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SOME SIMPLE MODELS FOR THE DYNAMICS OF CRACID POPULATIONS

A.P. DOBSON
University of Rochester
Rochester, USA

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Andrew Dobson,
Department of Biology,
University of Rochester,
Rochester,
NY 14627.

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ABSTRACT.

Members of the family Cracidae epitomize many of the problems conservation biologists have to face when trying to manage populations of endangered species. In the absence of complete sets of demographic data for any Cracid species, the development of simple mathematical models may allow us to ascertain which life history parameters are most important in determining the ability of populations to persist. Models may also suggest ways by which management techniques may most effectively monitor and maintain any particular species in a specific region.

In this paper some models are developed which initially consider the dynamics of cracids in the absence of any density dependent effects. These models are used to determine how fecundity and age at first reproduction constrain adult survival rates in cracid populations. The models are then extended to include in a very general form of density dependent recruitment. Here it is suggested that interactions between the quality of available territories and the behavior which govern habitat choice may provide an important mechanism by which recruitment is regulated. As these mechanisms are very important in determining both the level of hunting a population can sustain and its response to habitat fragmentation, it is important that more empirical work be done to determine the nature of this relationship. Finally, the dynamic consequences of various Allee effects are briefly discussed.

ABSTRACT IN SPANISH

Los miembros de la familia Cracidae resumen varios de los problemas que los biólogos de Conservación tienen que enfrentar cuando tratan de manejar poblaciones de especies amenazadas en ausencia de los datos mas básicos de demografía. Parece poco probable que alguna vez se tengan series completas de datos demográficos para cualquier especie de crácido. Sin embargo, el desarrollo de modelos matemáticos simples para poblaciones de crácidos, nos puede permitir identificar cuales son los parámetros mas importantes de la historia natural que determinan la habilidad para persistir de una población, y como el manejo podría monitorear y mantener más efectivamente, cualquier especie en particular en una región específica. En este artículo se han desarrollado algunos modelos simples, los cuales inicialmente consideran la dinámica de los crácidos en la ausencia de efectos dependientes de la densidad. Estos modelos son usados para determinar cómo la fecundidad y la edad de la primera reproducción restringen la tasas de supervivencia de adultos en las poblaciones de crácidos. Los modelos son después extendidos para incluir una forma muy general de reclutamiento dependiente de la densidad. Se sugiere que las interacciones entre la calidad de los territorios disponibles y el mecanismo de selección del hábitat pueden proveer un importante mecanismo por el cual el reclutamiento es mediado en crácidos. Así como este mecanismo es muy importante en determinar tanto, el nivel de cacería que una población puede sostener y su repuesta a la fragmentación del hábitat, es importante que se haga más trabajo empírico para determinar la naturaleza de esta relación. Finalmente, las consecuencias dinámicas de varios "efectos de Allee" son discutidas brevemente.

Introduction.

Members of the family Cracidae epitomize many of the problems conservation biologists have to face when trying to manage populations of endangered species in the absence of any basic demographic data. All the members of the family are relatively large, they usually form a significant fraction of the biomass of the avifauna in any region where they occur (Terborgh, 1986), more significantly their size considerably increases their attraction to hunters. Although it is likely that most populations can withstand some level of harvesting, ascertaining the level of exploitation a population can sustain requires detailed knowledge of both basic demography and the biological factors which determine the relationship between recruitment and population density. It seems unlikely that complete sets of demographic data will ever be available for any Cracid species. However, the development of simple mathematical models for cracid populations may allow us to determine which life history parameters are most important in determining the ability of the population to persist and how management may most effectively monitor and maintain any particular species in a specific region.

The paper is organized as follows: initially some simple models are developed which consider the dynamics of Cracids in the absence of any density dependent effects. These models are used to determine how fecundity and age at first reproduction constrain adult survival rates in cracid populations. The models are then extended to include in a very general form of density dependent recruitment. Here it is suggested that interactions between the quality of available territories and the behavioral cues used to determine habitat choice may provide an important mechanism by which recruitment is mediated in cracids. As this mechanism is very important in determining both the level of hunting a population can sustain and its response to habitat fragmentation, it is important that more empirical work be done to determine the nature of this relationship. Finally, the dynamic consequences of various Allee effects are briefly discussed.

