11

Animal Breeding Systems, Hunter Selectivity, and Consumptive Use in Wildlife Conservation

Correigh Greene
James Umbanhowar
Marc Mangel
Tim Caro

Multiple-Use Areas

Wild animal and plant populations are protected from development and agriculture in a number of ways, ranging from strict nature reserves and national parks that are managed for wilderness protection and nonconsumptive recreation, to multiple-use areas from which species or products are extracted (IUCN/UNEP/WWF, 1991). In the face of the growing human population, much of the world's animal and plant diversity will in the future be found within protected areas, so the efficacy with which different forms of protection conserve biodiversity is now of central concern (Meffe and Carroll, 1997). In the long term, we will need to determine whether wildlife populations protected in national parks suffer less attrition than those protected in multiple-use areas and which types of multiple-use areas are best.

To date, most studies of consumptive use of plants and animals have been from an economic perspective. These studies have attempted to quantify resource availability (e.g., Lawrence et al., 1995) and assign economic weighting to products (e.g., Peters et al., 1989; Balick and Mendelsohn, 1992), and hence examine whether exploitation is sustainable in economic terms (Clark, 1985, 1990; Redford and Padoch, 1992). Viewing natural resources solely from an economic standpoint does not necessarily ensure biological sustainability, and therefore, if multiple-use areas are to be an effective conservation tool, they must support viable populations of species in the long term.

Consumptive Use of Animals: Classical Conservation Approaches

Consumptive use of animals includes subsistence hunting by indigenous people (Marks, 1973; Kaplan and Kopischke, 1992), local market hunting (Glanz, 1991), ranching (Ojasti, 1991), sport hunting (Anderson, 1983; Cumming, 1989; Metcalfe, 1994), and commercial harvest (Lewis et al., 1990; Thomsen and Brautigam, 1991). To assess the effects of con-

sumptive use on terrestrial animal populations, some researchers have compared densities in areas of differing hunting intensity (Freese et al., 1982; Peres, 1990; Fragoso, 1991). Although prey populations are often smaller in hunted areas (but see Harcourt, chapter 3, this volume), reduction in density does not mean that hunting is unsustainable. To address this possibility, studies have examined how kills per unit effort (assumed to be a measure of abundance) change over time. Vickers (1991), for example, concluded that the Siona-Secoya people in northeastern Ecuador were not depleting their mammalian or avian prey because, for most species, returns per unit effort remained fairly constant over a decade.

Other studies have employed indirect methods and comparative data to determine re-productive parameters of prey populations and hence sustainable offtake levels. Robinson and Redford (1986, 1991a) calculated species densities in neotropical forests using body weights and intrinsic rates of natural increase and hence estimated production rates per unit area. Several studies have used Robinson and Redford's model to estimate potential harvests. For example, Fa et al. (1995) surmised that five primates and one ungulate species were being overhunted on the Island of Bioko, equatorial Guinea, but that few species were being overhunted on mainland Rio Muni. FitzGibbon et al. (1995) determined that yellow baboons *Papio cynocephalus* and Sykes' monkey *Cercopithecus mitis* were being over-hunted in Kenya's Arabuko-Sokole Forest, but offtake rates for elephant shrews, squirrels, and duikers (*Cephalophus* spp.) were sustainable.

Using more direct methods, Bodmer (1994; see also Bodmer et al., 1994) examined whether Amazonian wildlife could be harvested commercially without rendering species vulnerable to local extinction. Bodmer gathered data on mammal densities in the Reserva Comunal Tamshiyacu-Tahuayo in northeast Peru by walking line-transects and calculated reproductive rates by autopsying shot females. This allowed him to determine the magnitude of harvest that the population might sustain. In this study he also measured the actual number of animals hunted in an area. By comparing this with animal densities and production rates, it was possible to determine which species were being harvested on a sustainable basis and which were overexploited. He found that tapirs *Tapirus terrestris* and primates were overhunted, whereas peccaries *Tayassu tajacu* and *T. pecari* and brocket deer *Mazama americana* and *M. gouazoubira* were probably being hunted sustainably. Bodmer's study is unusual because it measured mammal densities, calculated production rates, and measured offtake simultaneously.

Data on animal densities and hunting rates are difficult to collect, but they represent a major step in both assessing the biological sustainability of consumptive animal use and in recommending appropriate offtake levels in multiple-use areas. A tentative conclusion emerging from studies in the Neotropics is that seasonal habitats are more likely to contain large-bodied species with high rates of population increase that can tolerate some sort of sustainable harvest. Species-diverse habitats, such as tropical rainforests, on the other hand, do not contain single species at high enough densities and with the population growth rates to be commercially exploitable. Neotropical forests are therefore more likely to be impor-tant for subsistence hunters who harvest a diversity of species (Robinson and Redford, 1991b). These generalizations should be treated cautiously, however, because aside from Bodmer's study, most attempts to derive estimates of harvest potential are crude and fail to take account of numerous human factors or the biology of prey animals (FitzGibbon, chap-ter 16, this volume).

Two important factors are hunter selectivity and animal breeding system. In general, an-imal harvest in buffer zones or multiple-use conservation areas takes three forms: (1) non-selective hunting, where subsistence hunters (or poachers) kill the first individual they en-

counter or that fall into their traps, regardless of age or sex (see Arcese et al., 1995; Campbell and Hofer, 1995); (2) hunting of adult males, as exemplified by tourist hunters shooting ungulates (Ginsberg and Milner-Gulland, 1994); and (3) selectively hunting adults of either sex (Marks, 1973; Alvard, chapter 17, this volume).

The range of breeding systems of commonly exploited species include harem and resource-defense polygyny, as exhibited by most mammals, and monogamy as found in many birds (Greenwood, 1980). Within these systems, species may exhibit particular behavioral and life-history strategies that have population consequences. In some species, resource competition or kin selection may cause females in larger harems to have lower fecundity than those in smaller harems (Clutton-Brock et al., 1982). Certain exploited carnivores and primates exhibit high levels of infanticide, usually by males (Hausfater and Hrdy, 1984). Other species show reproductive suppression in which only the dominant male and female normally breed (Creel and Creel, 1989). The ability of a population to sustain a given level of harvest depends, in part, on the interaction of both hunter selectivity and breeding system. This level directly affects the economic returns of harvest and hence its efficacy as a conservation strategy.

In this chapter, we explore the interactions of breeding systems and hunting selectivity on the ability of mammals to withstand different forms of hunting and hence highlight differences in sustainable offtake levels for commonly hunted species. We first develop a series of models showing how population growth rate responds to different hunting regimes, and then we examine how polygyny, infanticide, and reproductive suppression affect growth rates of hunted populations. Next, we use these models to examine the effect of legal hunting on three carnivore and three ungulate species hunted in Africa. These species were chosen because they have different breeding systems, their reproductive parameters are reasonably well documented, and two of them bring in substantial revenue from hunting. In the final section, we apply this information to the Selous Game Reserve in Tanzania, the world's largest hunting reserve. In Selous, population sizes of ungulates have been surveyed from the air (Caro et al., in press a,b) and those of carnivores estimated from the ground (Creel and Creel, 1996). We use our models to evaluate whether current tourist hunting levels will allow these six species to replace themselves sustainably in the Selous (i.e., whether they have a population growth rate > 1) and to make general recommendations for management of large mammal populations.

Examining Effects of Mating Systems Using Demographic Models

Classical Approaches Based on Life Tables

The classical approach based on life tables would typically begin with schedules of female fecundity (usually assuming a 50:50 natal sex ratio) and survivorship. These give the reproduction at each age and survival to that age. From fecundity and survivorship schedules, one can compute expected lifetime reproduction, R_0, of an individual and the instantaneous rate of increase, which is the solution of the Euler-Lotka equation (Gotelli, 1995).

The classical approach lacks any explicit recognition of mating system, except possibly in the inclusion of sex ratio. Depending on the specific mating system, R_0 computed independently for females and males might differ, especially if mean or variance in reproductive success differs between sexes (cf. Trivers, 1972). For example, Waser et al. (1995) cal-

culated R_0 for dwarf mongooses *Helogale parvula* to be 1.06 based on females but 0.94 based on males. Under such a circumstance, one can only say that the population growth rate is close to 1, and more precise statements, especially regarding whether the population is slightly growing or declining, are not possible if the variance in these rates is unknown.

Sex differences in population growth rate would not be a problem if, as is generally assumed, females solely limit population growth due to control of offspring production and recruitment. However, current theory on the evolution of mating systems predicts several circumstances in which males may limit population growth: when males provide significant parental care, as is often the case in monogamous, polyandrous, and some polygynous systems (Emlen and Oring, 1977), or when male dispersion is large relative to female dispersion (Clutton-Brock, 1989). In such cases, differential offtake of males could reduce population growth but would not be detected by classical life-table analysis.

The second problem with classical approaches is that, except for monogamous species, the empirical fecundity and survivorship schedules incorporate the result of the mating system. Because of that, they are not useful for predicting how the population characteristics will respond to changes. For example, a 10% hunting offtake of male lions *Panthera leo* will reduce survivorship accordingly, but the response of the mating system to this reduction may also be increased infanticide due to greater turnover in harem-holding males, which is difficult to predict a priori. Thus, one cannot simply reduce the survivorship schedule by 10% and assert that the new growth rates have not been otherwise affected.

Incorporating Breeding Systems into Age- and Stage-Structured Models

The age-based or stage-based approach to life history and conservation described in the previous section treats all individuals at the same age or stage as if they were identical. However, individuals of the same age may vary in physiological condition (reviewed in Mangel and Clark, 1988; Mangel and Ludwig, 1992; McNamara and Houston, 1996), and subpopulations may vary in the type of breeding system. While other population models have explicitly examined how both sexes influence population dynamics (Beddington, 1974; Beddington and May, 1980; Charlesworth, 1980; Burgoyne, 1981; Caswell and Weeks, 1986; Starfield et al., 1981; Starfield and Bleloch, 1991), few of these models incorporate the specific breeding system (however, see Caswell and Weeks, 1986). In this section, we show how breeding system can be incorporated into classical age- and stage-based approaches to life history and conservation. Like classical approaches, we use a population-level model without spatial dynamics, stochasticity, or density dependence to study the interaction of breeding system and hunting mortality. Our intention is produce a relatively simple, general model; possible modifications such as density dependence and spatial structure are discussed later.

The Fundamental Variables

The fundamental time unit in the model is the length of the birth interval (interbirth interval; IBI). In some species, the IBI is 1 year. In other species that have multiple litters per year, the IBI can be less than 1 year. We measure time, t, in multiples of the IBI. The fundamental population variables are the sizes of birth, juvenile, and adult populations at any time t (table 11-1). We denote the birth populations by

Table 11-1 Variables used in the text and their definitions.

Variable	Definition
a	Adult age class
$A_M(t), A_F(t)$	Total male and female adults at interval t
$A_m(t,a), A_f(t,a)$	Number of male or female adults in class a at interval t
$B_m(t), B_f(t)$	Number of male or female birth class individuals at interval t
F, f	Females
H	Total hunting intensity
h	Harem size
$H_{jm}, H_{jf}, H_{am}, H_{af}$	Hunting intensity of male and female juveniles and adults
i	Probability of takeover following death of a male in a coalition
j	Juvenile age class
$J_M(t,j), J_F(t,j)$	Total male and female juveniles at interval t
$J_m(t,j), J_f(t,j)$	Number of male and female juveniles in class j at interval t
λ	Population growth rate
$m(a)$	Fecundity of class a
M, m	Males
$P(t)$	Total population at interval t
P_H	Total hunted population
$\theta_{jm}, \theta_{jf}, \theta_{am}, \theta_{af}$	Hunting selectivity of male and female juveniles and adults
r	Proportion of birth class born that are male
R	Total reproduction
$\rho_m(a), \rho_f(a)$	Survivorship of male and female adults of class a
s_f, s_m	Survivorship of birth class individuals
$\sigma_m(j), \sigma_f(j)$	Survivorship of male and female juveniles of class j
t	Interbirth interval
τ	Average number of takeovers per male per interbirth interval

$B_f(t)$ = number of birth-class females at the start of interval t

$B_m(t)$ = number of birth-class males at the start of interval t.   (1)

After one birth interval, surviving offspring move into the juvenile class, where they remain for j_{max} birth intervals. Hence, if juvenile populations are described by

$J_f(t,j)$ = number of female juveniles in class j at the start of interval t

$J_m(t,j)$ = number of male juveniles in class j at the start of interval t (2)

the total juvenile populations are

$$J_F(t) = \sum_{j=1}^{j_{max}} J_f(t,j) \text{ and } J_M(t) = \sum_{j=1}^{j_{max}} J_m(t,j)$$ (3)

for females and males, respectively. Because we track sexes separately, we need not assume that j_{max}, the number of IBIs an individual spends as a juvenile, is the same for both sexes, but we do not add that complication here.

After j_{max} IBIs, individuals become adults. To track the different ages and sexes, we set

$A_f(t,a)$ = number of female adults in class a at the start of interval t

$A_m(t,a)$ = number of male adults in class a at the start of interval t.   (4)

Here $a = 1, \ldots a_{max}$, where a_{max} can be interpreted as the maximum adult life span or the age of reproductive senescence. As with j_{max}, it is possible that a_{max} differs between sexes. As with the juveniles, we denote the total adult male and female populations by $A_M(t)$ and $A_F(t)$, respectively.

