lelo S, Bomer M, 1993. Rabies in African wild dogs (*Lycaon pictus*) in the Serengeti region, Tanzania. *J Wild Dis* 29:396-402.
- Greene E, 1987. Individuals in an osprey colony discriminate between high and low quality information. *Nature* 329:239-241.
- Harcourt AH, 1995. Population viability estimates: theory and practice for a wild gorilla population. *Conserv Biol* 9:134-142.
- Kennedy S, 1990. A review of the 1988 European seal morbillivirus epizootic. *Vet Rec* 127:563-567.
- Lloyd M, 1967. Mean crowding. *J Anim Ecol* 36:1-30.
- Milner-Gulland EJ, Beddington JR, 1993. The exploitation of elephants for the ivory trade: an historical perspective. *Proc R. Soc Lond B* 252:29-37.
- Moehlman PD, 1979. Jackal helpers and pup survival. *Nature* 277:382-383.
- Moss CJ, Poole JH, 1983. Relationships and social structure in African elephants. Primate social relationships: an integrated approach (Hinde RA, ed). Oxford: Blackwell. 315-325.
- Parker ISC, 1979. The ivory trade. Washington, DC: U.S. Fish and Wildlife Service.
- Peters RH, 1983. The ecological implications of body size. Cambridge: Cambridge University Press.

- Poole JH, 1989a. The effects of poaching on the age structure and social and reproductive patterns of selected East African elephant populations. In: *The Ivory Trade and the Future of the African Elephant*, report no. 2 (Ivory Trade Review Group, ed).
- Poole JH, 1989b. Mate guarding, reproductive success and female choice in African elephants. *Anim Behav* 37:842-849.
- Reed JM, Dobson AP, 1993. Behavioural constraints and conservation biology: conspecific attraction and recruitment. *Trends Ecol Evol* 8:253-255.
- Roelke-Parker ME, Munson L, Packer C, Kock R, Cleaveland S, Carpenter M, O'Brien SJ, Pospischil A, Hofmann-Lehmann RH, Lutz H, Mwamengele GLM, Mgasa MN, Machange GA, Summers BA, Appel MJG, 1996. A canine distemper virus epidemic in Serengeti lions (*Panthera leo*). *Nature* 379:441-444.
- Rubenstein DI, Wrangham RW (eds), 1986. *Ecological aspects of social evolution: birds and mammals*. Princeton, New Jersey: Princeton University Press.
- Stacey PB, Koenig WD, 1990. *Cooperative breeding in birds: long-term studies of ecology and behavior*. Cambridge: Cambridge University Press.
- Stamps JA, 1987. Conspecifics as cues to territory quality. 1. A preference for previously used territories by juvenile lizards (*Anolis aeneus*). *Am Nat* 129:629-642.
- Taylor LR, 1961. Aggregation, variance and the mean. *Nature* 189:732-735.
- Taylor LR, Taylor RAJ, 1977. Aggregation, migration and population dynamics. *Nature* 265:415-421.
- Taylor LR, Woiwood IP, Perry JN, 1978. The density-dependence of spatial behaviour and the rarity of randomness. *J Anim Ecol* 47:383-406.
- Verner J, 1992. Data needs for avian conservation biology: have we avoided critical research? *Condor* 94:301-303.
- Wilcove DS, 1994. Turning conservation goals into tangible results: the case of the spotted owl and old-growth forests. In: *Large-scale ecology and conservation biology* (Edwards PJ, May RM and Webb NR, eds). Oxford: Blackwell Scientific; 313-329.
- Wilson EO, 1975. *Sociobiology: the new synthesis*. Harvard, Massachusetts: Belknap Press.