BASIC MODEL

The simplest model we could construct of a cracid population would need to consider age at first reproduction, annual fecundity, and rates of adult and immature survival. If we initially only consider the female section of the population then a suitable discrete equation model would be

$$N_{t+1} = s(A_t + I_t) + s^a iFA_{t-a-1} \qquad (1)$$

Here $\underline{s}$ is adult survival, $\underline{F}$ is annual fecundity (# of female chicks reared per female, $\underline{i}$ is the proportional survival rate of immature birds and $\underline{a}$ is age at first reproduction. The population is divided into three age classes, young of the year, immature birds, I_t, and the breeding adults, A_t. In the absence of hunting the population will either grow exponentially or decline to extinction. The growth rate, λ, is determined by solving the equation

$$\lambda = s^a iC/(\lambda - s) \qquad (2).$$

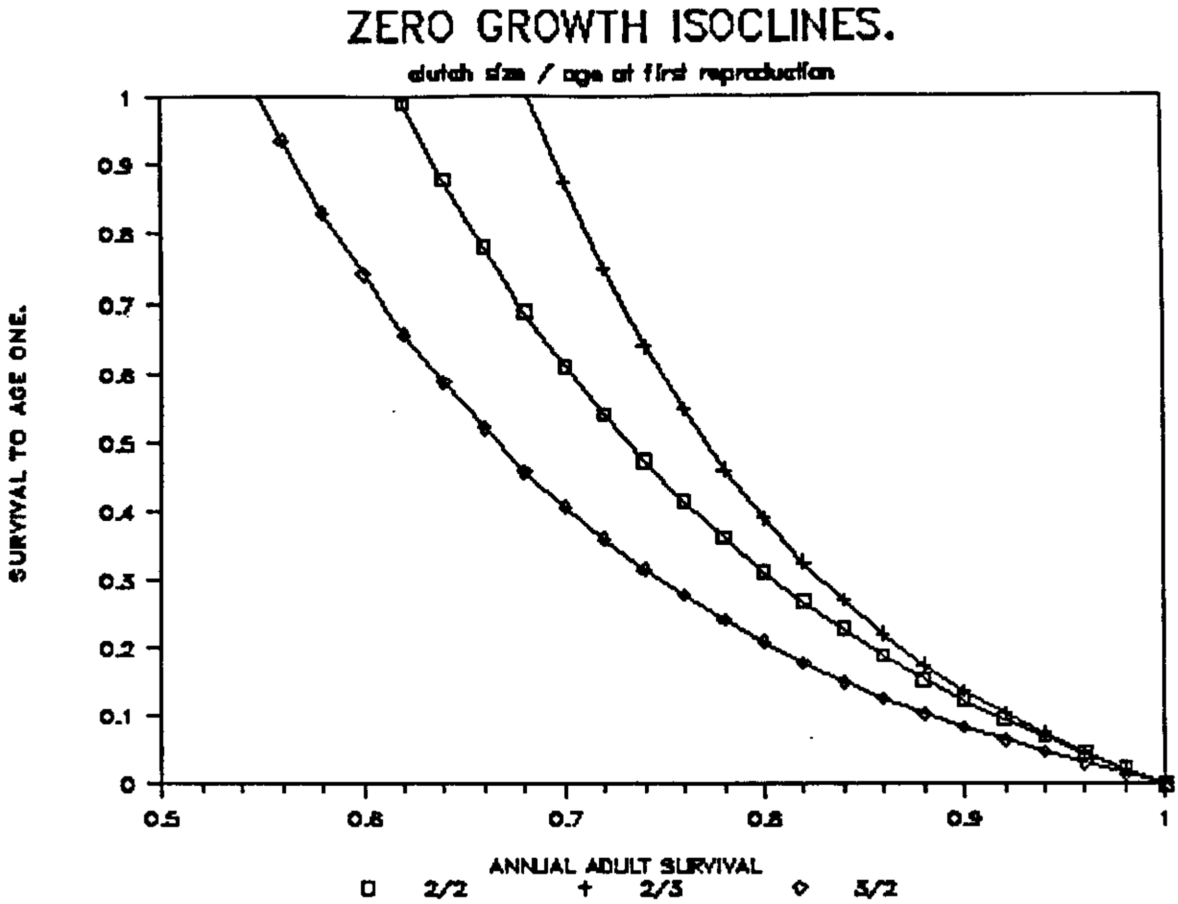

FIGURE 1. Isoclines for zero population growth in the basic model for different values of age at first reproduction, a, and clutch size, C. In all cases populations with values of s and i to the right of the line will grow, those to the left of the line will collapse to extinction.