In addition to j_{max} and a_{max}, we must specify fecundity and survivorship. Female fecundity depends, in principle, upon age, so we let

$$m(a) = \text{fecundity (number of offspring weaned) by a female of age } a. \quad (5)$$

To characterize survival in the absence of hunting, we assume that survivorship may vary among different stages, among age classes within each stage, and between sexes. For birth class individuals

$$s_f = \text{fraction of birth class females that survive to juvenile class 1}$$

$$s_m = \text{fraction of birth class males that survive to juvenile class 1}. \quad (6)$$

The survival of juveniles and adults in the absence of hunting depends in principle not only upon sex, but also upon age class:

$$\sigma_f(j) = \text{fraction of juvenile females in IBI class } j \text{ that survive to class } j + 1$$
$$\sigma_m(j) = \text{fraction of juvenile males in IBI class } j \text{ that survive to class } j + 1$$

$$\rho_f(a) = \text{fraction of adult females in IBI class } a \text{ that survive to class } a + 1$$
$$\rho_m(a) = \text{fraction of adult males in IBI class } a \text{ that survive to class } a + 1. \quad (7)$$

In these equations, IBI class $j_{max} = 1$ corresponds to adult class 1, and survival of adults past a_{max} is minuscule. In the simplest case, survivorship is constant within age class for juveniles and adults.

Hunting intensity may depend upon stage (birth class individuals are not hunted) and sex, but not upon IBI class within a stage, and is characterized by

$$H_{jf} = \text{hunting intensity on juvenile females}$$
$$H_{jm} = \text{hunting intensity on juvenile males}$$
$$H_{af} = \text{hunting intensity on adult females}$$
$$H_{am} = \text{hunting intensity on adult males}. \quad (8)$$

Hunting intensity is the proportion of individuals in a particular stage-sex class hunted, and the survivorship associated with hunting intensity, H_{ik} is $\exp(-H_{ik})$. We adopt this form because it is common in wildlife management and fisheries (e.g., Clark, 1990; Beverton and Holt, 1993) and because it reflects diminishing returns as hunting efforts increase.

The Population Dynamics and the Growth Rate
in the Basic Polygynous Model

We now describe the population dynamics, beginning with adults. Adults of age class a at time t must survive natural mortality and hunting intensity. In addition, adults of age class 1 are represented by the surviving juveniles of class j_{max}. Thus, for $a = 1$

$$A_f(t + 1,1) = \sigma_f(j_{max}) \exp(-H_{jf}) J_f(t,j_{max})$$

$$A_m(t + 1,1) = \sigma_m(j_{max}) \exp(-H_{jm}) J_m(t,j_{max}). \quad (9)$$

Subsequent ($a > 1$) adult age classes are determined by the number of adults surviving from the previous age class, so that for $a > 1$

$$A_f(t + 1,a) = \rho_f(a - 1) \exp(-H_{af}) A_f(t,a - 1)$$

$$A_m(t + 1,a) = \rho_m(a - 1) \exp(-H_{am}) A_m(t,a - 1). \tag{10}$$

Similarly, juveniles of the first IBI class ($j = 1$) are those surviving from the birth class

$$J_f(t + 1,1) = s_f B_f(t)$$

$$J_m(t + 1,1) = s_m B_m(t) \tag{11}$$

and for $j > 1$

$$J_f(t + 1,j) = \sigma_f(j - 1) \exp(-H_{jf}) J_f(t,j - 1)$$

$$J_m(t + 1,j) = \sigma_m(j - 1) \exp(-H_{jm}) J_m(t,j - 1). \tag{12}$$

If there are no differences in survival among age classes, then eqs. 9–12 simplify to dynamics in terms of the total population.

The computation of the birth age class proceeds in three steps. First, we compute the total number of males and females surviving through the time period:

$$A_M(t) = \sum_{a=1}^{a_{max}} \rho_m(a-1)\exp(-H_{am})A_m(t,a)$$

$$A_F(t) = \sum_{a=1}^{a_{max}} \rho_f(a-1)\exp(-H_{af})A_f(t,a). \tag{13}$$

Second, we compute the total reproduction, R, according to

$$R = \sum_{a=1}^{a_{max}} m(a)\rho_f(a)\exp(-H_{af})A_f(t,a). \tag{14}$$

Hence, reproduction is assumed to follow episodes of natural and harvest mortality.

Third, we correct for the effects of the mating system. The fundamental parameters describing the mating system in our model is harem size (see Caswell and Weeks, 1986), loosely defined as the number of females a male can fertilize. The basic model assumes that all females that are in harems reproduce and all adult males can hold harems. Thus, when harem size is h, reproduction will be limited by the smaller of two values: number of females, $A_F(t)$, or the number of females in harems, $hA_M(t)$. That is, all females reproduce if $hA_M(t) > A_F(t)$, and only a fraction, $[hA_m(t)]/[A_F(t)]$, reproduce otherwise. Assuming that neonatal sex ratio is a proportion, r, that is male,

$$B_f(t+1) = (1-r)R\min\left\{1, \frac{hA_M(t)}{A_F(t)}\right\}$$

$$B_m(t+1) = rR\min\left\{1, \frac{hA_M(t)}{A_F(t)}\right\} \tag{15}$$

Note that

$$R \min\left\{1, \frac{hA_M(t)}{A_F(t)}\right\} = \sum_{a=1}^{a_{max}} m(a)\rho_f(a)\exp(-H_{af})A_f(t,a)\min\left\{1, \frac{hA_M(t)}{A_F(t)}\right\}. \tag{16}$$

Thus, if the minimum is 1, eq. 16 is

$$R = \sum_{a=1}^{a_{max}} m(a)\ \rho_f(a)\exp(-H_{af})A_f(t,a) \tag{17}$$

which is the standard linear model for cohort analysis. However, the mating system introduces a nonlinearity via eq. 15. Caswell and Weeks (1986) provide a similar method for incorporating both males and females into cohort analysis using a harmonic mean function instead of the minimum function that we use.

At any time, t, the total population size is

$$P(t) = B_f(t) + B_m(t) + \sum_{j=1}^{j_{max}} J_f(t,j) + J_m(t,j) + \sum_{a=1}^{a_{max}} A_f(t,a) + A_m(t,a). \tag{18}$$

The growth rate of the population is

$$\lambda(t) = \frac{P(t)}{P(t-1)} \tag{19}$$

which may approach a constant λ as time increases if the population is increasing. Because of the nonlinearity due to the mating system, the growth rate changes over time when the population is decreasing. To account for this, we report the average growth rate of the population after 20 IBIs for up to 300 IBIs.

Equations 9–19 constitute the "basic model." We first present results from the basic model, then results of various modifications: fecundity depends on harem size, infanticide, and reproductive suppression. For each modification, we consider a completely protected population and then three different types of hunting: trophy hunting of adult males (hereafter termed "male hunting"), trophy hunting of adults of both sex ("adult hunting"), and hunting of juveniles and adults of both sex ("subsistence hunting"). In order not to confound adding sex and stage classes with increasing harvest intensity, we kept harvest intensity on the population as a whole constant by proportioning harvest to specific stages based on their size. We introduce hunting selectivities $\theta_{ik} = 1$ if a particular sex and age class is hunted and $\theta_{ik} = 0$ otherwise, where i = a or j (adult or juvenile) and k = m or f (male or female). Suppose that the total hunting intensity is H. The total hunted population is

$$P_H = J_F(t)\theta_{jf} + J_M(t)\theta_{jm} + A_M(t)\theta_{am} + A_F(t)\theta_{af} \tag{20}$$

and hunting intensity for each stage-sex class is

$$H_{jf} = H\,J_F(t)\ \theta_{jf}/P_H$$
$$H_{jm} = H\,J_M(t)\ \theta_{jm}/P_H$$
$$H_{af} = H\,A_F(t)\ \theta_{af}/P_H$$
$$H_{am} = H\,A_M(t)\ \theta_{am}/P_H \tag{21}$$

Several assumptions of this model could affect our predictions of the population dynamics. First, the deterministic population approach assumes that values of survivorship and fecundity are constant within a particular age–sex class and that all adult males have an equal probability of obtaining harems independent of age (but see appendix 1). In addition, harem size is invariable, altho**gh we show how this assumption can be partially relaxed below. Because birth class individuals are not tied to specific adults, this model assumes no parental care. In addition, this model assumes no selectivity of hunting mortality within particular age–sex classes. For example, harem-holding males are no more likely to be hunted than males lacking harems.

The discrete time approach assumes that reproduction occurs after natural and hunting mortality and that the rate of harvest mortality is in terms of the interbirth interval. In general, harvest mortality is on a per annum basis, while a particular species may reproduce more or less than once per year. This difference can be corrected by modifying harvest mortality accordingly; hence, if a given species reproduces four times per year, its harvest rate should divided by four to match its reproductive rate.

In the basic model, we assume that sex ratio at birth is 50:50 and $j_{max} = 2$, $a_{max} = 10$. For simplicity of presentation, we also assume that survivorship does not vary for different juvenile or adult IBI classes and that adult fecundity remains constant across different adult age classes. Thus, in the absence of hunting mortality, we still must specify the birth, juvenile, and adult sex-dependent survival and fecundity. For most mammals, males have lower survivorship than females (Clutton-Brock, 1988). We take this into account for juvenile and adult age classes, such that $s_f = s_m = 0.7$, $\sigma_f(j) = 0.8$, $\sigma_m(j) = 0.5$ (for all $j = 1$ to j_{max}), $\rho_f(a) = 0.8$, and $\rho_m(a) = 0.7$ (for all $a = 1$ to a_{max}). We assigned $m(a) = 3$ for all models except reproductive suppression, in which case $m(a) = 10$. All models detailed below were simulated with all cohorts of each sex having 100 individuals at $t = 1$.

Model Results

The Basic Model

In the absence of hunting, the population growth rate for the basic model increases for small harem sizes and levels off at $h = 5$ (fig. 11-1). The lower population growth rates for small harem sizes are the result of the lower survivorship of males. This is due to an Allee effect: there are not enough males to fertilize females when harem size is less than five and male survivorship is low. If survivorship were the same for both sexes, population growth would be equal for all harem sizes (resulting in a straight line). Although the Allee effect controls reduced growth rates for populations having small harems in our model, other mechanisms including absence of necessary paternal care could account for this pattern in reality.

For all methods of hunting ($H = 0.15$), small harem sizes (less than six females) have lower growth rates than large harem sizes, again a reflection of the fact that lower male survivorship results in some females not reproducing when harem size is small. The impact of hunting is particularly evident for monogamous species ($h = 1$), which, as shown in fig. 11-1, decline even in the absence of hunting. Male hunting is especially detrimental to monogamous species because fertilizations are equally limited by males and females. However, male hunting exerts less of an impact on large harem sizes; indeed, it approaches levels of no hunting. In contrast, adult hunting and subsistence hunting slightly reduce growth rates
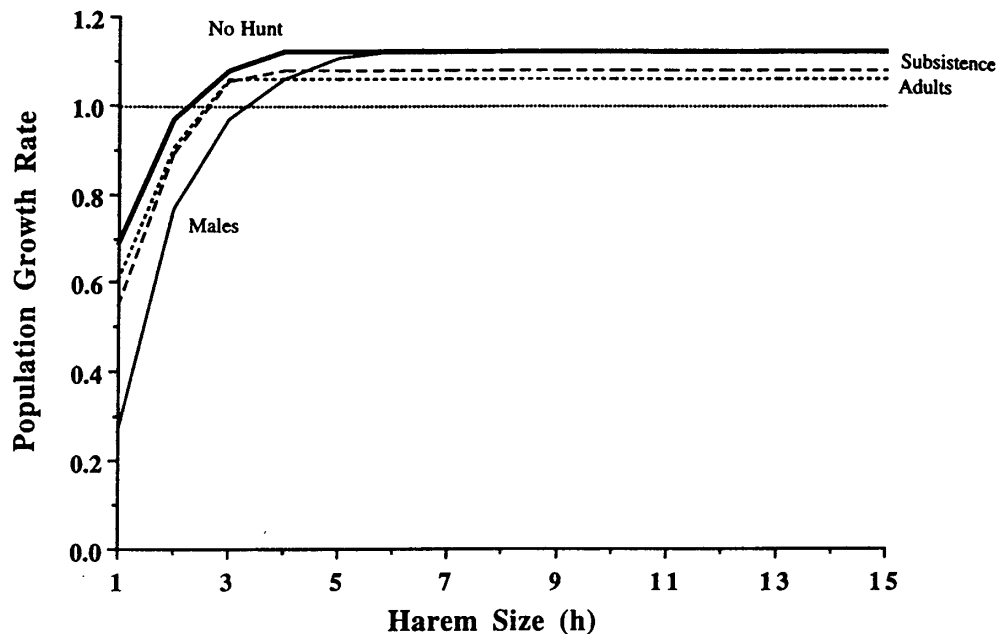
Figure 11-1 Population growth rate as a function of harem size using the basic model when hunting intensity (H) is either zero (no hunt) or 0.15 (all other lines). We consider three different types of hunting: adult males (male), adults of either sex (adult) and juveniles and adults of either sex (subsistence). The dashed horizontal line indicates the boundary between increasing and decreasing population change.

for large harem sizes. Differences between hunting methods are magnified for smaller harem sizes and reduced at larger harem sizes (table 11-2).

When harem size is constant at a moderate size ($h = 5$), male hunting is more sustainable: it has replacement population growth rates over a wider range of hunting intensities than adult hunting and is only slightly less sustainable than subsistence hunting (fig. 11-2). This results primarily because females are less affected when only males are hunted. Note that at this harem size, growth rates are near the maximum for any harem size (compare with fig. 11-1); at smaller harem sizes, male hunting is less sustainable because hunting effort is spread over fewer classes of individuals and because not enough males survive to fertilize all available females for a larger number of harem sizes.

These results have several implications. First, population sustainability depends on the particular breeding strategy and the hunting effort on the population. In particular, while highly polygynous species are relatively unaffected by male hunting, monogamous species are much more susceptible to such hunting. Furthermore, if natural survivorship is lower for males than for females, male hunting will reduce growth rates of monogamous species more than polygynous species. These generalizations depend to some extent upon sex- and age-specific survivorship patterns, sex-specific j_{max} and a_{max}, and age-specific fecundity. For example, results in fig. 11-1 show that monogamous species cannot have positive population growth rates, but if the fecundity and survivorship schedules had higher values, λ could exceed 1.0.

The basic model shows that while different types and intensities of hunting result in different reductions in population growth, harem size affects population growth only for low harem sizes. Figure 11-1 suggests that harem size may change in response to increased mor-

Table 11-2 Effects of different aspects of breeding system and harem size on populations' responses to three types of hunting, shown in order of the greatest population impact to the least impact.

Breeding system	Harem size[a]	Negative effects
Basic polygyny	Small	**Male**>Adult>Subsistence
	Large	Adult>Subsistence>Male
Fecundity depends on harem size	Small	**Male**>Adult>Subsistence
	Large	**Adult**>Subsistence>Male
Infanticide	Small	**Male**>Adult>Subsistence
	Large	**Adult**>Subsistence>Male
Reproductive suppression	Small	Male>Adult>Subsistence
	Large	**Adult**>Subsistence>Male

A hunting method is in boldface when the breeding system is particularly sensitive to it.

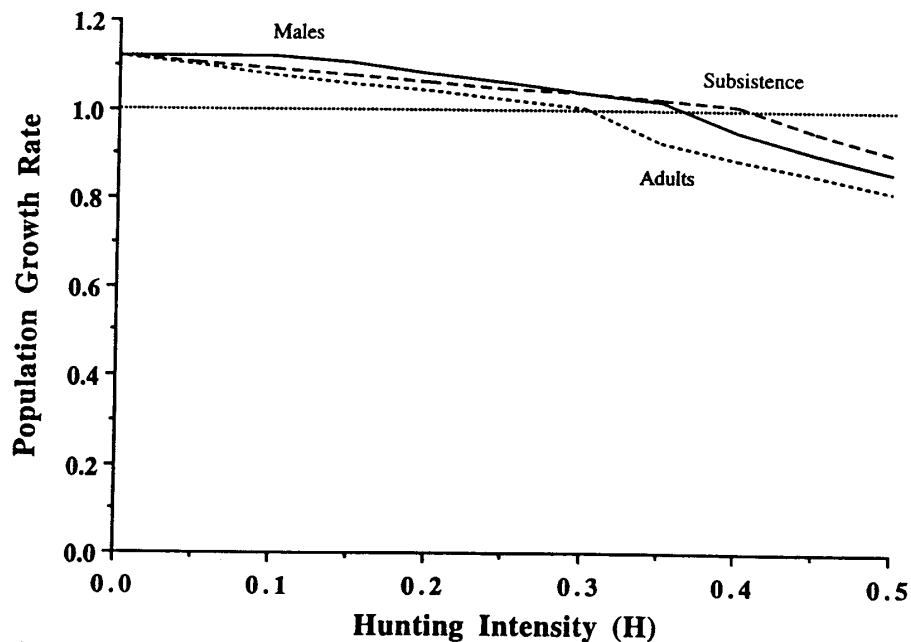[a]Small = < 4 or 5 females, large = > 4 or 5 females.

Figure 11-2 Population growth rate as a function of hunting intensity when harem size is held constant at five females and adult males (males), adults of either sex (adults), and juveniles and adults of either sex (subsistence) are hunted. The dashed horizontal line indicates the boundary between increasing and decreasing population change. Demographic parameters are identical to those used for fig. 11-1.

tality due to the fact that larger harems have higher growth rates. This change depends largely on the variability of the mating system. For the sake of generality, we assume that harem size remains stable, but we recognize that intraspecific variation may result in changes of breeding system (and hence harem size) in response to demographic changes. We now consider variations of the basic model: fecundity varies as a function of harem size, infanticide by males, or reproductive suppression where only one male and one female in a group breed.

Fecundity Depends on Harem Size

Fecundity may decrease in larger harems as females compete for resources or partition effort among other related individuals in the group (Downhower and Armitage, 1971; Armitage, 1986). Declining relationships between fecundity and group size have been noted in a number of species, including marmots *Marmota flaviventris* (Downhower and Armitage, 1971), wolves *Canis lupus* during prey shortages (Harrington et al., 1983), red deer *Cervus elaphus* (Clutton-Brock et al., 1982), and many primates (Van Schaik, 1987). In these and other species for which fecundity varies inversely with harem size, this relationship is likely a case of density dependence. For the purposes of modeling, however, we take a frequency-dependent approach. For species in which fecundity decreases with harem size,

$$\text{fecundity at age } a = m(a)\left(1 - \frac{h}{h_{max}}\right) \tag{22}$$

where h_{max} is the harem size at which no females are reproductive ($h \leq h_{max}$). We use this modification in eq. 15. Demographic parameters are identical to those used in the basic model.

When fecundity declines with harem size (fig. 11-3), the population growth rate is lower than for the basic model, especially at large harem sizes, because of the density dependence in fecundity associated with large harem sizes. In this case, a window of population growth exists, bounded by the lowest harem size at which males can fertilize all females and the largest harem size in which females cease to be productive. As in the frequency-independent case, monogamous species or populations are more sensitive to male mortality than polygynous ones, and if natural mortality is higher for males than for females, a proportionally lower growth rate will exist relative to polygyny. In this case, low degrees of polygyny are most favorable for population growth.

Although the same dome-shaped pattern of population growth rate across harem sizes exists for all hunting methods, the harem size at which hunting is most sustainable varies. For a particular hunting intensity, male hunting is again less sustainable at low harem sizes because many females remain unfertilized, but population growth rates approach natural mortality at high harem sizes. Adult hunting and subsistence hunting become sustainable at lower harem sizes because more females are fertilized, but the existence of fewer females reproducing in the population results in both hunting methods never approaching natural levels, in contrast to male hunting. At a moderate harem size ($h = 5$), subsistence hunting is more sustainable across different hunting intensities than male hunting and adult hunting (fig. 11-4) because the hunting mortality is spread over individuals.
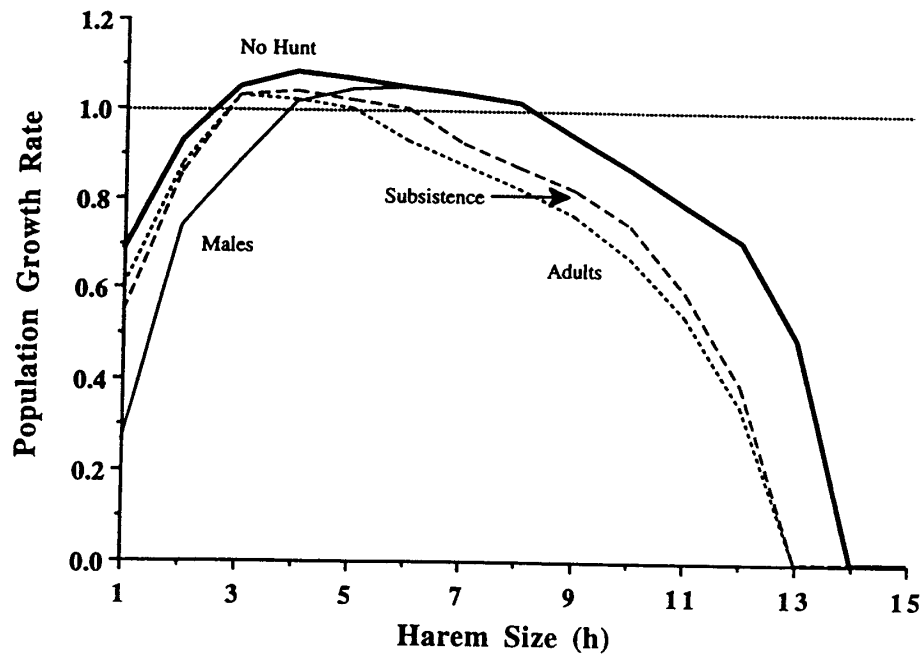
Figure 11-3   Population growth rate as a function of harem size when fecundity varies inversely with harem size and males, male and female adults, or all adults and juveniles (subsistence) are hunted ($H = 0.15$) or when there is no hunting ($H = 0$). The dashed horizontal line indicates the boundary between increasing and decreasing population change.
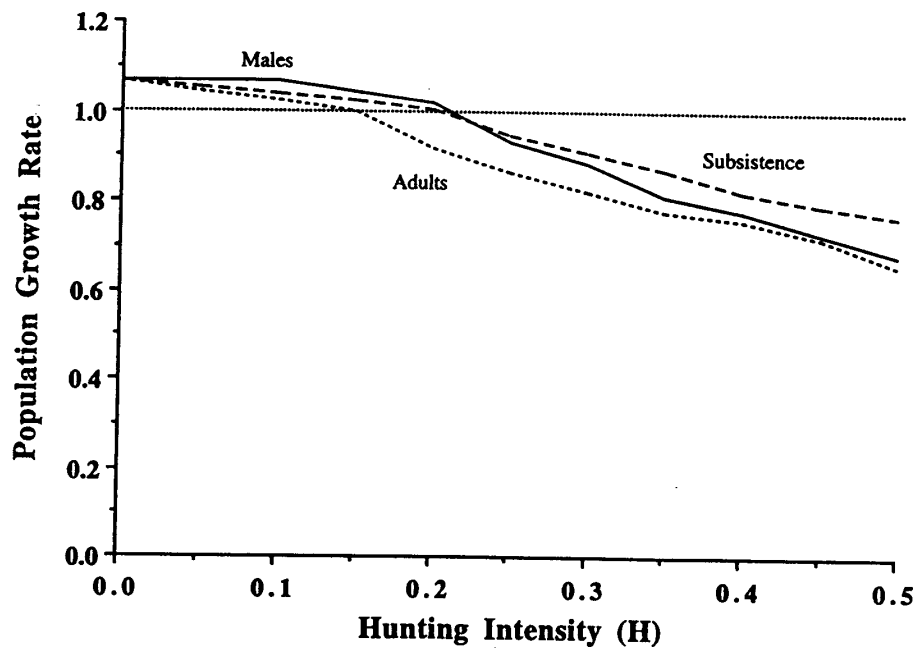

Figure 11-4   Population growth rate as a function of hunting intensity when fecundity varies inversely with harem size and harem size is held constant at five females and there are three different types of hunting. The dashed horizontal line indicates the boundary between increasing and decreasing population change.

Infanticide

In some infanticidal species, the death of a male controlling a harem leads to reproductive failure for that harem because the incoming male kills some or all the infants of the harem (Hausfater and Hrdy, 1984; Parmigiani et al., 1992). Because of this, female reproduction is tied to male survivorship, which is

$$S_M(t) = \frac{\sum_{a=1}^{a_{max}} \rho_m(a)\exp(-H_{am})A_m(t,a)}{A_M(t)}. \tag{23}$$

In this case, we find it easier to separate the analysis into two cases. First, if $A_F(t) > hA_M(t)$, then there is an "excess" of females, in the sense that all males hold harems. In such a case (e.g., when male mortality is extremely high), only a fraction $[hA_M(t)/A_F(t)]$ of the females are reproductive and there is no infanticide, so number of birth class individuals is

$$B_f(t+1) = (1-r)R\frac{hA_M(t)}{A_F(t)}$$

$$B_M(t+1) = rR\frac{hA_M(t)}{A_F(t)}. \tag{24a}$$

However, if $A_F(t) < hA_M(t)$, all females are reproductively active, but the death of a male leads to the loss of the reproduction of all females in that harem, so that

$$B_f(t+1) = (1-r)R\,S_M(t)$$

$$B_m(t+1) = r\,R\,S_M(t). \tag{24b}$$

We assume that survival does not differ within juvenile or adult age classes and demographic parameters are identical to those used for the basic model. In contrast to other models of infanticide (e.g., Starfield et al., 1981; Starfield and Bleloch, 1991), our model assumes that harem holders and nomads have no differences in either natural or hunting mortality.