As the population will only grow when $\lambda>1$, populations will only persist when

$$C > (1-s)/s^{a}i \qquad (3).$$

The interaction between these various parameters in illustrated in Figure 1 for different clutch sizes and ages at first reproduction. The figure emphasizes the importance of both high adult survival rates and high levels of immature survival in determining the ability of cracid populations to persist. In the absence of the large levels of parental care, it seems unlikely that immature survival rates would be high enough to allow species with such low fecundity to persist. As most cracids reproduce for the first time at least at age three and have clutch sizes of two to three eggs (Delacour & Amadon 1973), it would seem likely that rates of adult and immature survival have to be greater than around eighty percent per annum.

EXPLOITED CRACID POPULATIONS

A simple form of hunting mortality can be included into the basic model by assuming that in any year a number of hunters, H, each puts an effort, e, into trying to catch birds. Here effort can be measured in days spent hunting. More complex models could consider the case when hunters try and obtain a constant yield from the population (see Beddington & May, 1977), when in general exploitation more rapidly drives the population to extinction. Here we will concentrate on the former case and rewrite Eqn 1 as

$$N_{t+1} = s(A_t + I_t) + s^a iFA_{t-a-1} - eHN_t \qquad (4).$$

We can use this equation to examine how variations in parameters such as survival and age at first reproduction effect the levels of harvesting a population can sustain (Fig 2). Essentially, these calculations suggest that available yield is linearly dependent upon clutch size and immature survival rate, but non-linearly dependent upon adult survival and age at first reproduction. The sustainable level of hunting in our ideal density

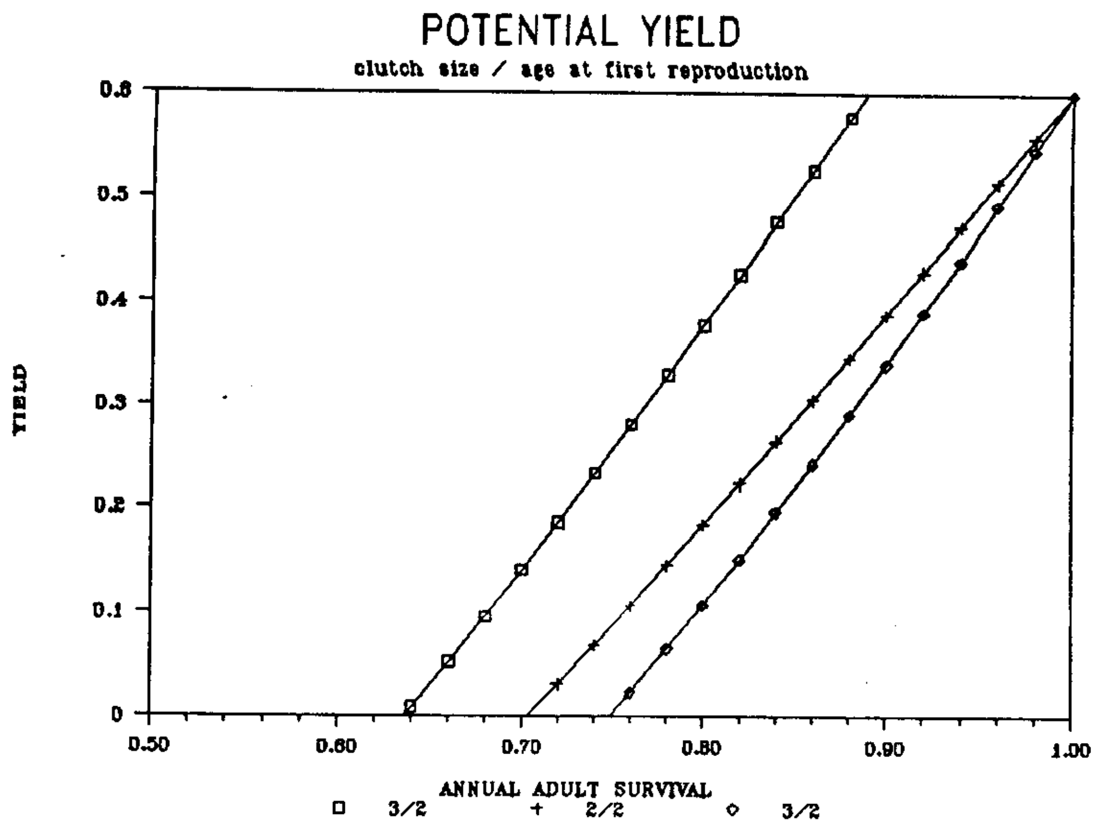

FIGURE 2. Levels of potential yield for idealized cracid populations with different clutch sizes and age at first reproduction. The horizontal axis gives the adult survival rate (proportional first year survival, i = 0.6), the vertical axis depicts the yield as a proportion of the adult population removed by hunters. The plotted lines are isoclines for the yield which will maintain the population at a 'stable' density. Yields greater than this will cause the population to collapse.

independent population is thus very dependent upon small variations in adult survival and in the absence of any accurate estimates of this parameter, it would be unwise to set acceptable levels of harvesting until more is known about basic cracid demography.

BASIC MODEL WITH SIMPLE DENSITY DEPENDENCE

In the absence of hunting, the number of cracids in an area is likely to be determined by interactions between available resources, such as breeding habitat, and the ability of the birds to exploit these resources. Although nothing is known about the way that regulation operates in cracid populations, it is possible that variation in the quality of different patches as potential territories may interact with the mechanisms of habitat choice to produce a per capita reduction in mean reproductive success as population density increases. Figure 3 illustrates how such an effect might operate. Essentially, it is assumed that when population density is very low only the best parts of the habitat are used as breeding territories. At higher population densities, territories become established in lower quality habitat and mean recruitment decreases. Similar reductions in mean fecundity with increasing population density could be produced by social systems which allow different proportions of the population to reproduce at different population densities (see Dobson & Lyles, 1988). Determining which mechanisms are operating and their relative importance in different populations requires detailed long term studies.

The recruitment curves produced by this simple 'habitat choice' model of regulation may be included into our basic model using a function suggested by Sheperd (1982) for fish populations. The function is particularly flexible in that one of its parameters varies with the total level of habitat or resource available, K; while a second parameter, b, allows the population to be either only weakly linked to available resources ($b<1$), or more tightly linked to available resources. Here the magnitude of