The effects of harem size on population growth in an infanticidal species are qualitatively similar to those for the basic model. Without a harvest, larger harem sizes generally have higher growth rates, leveling off at four females (fig. 11-5). When harem size is low, population growth is less than two, due mostly to males limiting reproduction. When harem size is greater than two, the population is increasing, and increases in harem size have little effect on population growth. Note that unlike the basic model, the maximum population growth rate occurs at $h = 3$ and levels off at a lower population growth rate thereafter, a result of the change in the birth equation from eq. 24a to 24b.

The effects of hunting on the infanticidal species are qualitatively different from the basic model. Harvests of females and juveniles still reduce population growth as in the basic model, but hunting only males reduces growth rate over all large harem sizes. These patterns contrast with the basic model (fig. 11-1), which shows that at large harem sizes, populations are very resilient to hunting of males. At $h = 5$, hunting males can cause the population growth rate to be greater than in an unhunted population, due to the fact that with moderate hunting of males, there are no extra males and consequently, no infanticide. When harem size is fixed ($h = 5$) and hunting intensity is increased (fig. 11-6), harvest of all adults
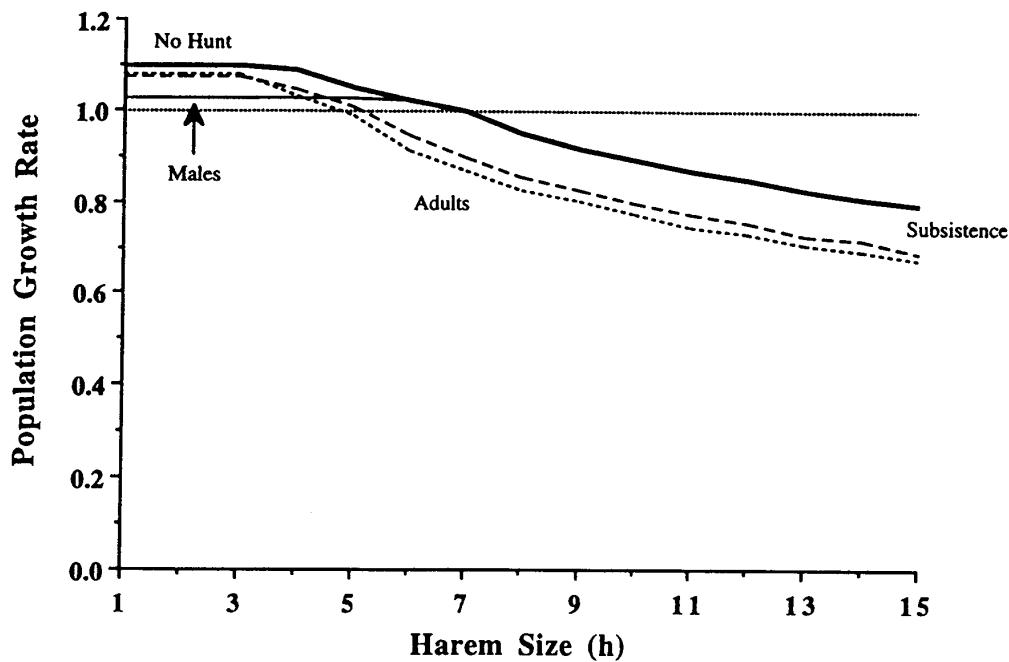
Figure 11-5 Population growth rate of an infanticidal species as a function of harem size when hunting intensity (*H*) is either zero (no hunt) or 0.15 (all other lines). We consider three different types of hunting: adult males (male), adults of either sex (adult) and juveniles and adults of either sex (subsistence). The dashed horizontal line indicates the boundary between increasing and decreasing population change.
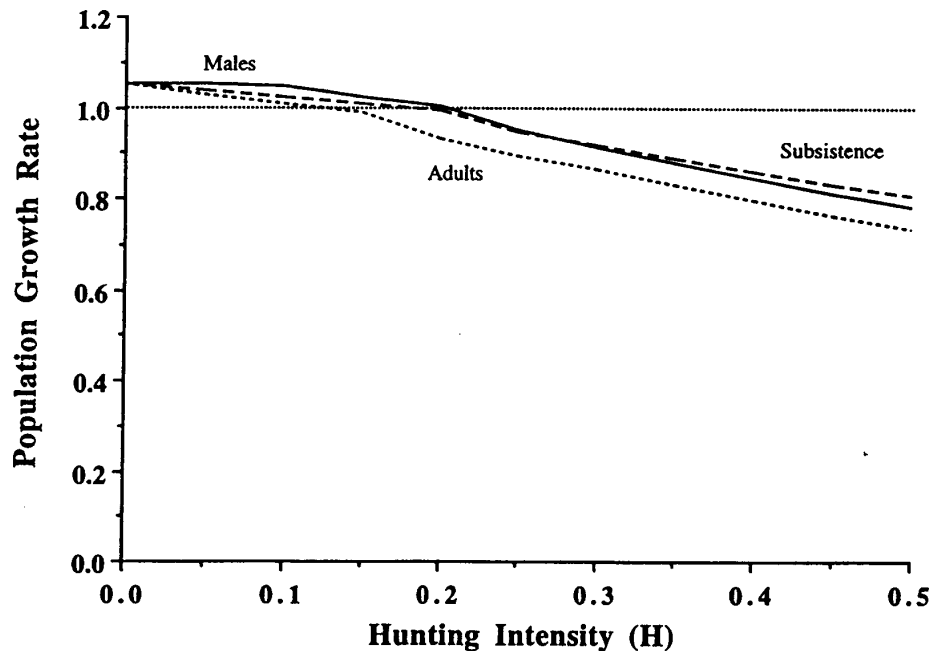

Figure 11-6 Population growth rate in an infanticidal species as a function of hunting intensity (*H*). We consider three different types of hunting: adult males (male), adults of either sex (adult) and juveniles and adults of either sex (subsistence). Harem size is constant at five females. The dashed horizontal line indicates the boundary between increasing and decreasing population change.

285

is the less sustainable than other hunting methods because adult hunting results in populations declining over a wider range of hunting intensity values. This is true because (1) females control fecundity by bearing young and (2) the maximum population growth rate occurs when $A_F(t) > hA_M(t)$ (i.e., there is no infanticide), which is less likely to occur when females are hunted in addition to males. Subsistence hunting is less sustainable than male hunting for similar reasons, although the proportionally lower hunting mortality of females causes subsistence hunting to be more sustainable than hunting of both sexes.

The population dynamics of infanticidal species are changed if there are male coalitions (as in lions) or if takeovers occur without the death of a harem-holding males. These additional factors are discussed in appendix 2.

Reproductive Suppression

In the case of reproductive suppression, only one female in the harem is reproductively active. In such a case, each harem receives only $1/h$ of the potential reproduction. Consequently, eq. 15 becomes

$$B_f(t) = (1-r)R\frac{1}{h}\min\left\{1,\frac{hA_M(t)}{A_F(t)}\right\}$$

$$B_m(t) = rR\frac{1}{h}\min\left\{1,\frac{hA_M(t)}{A_F(t)}\right\}. \tag{25}$$

Note that unlike the basic model, we divide the number of females by harem size to determine the level of reproductive output. We can combine the mating system components into

$$\frac{1}{h}\min\left\{1,\frac{hA_M(t)}{A_F(t)}\right\} = \min\left\{\frac{1}{h},\frac{A_M(t)}{A_F(t)}\right\} \tag{26}$$

Thus, for moderately sized harems, the minimum in eq. 26 is almost certainly going to be $1/h$ unless the survivorship of males is very low. This has important consequences for the effects of harem size on population growth rate and for the effect of different types of harvesting on population growth rate.

In the absence of hunting, the population growth rate decreases monotonically as a function of harem size, falling below one for harems of seven or larger (fig. 11-7). In essence, the effect of reproductive suppression in such large harems is to reduce the number of potentially reproductive females to $1/h$ of the actual number (Caughley, 1994). Moderate hunting ($H = 0.15$) of adult males reduces the population growth rate when harems are small but has little effect for larger harems. On the other hand, including females in the hunt can cause the population growth rate to drop below one at a smaller harem size than if only males were hunted. The pattern for subsistence hunting is virtually indistinguishable from the pattern when all adults are taken.

When harem size is fixed (fig. 8-11), the population growth rate is essentially constant for moderate levels of hunting intensity on only males because it is the female population size that determines the growth rate. However, if females are included in the hunt, then the growth rate drops below one for modest levels of hunting. The implication is that if the harvest is guaranteed to be male only, then the population can sustain a relatively heavy har-
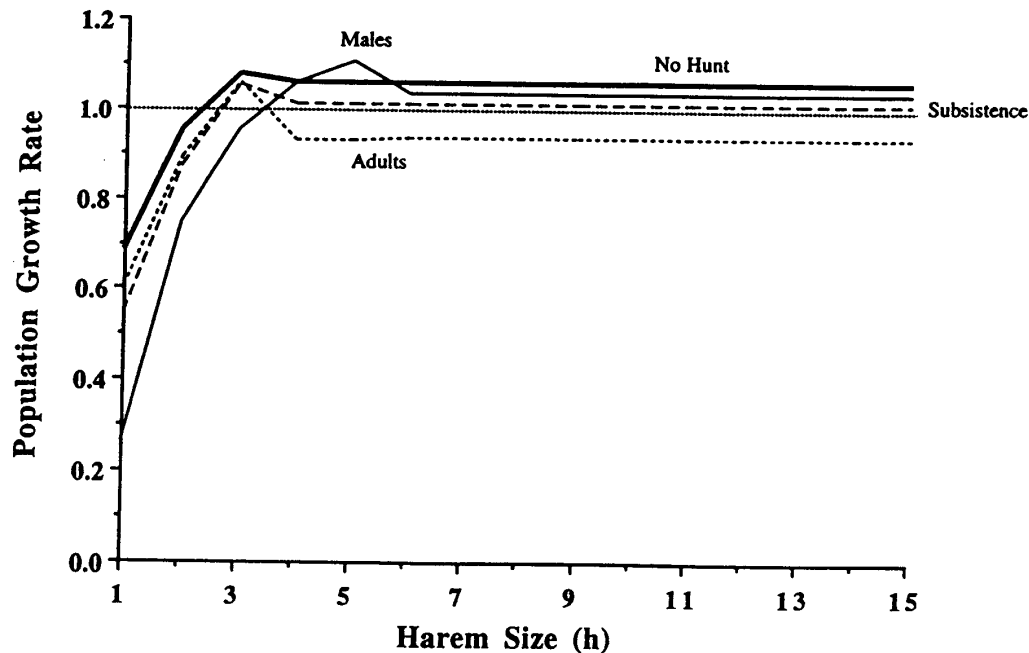
Figure 11-7 Population growth rate of a reproductively suppressed species as a function of harem size when hunting intensity is zero (no hunt) or 0.15. Demographic parameters are identical to those used for fig. 11-1, except that $m(a) = 10$. We consider three different types of hunting: adult males (male), adults of either sex (adult) and juveniles and adults of either sex (subsistence). The dashed horizontal line indicates the boundary between increasing and decreasing population change.

vest. However, if it is impossible to separate males and females in the hunt, then the harvest level must be much lower. For the parameters used to obtain the results shown in fig. 11-8, the harvest on adult males and females must approximate 0.12 to sustain a growth rate > 1. If only adult males were taken, the harvest could be as high as 0.2.

Summary

These models indicate that several breeding system attributes influence the magnitude of a population's response to hunting pressure (table 11-2). The response of the population to hunting pressure may vary greatly depending on the degree of polygyny and the extent of particular life-history strategies (e.g., reproductive suppression). Monogamous and weakly polygynous species are much more susceptible to male hunting than species characterized by large harems. Reduction of fecundity in larger harems results in less rapid population increases than weakly polygynous populations, although patterns for different hunting methods follow the basic model. Infanticide and reproductive suppression reduce the population's ability to withstand hunting, in the first case because loss of harem-holding males results in their replacement by infanticidal males,·and in the second because groups containing many nonbreeders are effectively similar to monogamous situations, which are themselves sensitive to offtake. Depending on harem size, hunting only males or adults of both sexes pose particular problems for infanticidal species with small and large harems, respectively. Even at large harem sizes, hunting adult males still reduces population growth
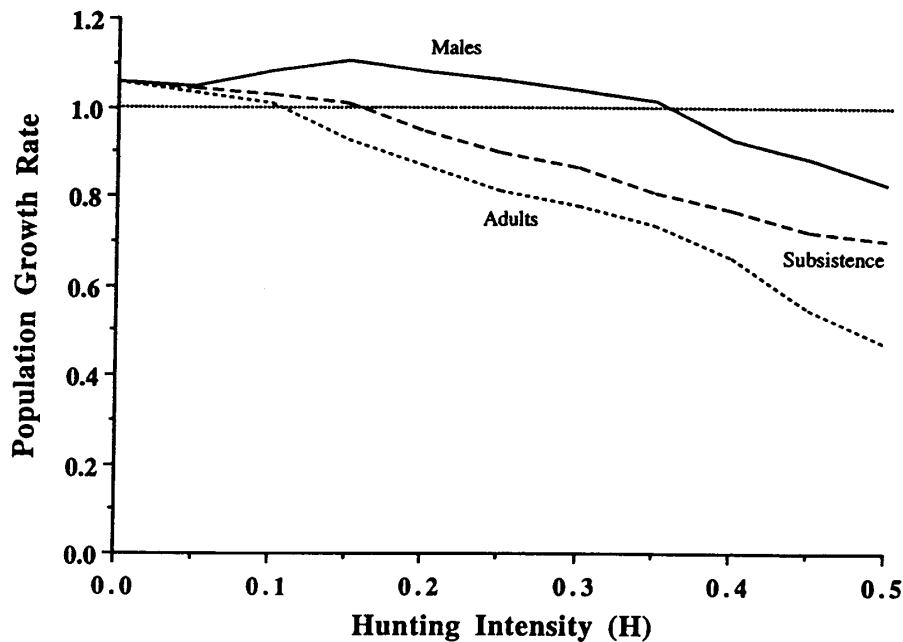
Figure 11-8   Population growth rate of a reproductively suppressed species as a function of hunting intensity (H) when harem size is five females. We consider three different types of hunting: adult males (male), adults of either sex (adult) and juveniles and adults of either sex (subsistence). The dashed horizontal line indicates the boundary between increasing and decreasing population change. Demographic parameters are identical to those used for fig. 11-1, except that $m(a) = 10$.

compared to species lacking infanticide. Hunting adults of both sexes also causes rapid population declines for reproductively suppressed species, but for different reasons: increasing hunting intensity on females may prevent an entire group from breeding if the breeding female is killed.