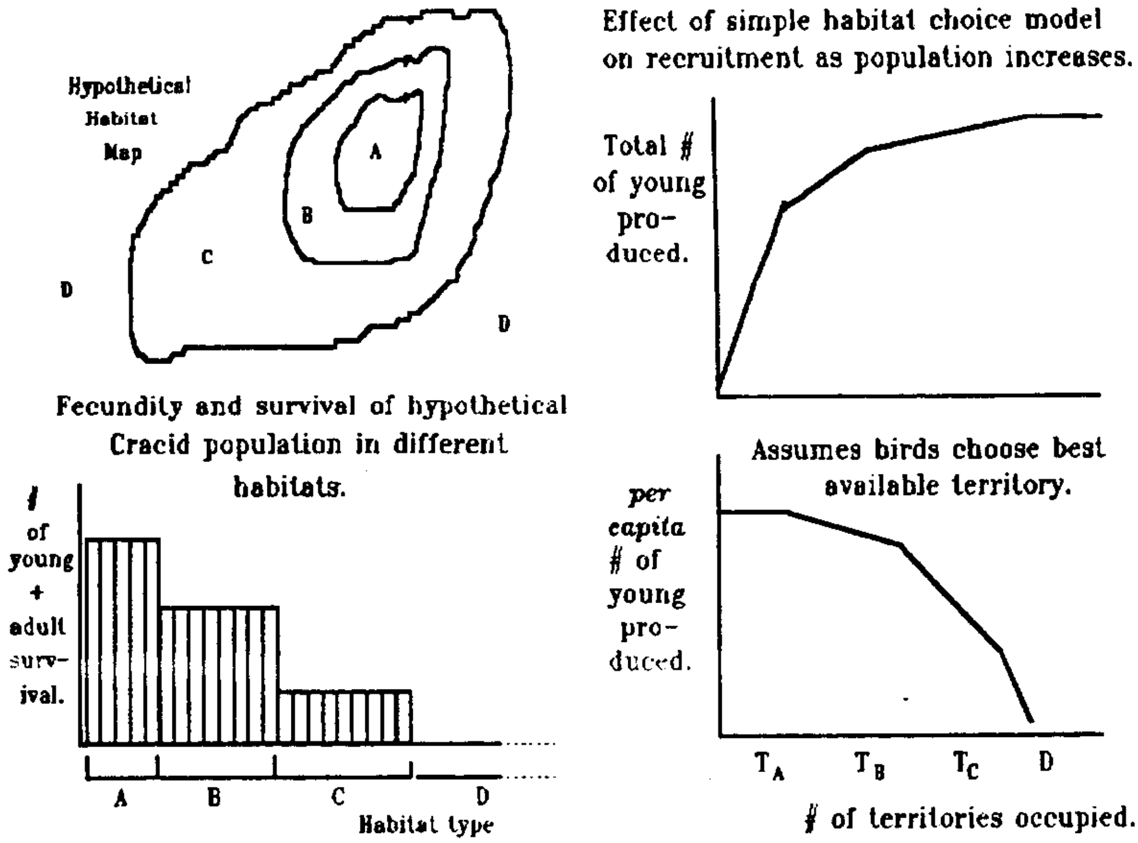

FIGURE 3. A simple graphical method of interpreting how habitats of different quality may determine recruitment in hypothetical cracid populations. The figure on the top left illustrates a hypothetical habitat divided into regions where the birds can either (A) breed at maximum fecundity, (B) breed at reduced fecundity, (C) survive, but unable to breed, and (D) unable to survive or breed. The bar chart below this illustrates this effect graphically, with patches of type A sustaining and producing the

most birds, while patches of type D sustain none. The graphs on the right illustrate how the birds ability to choose the best available habitat might produce a density dependent recruitment curve. It is important to note that this model assumes the birds are able to choose the best available territory; if this is not the case recruitment may only be weakly linked to population density.

'b' would be determined by the mechanism of habitat choice and variability in the quality of different territories (where quality is measured in units of offspring produced). The function takes the form

$$f(N) = 1 / (1 + (N/K)^b) \qquad (5).$$

The general shape of the function is illustrated in Figure 4 for different values of K and b. Here it is assumed that increases in adult density lead to reductions in the production and survival of young birds.