Applications

We now apply the models to six species of hunted African mammals that have reasonably well-documented demographic parameters and whose breeding systems vary. Although not all these species are regularly hunted (e.g., mongooses and hyenas), use of these species shows how modifications of the basic model can be used for particular animal populations.

Ungulates

Ungulates have an enormous diversity of breeding systems ranging from monogamy in the smaller species (Kleiman, 1977) to polygyny and lekking (Clutton-Brock, 1989; Clutton-Brock et al., 1993). We focus on three species, all of which are hunted only for males, but each having a different breeding system: impala *Aepyceros melampus,* buffalo *Syncerus caffer,* and dikdik *Madoqua kirki.*

Impala are characterized by resource-defense polygyny (Jarman, 1979) in which females form groups that wander between territories defended by dominant males. These

males mate with an average of 15 females per year (Murray, 1982), whereas many bachelors obtain no mates. We calculated a positive growth rate ($\lambda > 1.00$) based on this mating system, litter size of one young per female, and sex- and age-specific survivorship from Murray (1982) with longevity of females lengthened to 15 years (Skinner, 1989). We note that Murray's life-history data, in which female longevity is 10 years, do not produce a positive growth rate and that growth rates in general are extremely sensitive to this parameter.

Given life-history traits that result in a positive growth rate, impala populations could still grow even when adult males were completely hunted because of replacement by juvenile males capable of holding large harems. However, any inclusion of density dependence could make these very resilient populations sensitive to parameter changes. For example, if impala fecundity declines as a function of harem size, populations with large harem sizes generally decline. In addition, our model assumes that newly recruited adult males are equally capable of holding large harems as older males, an assumption that may well be false for polygynous species (Clutton-Brock et al., 1982). This assumption can be relaxed by introducing a parameter into eq. 15 capturing the lack in experience, $E(a)$, of newly recruited males relative to older males (see appendix 1). When this modification is used and hunting mortality, H, is set at 1.0 for all older adult males (all adult males hunted), growth rates become negative at $E(1) = 0.72$. In other words, if newly recruited males could achieve $> 72\%$ the number of matings older males achieve, the population would still increase. Given that new recruits are often much less capable of fertilizing females than are older males (e.g., Poole, 1989), the apparent resilience of the impala population to hunting in our model is misleading.

African buffalo form large mixed-sex herds (Sinclair, 1977; Mloszewski, 1983; Prins, 1996). Dominant males constitute about 10% of the herd and obtain most of the matings (Sinclair, 1977), with an average harem size of 4.4 per male (calculated from Mloszewski, 1983). Based on age- and sex-specific survivorship and average fecundity of 1.0 offspring per adult female per IBI estimated by Sinclair (1977), our population model predicted slightly growing populations ($\lambda = 1.07$) that were resilient to high levels of hunting effort because of high survivorship, the large number of adult age classes, and polygyny. Again, inclusion of density dependence in fecundity or lack of experience of newly recruited males can cause population declines.

Dikdik are small, territorial antelopes that form monogamous pair bonds (Komers, 1996). As shown earlier, monogamous species appear to be at a distinct population disadvantage when males are hunted; therefore, dikdik and other antelope such as duikers (*Cephalophus* spp., *Sylvicapra* spp.), suni *Neotragus moschatus*, and klipspringer *Oreotragus oreotragus* represent an especially interesting set of species to examine. Unfortunately, population data such as age- and sex-specific survivorship are extremely scanty for all these species. Hence, we used an amalgamation of dikdik and klipspringer demographic parameters to estimate population growth rates of dikdik. Dikdik females give birth twice per year (Komers, 1996), and we estimated that offspring have a survivorship of 0.55 using data within the range reported for several klipspringer populations (Dunbar, 1990). Tilson and Tilson (1986) observed that 85% and 69% adult male and female dikdiks, respectively, disappeared from territories over 25 months. As these data do not indicate which age classes experienced this mortality, we assumed this was a population average for adults. Calculations of population growth rates are further complicated because the number of juvenile and adult age classes and juvenile survivorship are unknown. We constructed age-specific survivorship by assuming no juvenile age classes, that adults lived up to 6 years, and that adult age-specific survivorship was high for both sexes over the first 2 years

of life ($\rho_f = \rho_m = 0.9$) and correspondingly lower at the remaining four age classes ($\rho_f = 0.36$ and $\rho_m = 0.16$). When the population age structure is taken into account, the average adult survivorship for the entire population closely matches the values reported by Tilson and Tilson (1986). These designations resulted in a slightly larger than replacement population growth rate ($\lambda = 1.01$).

Spotted Hyenas

Spotted hyenas *Crocuta crocuta* group in large clans of multiple males and females, with a few dominant males mating with the females (Frank et al., 1995). Even though the number of males per group is high, the harem size per male is still rather large (8–12) because most males in the group do not mate (Frank, 1986). Female spotted hyenas have high levels of androgens compared to other mammals, and as a result are dominant over most males and have masculinized genitalia (Frank, 1986). Because of these characteristics, it is difficult to distinguish male and female hyenas in the field, and as a result, individuals of both sexes are often shot.

As in most carnivore studies, collecting demographic data for both sexes has been difficult because male dispersal cannot usually be distinguished from death. Kruuk (1972) and Hofer and East (1995) nevertheless suggest a relatively constant mortality rate of 13% and 15% for males and female adults, respectively. We combined these estimates with known infant siblicide of 30% for the common litter size of two (Frank et al., 1995) to construct a life table for both sexes. Using these data, we estimate population growth rate of 1.03.

Lions

We adjusted the model with infanticide to fit the form of the data for lions in Packer et al. (1988). In particular, published data on fecundity and mortality of cubs generally include the effects of infanticide that occur in the population. Therefore, we could only model the additional infanticide that would occur with hunting of a population. We modified eq. 23 to reflect additional infanticide caused by hunting by multiplying total reproduction by $\exp(-H_{am})$, which reflects the change in survivorship as a result of hunting. We found that the population has a positive growth rate with no hunting ($\lambda = 1.10$) and that growth rate declines but remains 1.0 up to a harvest mortality of about 19% of the male population. This is equivalent to approximately 6% of the entire population due to the female-biased adult sex ratio. These models assume there is no population response to harvesting other than total changes in numbers of individuals. It is nevertheless known that lions produce male-biased sex ratios in larger litters (Packer and Pusey, 1987), and recent data indicate that populations of lions hunted for males produce an excess of male cubs (Creel and Creel, 1997). Incorporating this response into the model would substantially reduce the number of male lions that could be sustainably harvested (from 19% down to 12% with a natal sex ratio of 0.55) because the population would quickly become limited by females. Furthermore, male lions usually control harems in coalitions of individuals (Packer et al., 1988), and sustainable offtake is much reduced when this factor is incorporated in the model (appendix 2).

Dwarf Mongooses

Dwarf mongooses show strong reproductive suppression (Rood, 1980, 1990). We used data in Waser et al. (1995) in the model of reproductive suppression but made two changes. First,

we assumed that total reproduction is determined by the number of females at the start of interval t, rather than the number of surviving females. Hence, we modified eq. 14 to

$$R = \sum_{a=1}^{a_{max}} m(a)\exp(-H_{af})A_f(t,a).$$ (27)

Second, in order to use the empirical values for $m(a)$ (Waser et al., 1995), we recognize that the reported fecundities include the effect of reproductive suppression in harems. Consequently, we used the birth class equations of the basic model (eq. 15) instead of eq. 25. We assume that the harvest includes adults and juveniles of both sex. For our analyses, we assumed that only dominant individuals breed. Although both subordinate males and females occasionally breed (Keane et al., 1994), relaxing the above assumption (see Creel, chapter 10, this volume) effectively changes harem size from nine to eight females and hence has little effect on population growth rates. Our result is that $\lambda > 1.00$ as long as $H < 0.1$.

Hunted Populations in the Selous Game Reserve

We used the data on population growth rates to calculate rates of sustainable offtake for the six species described above in the Selous Game Reserve in Tanzania. Table 11-3 shows estimated population sizes for each species in the 41,245-km² area of the Selous Game Reserve, over which species were counted or estimated. Table 11-4 gives annual hunting levels and the percentage of the population that is legally hunted by tourists.

Ungulates were resilient to tourist hunting levels in the Selous Game Reserve, with the particular exception of monogamous antelope. Buffalo and impala have large harems and a relatively low hunting intensity in the Selous which prevent tourist hunting from having a significant impact. Current hunting effort (i.e., number of animals taken) is well below that which their population could sustain assuming no additional offtake through illegal

Table 11-3 Estimated population size of species in the Selous Game Reserve.

Species	Mating system	Estimated total adult population size	Estimated hunted population size[a]	Reference for population size
Impala	Highly polygynous	32,287	10,762[b]	Caro et al (in press a)
Buffalo	Mildy polygynous	69,219	23,073[b]	Caro et al (in press a)
Small antelope	Monogamous	436[c]	218[b,c]	Caro et al (in press a)
Spotted hyena	Highly polygynous	13,198	13,198	Creel and Creel (1996)
Lion	Polygynandrous and infanticide	4,537	1,747[b]	Creel and Creel (1996)
Dwarf mongoose	Monogamous and reproductive suppression	138,171	138,171	S. Creel (personal communication)

[a]Based on published estimates of adult sex ratios.
[b]As only adult males are hunted, these numbers represent the estimated number of adult males in the reserve.
[c]Estimated population size for all small antelopes (dikdik, duikers, oribi, klipspringer, and steenbok). Because these cryptic species are difficult to count in aerial censuses, the population size is certainly a great underestimate.

Table 11-4   Hunting parameters of species hunted in the Selous Game Reserve.

Species	Stage and sex hunted	Average offtake/year[a]	Hunting Mortality (%)[b]	Will legal offtake cause decline?
Impala	Adult males	118	1.10	No
Buffalo	Adult males	163	0.71	No
Small antelope	Adult males	46	21.10	Yes
Spotted hyena	Adult males and females	17	0.13	No
Lion	Adult males	42	2.40	No
Mongoose	Adult males and females	10[c]	0.01	No

[a]Derived from individuals legally shot between 1988 and 1992, from Caro et al. (in press b).
[b]Mortality is expressed as percent of stage and sex hunted per year.
[c]Estimated, based on information from S. Creel.

hunting. Small antelope populations were greatly affected by even slight changes in hunting effort; hunting effort of approximately 21% (that occurring in the Selous; see table 11-4) reduced population growth rates to < 1.0 (λ = 0.52). In fact, mortality rates > 1% cause populations to drop below replacement growth. Although these results may stem from lack of accurate demographic data and from seriously underestimating population sizes of small antelopes during aerial censuses, it is clear from the models that monogamous species are particularly sensitive to male offtake.

All three carnivore species modeled maintained positive growth rates under current Selous hunting levels. For spotted hyenas, our calculations indicate that hunting both sexes at hunting effort > 1% of the adult population will cause the population to decline. Thus, our model suggests that spotted hyenas are currently hunted at very conservative levels in the Selous. Dwarf mongooses live at high densities and are rarely hunted in the Selous. These two factors mean that offtake is far below what the population could sustain.

Lions live at relatively low densities compared to ungulates and are subject to reasonably strong hunting pressure. Nevertheless, our model suggests they can withstand current levels of hunting. These results run contrary to earlier findings which suggested that lions were being hunted at high levels throughout Tanzania (Caro et al., in press b) and that quotas in the northern part of the Selous were set too high (Creel and Creel, 1997). Modeling efforts by Starfield and Bleloch (1991), Starfield et al. (1981), and Venter and Hopkins (1988) predict that hunting harem-holding males increased infanticide and led to much lower population growth rates. Our model does not differentiate between harem-holding and bachelor males, and therefore harvest is proportioned to them according to their relative population sizes. If harem-holding males are actually more easily detected by hunters than nomads due to their association with prides, they may suffer a disproportionate amount of hunting, thereby reducing population growth. However, common hunting practices in which males are shot at bait stations may actually take harem holders and bachelors in proportion to their availability as assumed by our model.

In summary, our models suggest that these animals are being removed conservatively and therefore, from a conservation standpoint, are being hunted appropriately. The important exception is the hunting of small antelope, which may be sustainably hunted only if population estimates (table 11-3) are too small by a factor of at least 20. Our analyses are at a large scale because data on ungulate populations sizes were available only for the whole reserve, which forced us to combine hunting levels in different areas into one figure. At a small scale, it is known that hunting pressures differ according to region in the game re-

serve, with the eastern and northern section having a long history of sustained hunting pressure. Although our analyses examined only six species of mammals, it appears that tourist hunting in the Selous is an effective conservation tool because it generates substantial revenue for the Tanzanian government and occurs at levels that appear sustainable despite the different forms of hunting and variability of breeding systems in hunted species. We hesitate to recommend large increases in hunting intensity that our models suggest are possible for reasons that we discuss below.

Discussion: Strengths and Weaknesses of the Models

In this chapter we used a modeling approach to examine the impact of different types of hunting on animal populations and to investigate how breeding system modifies a population's ability to withstand hunting pressure. Models force one to formalize the logic of the relationships between the given parameters. Doing so may lead to unanticipated conclusions that are relatively straightforward after the fact. For example, the susceptibility of monogamy to male trophy hunting is a result that has long been overlooked by managers. The models we present are extremely flexible in that they are amenable to the numerous behavioral and life-history variations that complicate the population dynamics of real organisms. Other complications, such as environmental stochasticity and density dependence, could be incorporated to address the particular system that a researcher or manager is interested in modeling. Because the aim was to highlight the generality and flexibility of our approach, we did not explore the depth to which our model can be applied to population dynamics, but we encourage others to test its limits.

The problem of predicting natural population changes has been a continual challenge for biologists. These problems are further complicated by human-induced effects such as hunting. We argue that single-sex models do not characterize population dynamics very well because they do not take into account population-level effects of breeding systems and because current hunting practices may be targeted at different age–sex classes, and often those that are not incorporated into single-sex models. For example, a classical life-table model of lions not incorporating male hunting would be particularly egregious because it ignores consequences of the removal of harem-holding males (leading to infanticide) and because it ignores the number of available breeding males. While our model predicts that in such circumstances approximately 19% of adult males can be sustainably hunted, a naive life-table model would predict a much larger offtake without serious consequences. The need to examine population changes in terms of the dynamics of both sexes has been suggested by others (Beddington, 1974; Beddington and May, 1980; May and Beddington, 1980; Starfield et al., 1981; Starfield and Bleloch, 1991). These researchers have shown that population growth rates can be affected by changes in male and female availability and hence the operant sex ratio. In addition to effects caused by changes in sex ratio, our results reveal that the specific breeding system can play a critical role in population growth rates.

Our first result is that hunter selectivity at a given offtake level can be important. In particular, except for the case of reproductive suppression, we found that as hunting intensity increases, offtake of males or all adults causes a population to decline earlier than when offtake is spread over all juvenile and adult age and sex classes. Second, the models show that different types of hunting may have contrasting effects, depending on aspects of the breeding system. Monogamous and weakly polygynous species were more susceptible to hunting of males than strongly polygynous species, and species exhibiting reduced fecundity at

large harem sizes were more affected by hunting adults of both sexes than species for which this characteristic does not apply. Infanticidal species and reproductively suppressed species with moderate to large harem sizes were radically impacted by adult hunting, but could sustain higher intensities of hunting if hunters were able to select only males. These results suggests that other breeding systems not modeled here such as polyandry, polygynandry, protandry, and protogyny (see Vincent and Sadovy, chapter 9, this volume) need to be explored in a similar fashion. In particular, the effects of mate choice and alternative mating strategies on population growth rates in the face of hunting pressure need investigation. For example, if females are particularly choosy, populations may decline faster because the effective population size of males is much smaller than the actual size (see appendix 1).

Because our models lack certain complications, their application may not be appropriate for all conservation situations, and the models may require modification. First, density dependence can be important in exploited populations (Milner-Gulland, 1994; Milner-Gulland et al., 1995). In Tanzania, for example, population sizes of some mammals hunted in game reserves are high, matching those found in national parks (Caro et al., in press a). Density dependence could be added to the model if needed. For example, one version of our own models incorporating harem size dependence of fecundity involved a simple change of fecundity from an absolute value to a function of harem size. Although this change is technically a frequency-dependent change (because number of females in a harem, not female density, varies), true density-dependent modifications could be similarly added. In addition to fecundity, density dependence has been hypothesized to increase juvenile mortality, adult mortality, and even interbirth interval, and hence could have important population-level effects, especially when human harvest is considered (Beddington and Basson, 1994). However, density dependence should be tailored based on the specifics of the particular species; while inclusion of density dependence may make a model more realistic, it also makes it highly system specific.

Second, individual condition, which is averaged out in population-level models like ours, may have a large impact on population dynamics. For example, wounded individuals in hunted populations may survive but subsequently fail to breed. Other individual-based characteristics, such as alternative mating strategies, may be difficult to incorporate in our models (but see appendix 1 for an example of how age can be correlated with male mating success).

Third, the spatial structure of populations may be important. Many of the species favored by tourist and subsistence hunters live in groups and more than one individual is killed when a group is encountered, especially in the case of subsistence hunting. Selective removal of certain types of groups (bachelor males or harems) will affect a population's response to offtake. For example, female elephants in herds find it difficult to locate solitary roving males in heavily poached areas (Dobson and Poole, chapter 8, this volume). In addition, populations may become fragmented in multiple-use areas as regions of heavy exploitation expand around settlements (Alvard, chapter 17, this volume).

Fourth, random events, especially in small populations, could have large impacts on the sustainability of the population. This could be included in a straightforward manner by using frequency distributions for survivorship and then using Monte Carlo simulation to compute statistics for the population growth rate. In addition, several parameters in our model, especially harem size, fecundity, and survivorship, might be better characterized by distributions rather than mean values due to skewed reproductive success and survivorship in many polygynous species.

Our models are relatively data rich, and in applying them we found it difficult to obtain relevant demographic parameters. While age at first breeding and interbirth intervals were available from zoo and field records, survivorship curves for males and females, age-specific fecundity, and harem sizes had to be gleaned from field studies and were often unavailable. Indeed, our choice of species was in part restricted by the lack of high-quality, long-term field studies. We expect that similar difficulties would be faced in applying models to exploited mammals outside the tropics. Clearly, detailed life-history information is needed to make valid predictions of population dynamics that can be applied to real populations, although simplifications of our model are possible, as we have shown.

We were forced to make additional assumptions to apply the models to the Selous Game Reserve. First, we used reproductive data from populations studied in protected areas where exploitation is reduced (but see Hofer et al., 1993). The extent to which population parameters vary in different parts of a species' range and the influence of hunting on these parameters is recognized but poorly understood. The fact that hunted populations of lions produce male-biased sex ratios among cubs, (Creel and Creel, 1997) shows that this variation is likely to be important. Second, we assumed that sources of mortality in study populations from which reproductive data were obtained were the same as those in areas of exploitation, but this is unlikely. Poaching pressure is low in most protected areas but in multiple-use areas that are not protected by guards, poaching is higher (Caro et al., in press a), and this additional offtake will affect recruitment. While this may have relatively little impact on abundant populations, it could seriously impact species living at low density. In light of these assumptions, it seems prudent to conduct sensitivity analyses in future models that incorporate additional offtake by legal hunters and poachers and that allow for biologically sensible population responses to hunting pressure (Hilborn and Mangel, 1997). Other hunting practices, such as the culling of entire herds, should also be modeled.

Finally, these models consider the effects of hunting on animal populations alone. Tourist hunting is a large revenue source for many countries (Cumming, 1989), and the type of recommendations made and the degree to which they are implemented depend on the worth of individual animals removed from the population. For example, in Tanzania, lions and buffalo are critical species to tourist hunting; lions generate more than 12% of hunting revenue per annum (Creel and Creel, 1997). Incorporation of economic returns into models would have important effects on decision making. In particular, managers need to face the decision about how close to the boundary $\lambda = 1.00$ they are willing to operate for larger economic gain. When parameters vary, operating close to the boundary may bring in more revenue over the short term but could lead to long-term catastrophe.

Recommendations

A number of practical recommendations emerge from these findings. For moderately polygynous species, hunting that focuses on either males or on adults of both sexes has a greater effect on populations than hunting of all age–sex classes if hunting is carried out at high intensity (figs. 11-2, 11-4). Because tourist hunting is less sustainable than subsistence hunting from a population perspective, tourist hunting quotas should be set at a lower level than subsistence hunting quotas. However, as shown by our models, polygynous species with large harem sizes are more resilient to male trophy hunting than species with small harem sizes (figs. 11-1, 11-3). If managers lack specific demographic information but can influ-

ence quota limits for particular species, managers should curtail male trophy hunting of mongamous or weakly polygynous species and favor hunting of strongly polygynous species.

Furthermore, the decision to hunt either adult males or adult males and females is important in infanticidal and reproductively suppressed species. For both types of breeding systems, our conclusion that male hunting has less impact on population growth rates than hunting both sexes has important management consequences. In Tanzania, for example, male and female leopards *Panthera pardus* are sometimes shot because hunters find it difficult to distinguish the sexes. In contrast, only male lions are shot. Since both species are infanticidal (Caro and Durant, 1995), our model suggests that leopard populations are likely to suffer a greater reduction in growth rates than lion populations for a given number of hunting quotas (figs. 11-5, 11-6). As detailed studies of leopard demography are lacking, we recommend that tourist hunting of this species should be reduced to low levels until such data have been collected and evaluated.

Our models also suggest where future monitoring efforts should be directed. Monogamous and weakly polygynous species are particularly sensitive to hunting. Hence, we recommend that species in Africa with these breeding systems such as dikdik, klipspringer, oribi *Ourebia ourebi,* duiker, and reedbuck *(Redunca* spp.) should be monitored carefully in multiple-use areas. This will necessitate increasing use of ground counts rather than aerial surveys, which often fail to discern these species from the air (Caro et al., in press c). As noted above, infanticidal species that are hunted for both sexes should also be closely monitored.

Summary

Effectiveness of multiple-use areas as a conservation tool depends on harvesting populations sustainably. We incorporated mating systems into age- and stage-structured models to assess populations' responses to different types of hunting under different types of breeding systems. Hunting that removed either adult males or adults of both sexes reduced population growth rates at lower hunting intensities than did hunting of adults and juveniles of both sexes. Monogamous and weakly polygynous species were more sensitive to hunting offtake than strongly polygynous systems, although if fecundity declines with harem size, strongly polygynous species will have lower growth rates than weakly polygynous ones. Infanticidal species and reproductively suppressed species were particularly sensitive to offtake of adult males and females.

Models were applied to populations of polygynous spotted hyenas, impala, and buffalo, to monogamous small antelopes, infanticidal lions, and reproductively suppressed dwarf mongooses. Positive growth rates were predicted when empirical reproductive parameters were used in the model. Data on population growth rates were used to calculate sustainable offtake for these species in the Selous Game Reserve in Tanzania. Results showed that current tourist hunting levels there are conservative for most species. The modeling approach allows for the incorporation of mating system and life-history attributes into demographic analysis and can track interactions of such attributes and effects of different hunting methods. Our models do not include density dependence, physiological condition, or economic parameters, although in certain cases these variables could be added. The models may be difficult to apply to real-life situations because long-term demographic variables are available for only a few species. Nevertheless, our models do allow us to make recommenda-

tions about changing the form of hunting of certain infanticidal species and increasing the monitoring of monogamous species.

Appendix 1: Mate Choice and Intrasexual Competition

In many species, females choose mates among available males. Hence, although a particular male may be capable of breeding, it may actually achieve no matings because it lacked experience or capabilities that made it desirable to females. Such experience is age dependent in many species; older males achieve most of the matings, whereas younger males often have low reproductive success (Poole, 1989). This mating bias also is caused by intrasexual competition; very young and very old males may be excluded from mating by dominant, intermediately aged males.

These constraints could have population consequences. For example, our model of impala populations predicts that even when all adult males in the population are hunted in an interbirth interval, the population would be able to sustain itself because newly recruited juveniles could mate with all females in harems. In reality, female choice and lack of experience by these males would likely curtail the number of matings.