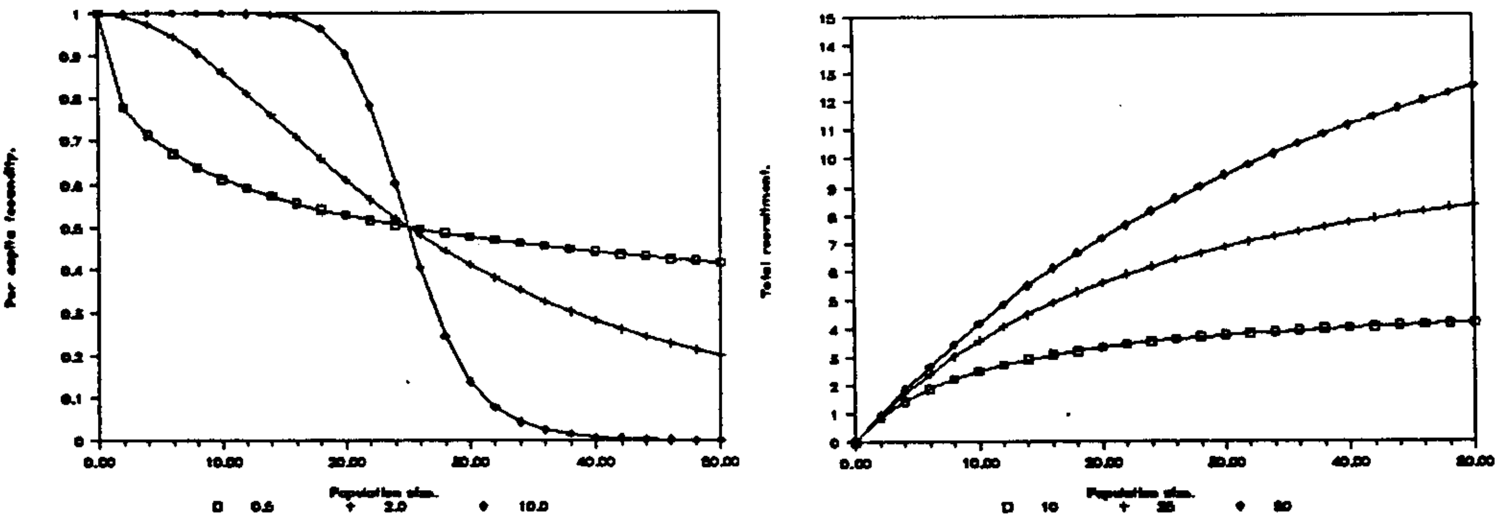

FIGURE 4. The shape of the recruitment function for different values of K and b. The upper figure illustrates the influence of K on total numbers of young recruited to the population; here b has been held constant at 1.0 and K set to 10, 20 and 50. The lower figure illustrates the influence of b on <u>per capita</u> recruitment; the curve is drawn for three values of b (0.5, 2.0 & 10.0); K has been held constant at 25. These curves should be compared to those produced by the 'habitat choice' model of figure 3.

THE EFFECT OF RECRUITMENT ON YIELD

The recruitment function can be substituted into our equation for growth in the presence of hunting to produce the following expression

$$N_{t+1} = s(A_t + I_t) + s^a iFA_{t-a-1}f(N_t) - eHN_t \quad (6).$$

This can then be solved to determine the equilibrium numbers of birds, N^*, in an exploited population

$$N^* = K \left(\frac{s^a iC}{1+eH-s} - 1 \right)^{1/b} \quad (7).$$

The effects of hunting on the system can now be examined by plotting out the decrease in population density as hunting pressure increases (Figure 5).