One way to model experience is to introduce a new parameter into the equations calculating number of birth-class individuals. Let experience, $E(a)$, represent the proportion of females in a harem that an adult male in age class a can actually fertilize, where $a = 1 \ldots a_{max}$. The appropriate modifications to the basic model are as follows. Because $E(a)$ affects the breeding system in an age-specific manner, experience is incorporated in the minimum rule of eq. 15:

$$B_f(t+1) = (1-r)R \min\left[1, h\frac{\sum_{a=1}^{a_{max}} E(a)A_m(t,a)}{A_F(t)} \right]$$

$$B_m(t+1) = r\,R \min\left[1, h\frac{\sum_{a=1}^{a_{max}} E(a)A_m(t,a)}{A_F(t)} \right]. \tag{28}$$

In the basic model, males are excluded when all harems are filled, but this exclusion is age independent. $E(a)$ weights the degree to which males of particular age classes are able to obtain harems and hence are included in the effective population.

Inclusion of experience has the effect of reducing population growth rate, depending on hunting mortality. Table 11-5 shows a manipulation of the impala population model that incorporates experience: $E(1)$ varies from 0.1 to 0.9 and is 1.0 for all other adult age classes. Thus, newly recruited adult males need one IBI to achieve full reproductive competency and are only a fraction as capable during their first breeding season. At high levels of hunting mortality (40% or higher), the impala population slowly declines when $E(1) < 0.5$. Experience should be regarded as a continuous trait that generally increases across age

Table 11-5 Population growth rate as a function of hunting mortality and $E(1)$, the experience of newly recruited adult males.

Hunting mortality	$E(1)$			
	0.2	0.4	0.6	0.8
0.3	1.000	1.000	1.000	1.000
0.4	0.969	1.000	1.000	1.000
0.5	0.955	1.000	1.000	1.000
0.6	0.946	1.000	1.000	1.000
0.7	0.937	1.000	1.000	1.000
0.8	0.932	0.964	1.000	1.000
0.9	0.928	0.954	1.000	1.000
1.0	0.924	0.947	0.970	1.000

groups. Consequently, the population growth rates reported in table 11-5 are probably too high. In general, a negative correlation between average harem size in a species and variation in $E(a)$ is expected because of increased mate choice and intrasexual competition that accompanies polygyny (Trivers, 1972). Measuring such parameters could be accomplished by comparing harem sizes, and perhaps more importantly, number of fertilizations, of adult males of different age.

Appendix 2: Infanticide Revisited

In the interest of brevity and generality, the initial model of infanticide only included a minimum of details concerning infanticide's population effects. Applying the model to lions revealed several ways that the model could accommodate added complexity. Lion males occur in coalitions of up to seven males (Packer et al., 1988). Adding coalitions alters the dynamics of infanticide in two ways. First, because more than one male controls a harem, a death does not lead automatically to a takeover and subsequent infanticide. Second, more males are tied to harems, so that each mortality has a higher chance of affecting a harem. We added two parameters to the model to accommodate male coalitions: c is the coalition size, and p is the probability that a death leads to a new coalition taking over a pride. In this case, assuming a linear relationship between mortality and probability of takeover, we replace eq. 24b with

$$B_f(t + 1) = (1 - r) R \{1 - pc[1 - S_M(t)]\}$$

$$B_m(t + 1) = r R \{1 - pc[1 - S_M(t)]\}. \tag{29}$$

We used data from Bygott et al. (1979) on how length of tenure changes between lion coalitions of different sizes to make a rough estimate of p. Using the data they presented, we estimated the probability that a coalition of a given size would survive one IBI after a hunting mortality. We then used data from Bygott et al. (1979) on the relative number of various sized coalitions to create a weighted mean of these probability over all coalition sizes. Using this estimate ($p = 0.75$), we obtained a value of 10% male hunting mortality (approximately 3% of the adult population) as the maximal offtake in the Selous before the lion population

will decline. This lower value compared to the simpler infanticide model suggests that the existence of male coalitions can make a population more susceptible to decline in the face of hunting mortality. Nonetheless, this value exceeds the 3–4% that Creel and Creel (1997) suggest is sustainable offtake in the Selous.

In many infanticidal species, infanticide also occurs when a bachelor male (or coalition, in the case of lions) displaces the harem-holding male (Hausfater and Hrdy, 1984). Undoubtedly, higher numbers of bachelor males (non–harem-holding males) will cause higher the rates of takeover attempts and subsequent infanticide. To predict how the relative number of males to females affects the rates of infanticide, consider a population that has A_F/h harems and A_M males, where there are $(A_M - A_F/h) = B$ bachelor males that do not hold a pride. If each male attempts on average τ takeovers per IBI and the attempts are evenly spread across all harems, then an individual harem faces $\{B/[A_F(t)/h]\}\tau$ turnover attempts, which simplifies to $[Bh\tau/A_F(t)]$. Furthermore, if each attempt succeeds with probability i, then a harem is held with probability $(1 - i)^{Bh\tau/A_F(t)}$. The resulting replacement to Eq. 24b is

$$B_f(t + 1) = (1 - r) R (1 - i)^{Bh\tau/A_F(t)}$$

$$B_m(t + 1) = r R (1 - i)^{Bh\tau/A_F(t)}. \tag{30}$$

Using the same parameter values as before and setting τ, the number of takeover attempts per male per IBI $= 1$ and the takeover probability $i = 0.15$, we simulated population dynamics using this model (fig. 11-9). The most obvious qualitative effect is a decline
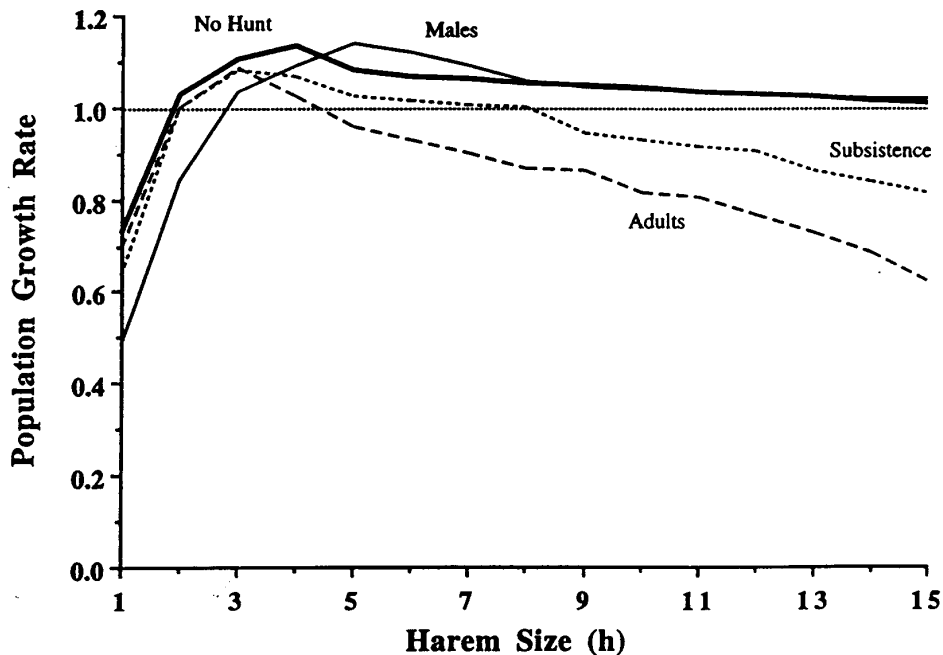

Figure 11-9   Population growth rate of an infanticidal species as a function of harem size when hunting intensity (H) is either zero (no hunt) or 0.15 (all other lines), and when $\tau = 1$ and $i = 0.15$ (see text for details). We consider three different types of hunting: adult males (male), adults of either sex (adult) and juveniles and adults of either sex (subsistence). The dashed horizontal line indicates the boundary between increasing and decreasing population change.
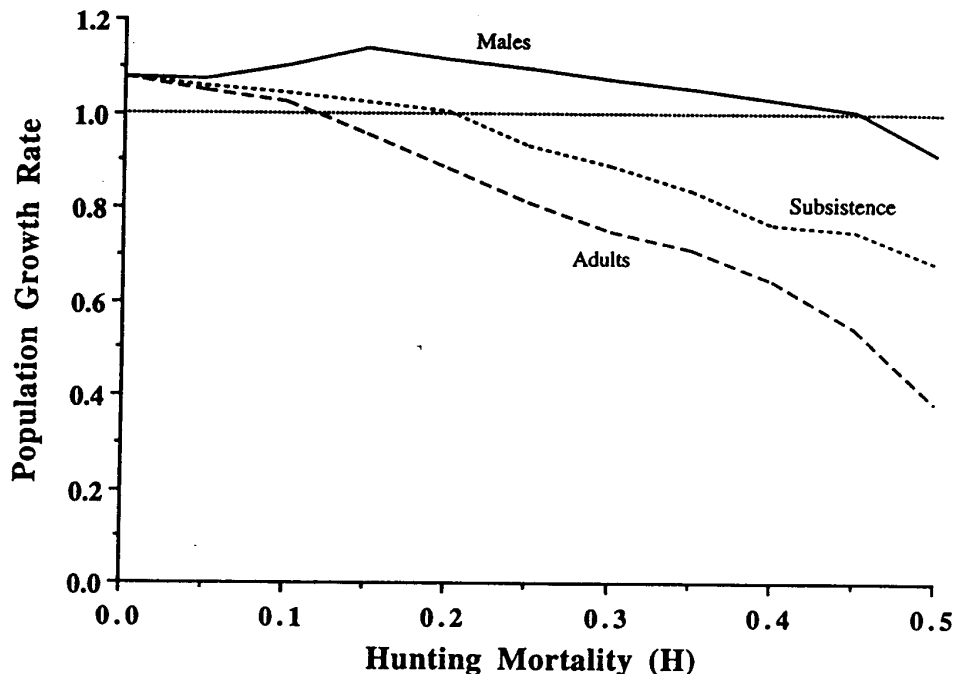
Figure 11-10 Population growth rate in an infanticidal species as a function of hunting intensity. Harem size is constant at five females, and $\tau = 1$ and $i = 0.15$ (see text for details). We consider three different types of hunting: adult males (male), adults of either sex (adult) and juveniles and adults of either sex (subsistence). The dashed horizontal line indicates the boundary between increasing and decreasing population change.

in population growth rate after harem size is greater than three or four females. At larger harem sizes, many males do not hold harems and increase the rate of takeover and subsequent infanticide. The effect of hunting (fig. 11-10) is qualitatively different from when infanticide only occurred after the death of the harem-holding male. Hunting of males is actually more sustainable than any other type of hunting, and in some cases may increase population growth rate. In this case, additional hunting reduces the large number of extra males, thereby reducing takeovers and infanticide. This result agrees with those of Starfield and Bleloch (1991), who showed that culling nomadic males led to increases in population growth (see also Venter and Hopkins, 1988). These results should be interpreted cautiously because the choice of values for τ and i were arbitrary. The actual dynamics of infanticide in the field have been difficult to analyze: it is rare to witness a takeover, and the results of the takeover are somewhat ambiguous (Packer and Pusey, 1984). However, this model can be used as a guide for further research into the dynamics of infanticide, especially for dealing with issues such as the frequency of takeover attempts and their success rate and how attempts and success change at different densities.

References

Anderson JL, 1983. Sport hunting in national parks: sacrilege or salvation? In: Management of large mammals in African conservation areas (Owen-Smith RN, ed). Pretoria: Haum; 271–280.

Arcese P, Hando J, Campbell K, 1995. Historical and present-day anti-poaching efforts in Serengeti. In: Serengeti II: Dynamics, management and conservation of an ecosystem (Sinclair ARE, Arcese P, eds). Chicago: University of Chicago Press; 506–533.

Armitage KB, 1986. Marmot polygyny revisited: determinants of male and female reproductive strategies. In: Ecological aspects of social evolution (Rubenstein DI, Wrangham RW, eds). Princeton, New Jersey: Princeton University Press; 303–331.

Balick MJ, Mendelsohn R, 1992. Assessing the economic value of traditional medicines from tropical rain forests. Conserv Biol 6:128–130.

Beddington JR, 1974. Age structure, sex ratio and population density in the harvesting of natural animal populations. J Appl Ecol 11:915–924.

Beddington JR, Basson M, 1994. The limits to exploitation on land and sea. Phil Trans R Soc B 343:93–98.

Beddington JR, May RM, 1908. A possible model for the effect of adult sex ratio and density on the fecundity of sperm whales. Rep Int Whal Comm 2:75–76.

Beverton RJH, and Holt SJ, 1993. On the dynamics of exploited fish populations. New York: Chapman and Hall.

Bodmer RE, 1994. Managing wildlife with local communities in the Peruvian Amazon: the case of the Reserva Comunal Tamashiyacu-Tahuayo. In: Natural connections: perspectives in community-based conservation (Western D, Wright RM, Strum SC, eds). Washington, DC: Island Press; 113–134.

Bodmer RE, Fang TG, Moya I I, Gill R, 1994. Managing wildlife to conserve Amazonian forest: population biology and economic considerations of game hunting. Biol Conserv 67:29–35.

Burgoyne GE Jr, 1981. Observations on a heavily exploited deer population. In: Dynamics of large mammal populations (Fowler CW, Smith TD, eds). New York: Wiley and Sons; 403–413.

Bygott JD, Bertram BCR, Hanby JP, 1979. Male lions in large coalitions gain reproductive advantages. Nature 282:839–841.