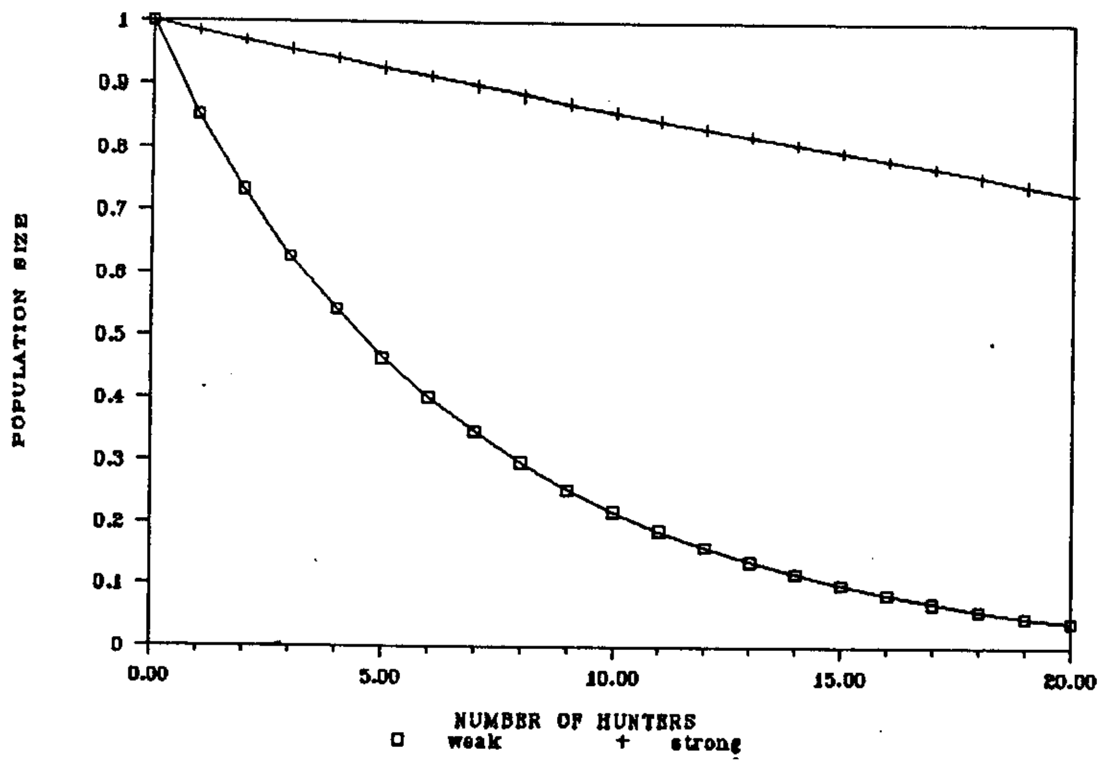

FIGURE 5. The effect of increased hunting intensity on populations with different shaped recruitment functions. Hunting intensity increases with the number of hunters, population size is calibrated as a proportion of population size in the absence of hunting. The curve for weak regulation has b = 0.5, that for strong regulation has b = 5.0.

The important point to emerge from this diagram is that populations that are tightly linked to their available resources (b>1) are much more resilient to exploitation, than populations with weaker regulation (b<1). A further important difference emerges when we consider the yield, or number of birds shot, at different intensities of hunting (Figure 6). This diagram suggests that tightly regulated populations will continue to produce increased yields as hunting pressure increases, while populations with weak regulation will initially give small increases which rapidly diminish as hunting pressure increases. Hence monitoring the interaction between hunting intensity and yield is a very powerful way of determining the strength of the regulation.

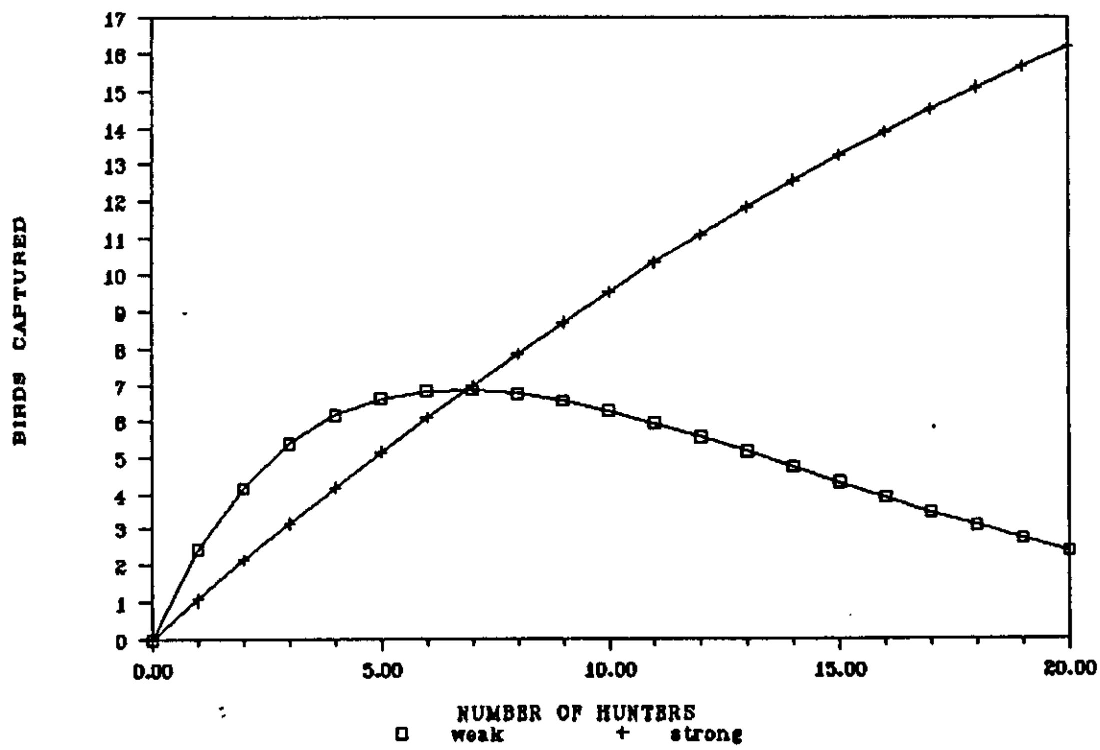

FIGURE 6. The effect of the two different recruitment functions on the yield, numbers of birds shot, as hunting intensity increases.