Campbell K, Hofer H, 1995. People and wildlife: spatial dynamics and zones of interaction. In: Serengeti II: Dynamics, management and conservation of an ecosystem (Sinclair ARE, Arcese P, eds). Chicago: University of Chicago Press; 534–570.

Caro TM, Durant SM, 1995. The importance of behavioral ecology for conservation biology: examples from Serengeti carnivores. In: Serengeti II: Dynamics, management, and conservation of an ecosystem (Sinclair ARE, Arcese P, eds.). Chicago: University of Chicago Press; 451–472.

Caro TM, Pelkey N, Borner M, Campbell KLI, Woodworth BL, Farm BP, ole Kuwai J, Huish SA, Severre ELM, in press a. Consequences of different forms of conservation for large mammals in Tanzania: Preliminary analyses. Afr J Ecol.

Caro TM, Pelkey N, Borner M, Severre ELM, Campbell KLI, Huish SA, ole Kuwai J, Farm BP, Woodworth BL, in press b. The impact of tourist hunting on large mammals in Tanzania: An initial assessment. Afr J Ecol.

Caro TM, Rejmanek M, Pelkey N, in press c. Which mammals benefit from protection in East Africa? In: Has the panda had its day? Future priorities for the conservation of mammal biodiversity (Entwhistle A, Dunstone N, eds). London: Chapman and Hall.

Caswell H, Weeks DE, 1986. Two sex models: chaos, extinction, and other dynamic consequences of sex. Am Nat 128: 707–735.

Caughley G, 1994. Directions in conservation biology. J Anim Ecol 63:215–244.

Charlesworth B, 1980. Evolution in age-structured populations. London: Cambridge University Press.

Clark CW, 1985. Bioeconomic modeling and fisheries management. New York: Wiley Interscience.

Clark CW, 1990. Mathematical bioeconomics, 2nd ed. New York: Wiley Interscience.

Clutton-Brock TH (ed), 1988. Reproductive success: studies of individual variation in contrasting breeding systems. Chicago: University of Chicago Press.

Clutton-Brock TH, 1989. Mammalian mating systems. Proc R Soc B 235:339–372.

Clutton-Brock TH, Albon SD, Guiness FE, 1982. Competition between female relatives in a matrilocal mammal. Nature 300:178–180.

Clutton-Brock TH, Deutsch JC, Nefdt RJC, 1993. The evolution of ungulate leks. Anim Behav 46:1121–1138.

Creel SR, Creel NM, 1989. Energetics, reproductive suppression, and obligate communal breeding in carnivores. Behav Ecol Sociobiol 28:263–270.

Creel SR, Creel NM, 1996. Limitation of African wild dogs by competition with larger carnivores. Conserv Biol 10:526–538.

Creel S, Creel NM, 1997. Lion density and population structure in the Selous Game Reserve: evaluation of hunting quotas and offtake. Afr J Ecol. 35:83–93.

Cumming DHM, 1989. Commercial and safari hunting in Zimbabwe. In: Wildlife production systems: economic utilization of wild ungulates (Hudson RJ, Drew KR, Baskin LM, eds). Cambridge: Cambridge University Press; 147–169.

Downhower JF, Armitage KB, 1971. The yellow-bellied marmot and the evolution of polygamy. Am Nat 105:355–370.

Dunbar RIM, 1990. Environmental determinants of fecundity in klipspringer (Oreotragus oreotragus). Afr J Ecol 28:307–313.

Emlen ST, Oring LW, 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223.

Fa JE, Juste J, Perez de Val J, Castroviejo J, 1995. Impact of market hunting on mammal species in Equatorial Guinea. Conserv Biol 9:1107–1115.

FitzGibbon CD, Mogaka H, Fanshawe JH, 1995. Subsistence hunting in Arubuko-Sokole Forest, Kenya, and its effects on mammal populations. Conserv Biol 9:1116–1126.

Fragoso JMV, 1991. The effects of hunting tapirs in Belize. In: Neotropical wildlife use and conservation (Robinson JG, Redford KH, eds). Chicago: University of Chicago Press; 154–162.

Frank LG, 1986. Social organization of the spotted hyaena Crocuta crocuta. II. Dominance and reproduction. Anim Behav 34:1510–1527.

Frank LG, Holekamp KE, Smale L, 1995. Dominance, demography, and reproductive success of female spotted hyenas. In: Serengeti II: Dynamics, management and conservation of an ecosystem (Sinclair ARE, Arcese P, eds). Chicago: University of Chicago Press; 364–384.

Freese CG, Heltne PG, Castro N, Whitesides C, 1982. Patterns and determinants of monkey densities in Peru and Bolivia, with notes on distribution. Int J Primatol 3:53–90.

Ginsberg JR, Milner-Gulland EJ, 1994. Sex-biased harvesting and population dynamics in ungulates: implications for conservation and sustainable use. Conserv Biol 8:157–166.

Glanz WE, 1991. Mammalian densities at protected versus hunted sites in Central Panama. In: Neotropical wildlife use and conservation (Robinson JG, Redford KH, eds). Chicago: University of Chicago Press; 236–252.

Gotelli N, 1995. A primer of ecology. Sunderland Massachusetts: Sinauer Associates.

Greenwood PJ, 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140–1162.

Harrington FH, Mech LD, Fritts SH, 1983. Pack size and wolf pup survival: their relationship under varying ecological conditions. Behav Ecol Sociobiol 13:19–26.

Hausfater G, Hrdy SB (eds), 1984. Infanticide: comparative and evolutionary perspectives. New York: Aldine.

Hilborn R, Mangel M, 1997. The ecological detective. Confronting models with data. Princeton, New Jersey: Princeton University Press.

Hofer H, East M, 1995. Population dynamics, population size, and the commuting system of Serengeti spotted hyenas. In: Serengeti II: Dynamics, management and conservation of an ecosystem (Sinclair ARE, Arcese P, eds). Chicago: University of Chicago Press; 332–363.

Hofer H, East M, Campbell KLI, 1993. Snares, commuting hyaenas, and migrating herbivores: humans as predators in the Serengeti. Symp Zoo Soc Lond 65:347–366.

IUCN/UNEP/WWF, 1991. Caring for earth: a strategy for sustainable living. Gland: International Union for the Conservation of Nature and Natural Resources.

Jarman MV, 1979. Impala social behaviour: territory, hierarchy, mating, and the use of space. Berlin: Verlag Paul Parey.

Kaplan H, Kopischke K, 1992. Resource use, traditional technology, and change among native peoples of lowland South America. In: Conservation of neotropical forests: working from traditional resource use (Redford KH, Padoch C, eds). New York: Columbia University Press; 83–107.

Keane B, Waser PM, Creel SR, Creel NM, Elliot LF, Minchella DJ, 1994. Subordinate reproduction in dwarf mongooses. Anim Behav 47:65–75.

Kleiman DG, 1977. Monogamy in mammals. Q Rev Biol 52:39–69.

Komers PE, 1996. Obligate monogamy without parental care in Kirk's dikdik. Anim Behav 51:131–140.

Kruuk H, 1972. The spotted hyena: a study of predation and social behavior. Chicago: University of Chicago Press.

Lawrence DC, Leighton M, Peart DR, 1995. Availability and extraction of forest products in managed and primary forests around a Dayak village in west Kalimantan, Indonesia. Conserv Biol 9:76–88.

Lewis D, Kaweche GB, Mwenya A, 1990. Wildlife conservation outside protected areas—lessons from an experiment in Zambia. Conserv Biol 4:171–180.

Mangel M, Clark CW, 1988. Dynamic modeling in behavioral ecology. Princeton, New Jersey: Princeton University Press.

Mangel M, Ludwig D, 1992. Definition and evaluation of behavioral and developmental programs. Annu Rev Ecol Syst 23:507–536.

Marks SA, 1973. Prey selection and annual harvest of game in a rural Zambian community. E Afr Wildl J 11:113–128.

May RM, Beddington JR. 1980. The effect of adult sex ratio and density on the fecundity of sperm whales. Rep Int Whal Comm 2:213–217.

McNamara JM, Houston AI, 1996. State dependent life histories. Nature 380:215–221.

Meffe GK, Carroll RC, 1994. Principles of conservation biology. Sunderland, Massachusetts: Sinauer Associates.

Metcalfe S, 1994. The Zimbabwe communal areas management programme for indigenous resources (CAMPFIRE). In: Natural connections: perspectives in community-based conservation (Western D, Wright RM, Strum SC, eds). Washington, DC: Island Press; 161–192.

Milner-Gulland EJ, 1994. A population model for the management of the Saiga antelope. J App Ecol 31:25–39.

Milner-Gulland EJ, Bekenov AB, Grachov YA, 1995. The real threat to Saiga antelopes. Nature 377:488–489.

Mloszewski MJ, 1983. The behaviour and ecology of the African buffalo. Cambridge: Cambridge University Press.

Murray MG, 1982. The rut of impala: aspects of seasonal mating under tropical conditions. Z Tierpsychol 59:319–337.

Ojasti J, 1991. Human harvest of capybara. In: Neotropical wildlife use and conservation (Robinson JG, Robinson KH, eds). Chicago: University of Chicago Press; 234–252.

Packer C, Pusey AE, 1984. Infanticide in carnivores. In: Infanticide: comparative and evolutionary perspective (Hausfater G, Hrdy SN, eds). New York: Aldine; 43–64.

Packer C, Pusey AE, 1987. Intrasexual cooperation and the sex ratio in African lions. Am Nat 130:636–642.

Packer C, Herbst L, Pusey AE, Bygott JD, Hanby JP, Cairns EJ, Borgerhoff Mulder M, 1988. Reproductive success of lions. In: Reproductive success: studies of individual variation in contrasting breeding systems (Clutton-Brock TH, ed). Chicago: University of Chicago Press; 363–383.

Parmigiani S, vom Saal F, Svare B (eds). 1992. Infanticide and parental care. London: Harwood Academic Press.

Peres CA, 1990. Effects of hunting on western Amazonian primate communities. Biol Conserv 54:47–59.

Peters CM, Gentry AH, Mendelsohn RO, 1989. Valuation of an Amazonian rainforest. Nature 339:655–656.

Poole JH 1989. Mate guarding, reproductive success and female choice in African elephants. Anim Behav 37:842–849.

Prins HHT, 1996. Ecology and behaviour of the African buffalo. London: Chapman and Hall.

Redford KH, Padoch C (eds), 1992. Conservation of neotropical forest: working from traditional resource use. New York: Columbia University Press.

Robinson JG, Redford KH, 1986. Intrinsic rate of natural increase in neotropical forest mammals: relationship to phylogeny and diet. Oecologia 68:516–520.

Robinson JG, Redford KH, 1991a. Sustainable harvest of neotropical forest mammals. In: Neotropical wildlife use and conservation (Robinson JG, Redford KH, eds). Chicago: University of Chicago Press; 415–429.

Robinson JG, Redford KH, 1991b. The use and conservation of wildlife. In: Neotropical wildlife use and conservation (Robinson JG, Redford KH, eds). Chicago: University of Chicago Press; 3–5.

Rood JP, 1980. Mating relationships and breeding suppression in the dwarf mongoose. Anim Behav 28:143–150.

Rood JP, 1990. Group size, survival, reproduction, and routes to breeding in dwarf mongooses. Anim Behav 39:566–572.

Sinclair ARE, 1977. The African buffalo: a study of resource limitation of populations. Chicago: University of Chicago Press.

Skinner JD, 1989. Game ranching in southern Africa. In: Wildlife production systems: economic utilization of wild ungulates (Hudson RJ, Drew KR, Baskin LM, eds). Cambridge: Cambridge University Press; 286–306.

Starfield AM, Bleloch AL, 1991. Building models for conservation and wildlife management, 2nd ed. Edina, Minnesota: Burgess International Group.

Starfield AM, Furniss PR, Smuts GL, 1981. A model of lion population dynamics as a function of social behavior. In: Dynamics of large mammal populations (Fowler CW, Smith TD, eds). New York: Wiley and Sons; 121–134.

Thomsen JB, Brautigam A, 1991. Sustainable use of neotropical parrots. In: Neotropical wildlife use and conservation (Robinson JG, Redford KH, eds). Chicago: University of Chicago Press; 359–379.

Tilson RL, Tilson JW, 1986. Population turnover in a monogamous antelope (*Madoqua kirki*) in Namibia. J Mammal 67:610–613.

Trivers R, 1972. Parental investment and sexual selection. In: Sexual selection and the descent of man 1871–1971 (Campbell B, ed). Chicago: Aldine; 136–179.

Van Schaik CP, 1987. Why are diurnal primates living in groups? Behaviour 87: 120–144.

Venter J, Hopkins ME, 1988. Use of a simulation model in the management of a lion population. S Afr J Widl Res 18:126–130.

Vickers WT, 1991. Hunting yields and game composition over ten years in an Amazon indian territory. In: Neotropical wildlife use and conservation (Robinson JG, Redford KH, eds). Chicago: University of Chicago Press; 53–81.

Waser PM, Elliott LF, Creel NM, Creel SR, 1995. Habitat variation and mongoose demography, In: Serengeti II: Dynamics, management and conservation of an ecosystem (Sinclair ARE, Arcese P, eds). Chicago: University of Chicago Press; 421–447.