In the absence of any knowledge about the form of this relationship, it is impossible to determine the levels of regulation a population can sustain. As it has been fairly arduous to determine how density dependence operates in well studied bird populations (Stenning, Harvey & Campbell, 1988), this suggests that regulation may well be relatively weak ($b<1$). If this is the case for cracid populations, they will not respond favourably to exploitation.

The shape of the recruitment function may also be important in determining how the population responds to fragmentation and loss of habitat. Although Eqn 7 would initially seem to suggest that reductions of habitat give rise to proportionally similar decreases in population density, this will only be the case if there is no change in the value of 'b'. If loss of habitat leads to changes in the shape of the recruitment function, which may be the case if the population is regulated by some form of territoriality, then changes in cracid density that result from habitat fragmentation will be hard to predict. More specifically, if loss of habitat leads to increases in the strength of regulation (b increases), then rate of population decline will proceed more rapidly than the rate of habitat loss.

ALLEE EFFECTS

A second form of density dependence may be important in determining the dynamics of heavily exploited populations or populations which live in highly fragmented habitats. These effects begin to be important when population density is sufficiently low that individuals have difficulty finding potential mates during the breeding season. Such effects also determine the number of birds required to successfully reintroduce a population. Dynamic models can be developed for these effects using some functions originally described by May (1977). They have been applied by Dobson & Lyles (1988) to data from endangered primate populations and by Lande (1987) for hypothetical territorial species. The most important feature of these models is that they allow a threshold to be determined, below which a population will collapse to extinction, even in the absence of further exploitation or loss of habitat. This threshold is lower for promiscuous, group living species than for monogamous, more solitary species. Although most cracids have been believed to be monogamous, recent work on the Yellow-knobbed Curassow (Strahl, Silva & Buchholz, this volume) suggests that polygamy may be more common than had been previously thought.

DISCUSSION

Although the ultimate goal of cracid conservation would be to set aside large areas of land where absolutely no hunting occurs, this ideal situation is unlikely to be met in other than a few isolated cases. Instead, it seems likely that diminishing amounts of habitat will support relatively isolated populations that are exploited by hunters at levels determined by human population densities. Although all conceivable effort should be made to eliminate hunting, it may be useful to monitor whatever hunting remains as actively as possible as these data provide invaluable information about the relative abundance of birds in a region and their rates of recruitment at different levels of exploitation. Similarly, in many places the locals who hunt the birds will have a detailed knowledge of the natural history of the species, this should be capitalized on by the those concerned with conserving and managing the population. This research may then be complemented by further research to determine how important habitat quality and habitat choice are in mediating relationships between population density and rates of reproduction. Here ascertaining whether the birds utilize environmental or intraspecific cues when choosing suitable nest sites (Carenter, 1987; Stamps 1988) might considerably alter the efficacy of different management strategies. If birds utilize environmetal cues in determining where to breed, management should concentrate on preserving those features of the habitat which are most attractive to the resident cracid species. In contrast, if intraspecific cues are important in choice of nesting site then management may be able to artificially attract birds to previoulsy uncolonized areas of habitat by using recorded calls. This area of cracid biology would also benefit from further experimental work.

CONCLUSIONS AND RECOMMENDATIONS.

The models discussed in this paper emphasize several important areas of cracid population biology that require either further experimental examination or the reconsideration of previously collated data. It is of prime importance that we obtain for as many species as possible estimates of survival (for both adults and immatures), fecundity and age at first reproduction. Although this may be impossible for some species, it may be possible to extrapolate estimates of these parameters from data sets which compare these values for species with different body sizes.

A second priority concerns determining the relationship between population density and recruitment. This requires research on two fronts: paradoxically it is important for park wardens and reserve managers to try and obtain some information on levels of hunting intensity and yield obtained by hunters. Although this may have to be obtained covetously, it is invaluable in determining an important component of population regulation. When complimented with scientific studies to determine the actual mechanisms by which density dependence operates, it should be possible to build up a more precise assessment of how a population will respond to changes in hunting pressure or loss of habitat. In most cases it could be argued that in the absence of any data on 'stock-recruitment' relationships the population should not be exploited at all.

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