

THE INFLUENCE OF HUNTING PRESSURE ON THE SOCIAL BEHAVIOR OF VERTEBRATES

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RESUMO

A Influência da Pressão Humana de Caça sobre o Comportamento Social de Vertebrados

O estudo da influência da pressão humana de caça sobre o comportamento social de vertebrados requer um conhecimento prévio sobre a própria pressão de caça e sobre o comportamento social da(s) espécie(s) em questão. A literatura sobre o assunto é relativamente escassa. A maioria dos trabalhos é restrita a alterações demográficas populacionais e são geralmente espécie-específicas. A pressão humana de caça pode afetar não apenas a demografia mas também aspectos do comportamento social como cuidado paterno, territorialidade, comportamento reprodutivo, tamanho de grupo, comportamento de marcação de território, sistema reprodutivo e competição intra-específica. A presença de caçadores em uma área pode levar os animais a se deslocar para fora de seus territórios ou áreas originais, o que pode resultar em quebra da estrutura social, com efeitos a longo prazo na demografia da população local e vizinha, ampliando assim o efeito da pressão de caça. Por outro lado, a retirada de indivíduos em populações territoriais pode ser compensada pela existência de indivíduos excedentes que não possuem território. Da mesma forma, ela pode ser compensada em algumas espécies por um aumento na atividade reprodutiva. A compreensão das implicações da pressão de caça no comportamento social de vertebrados pode ser decisivo para o estabelecimento de programas de caça controlada. Experimentos manipulativos podem auxiliar na compreensão de tais interações. A ocorrência de alterações qualitativas e quantitativas no comportamento social de vertebrados, causadas direta ou indiretamente por pressão humana de caça é revista e analisada neste trabalho.

Palavras-chave: pressão de caça, comportamento social, vertebrados.

ABSTRACT

The study of the influence of human hunting pressure on the social behavior of vertebrates requires a large background on both the hunting pressure and the social behavior of the species. Literature about this subject is relatively scarce. Most of the papers are restricted to shifts in demography, and are generally "species-specific". However, human hunting pressure can not

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only affect demography but also some factors of the social behavior of a species such as parental care, territoriality, reproductive behavior, group-size, fraying behavior, mating system, and intraspecific competition. The presence of hunters in the area can lead the animals to move out of their original home-rangers. This can breakup the social structure and can cause long-term effects on the demography of hunted as well as nearby populations, amplifying the impact of hunting. On the other hand, harvest can be compensated in territorial species by "surplus population" of non-territorial individuals. Moreover, alternatively, an increase in the reproductive activity, as a response to hunting pressure, can compensate its effects in some species. Understanding the implications of hunting pressure in the social behavior of vertebrates might be decisive to the establishment of wildlife management and conservation programs. Manipulative experiments might help us to model such complex interactions. The occurrence of qualitative and quantitative changes in vertebrate social behavior directly or indirectly related to human hunting pressure is reviewed and analyzed in this paper.

Key words: hunting pressure, social behavior, vertebrates.

INTRODUCTION

The biological and cultural evolution of humans has been extremely influenced by their relationships with other animals (Eltringham, 1984). Ancient cultures relied on animals for many needs of human existence like meat for food, skins for clothing, fat for fuel, and bones, antlers and horns for tools and weapons. During the ages in which hunting was the main livelihood of humans, a progression of inventions continually improved the efficiency of hunters (Robinson and Bolen, 1989). There is some controversy about the real impact of primitive cultures on wildlife populations. Martin (1971) proposed that the growth and spread of human population may have caused the extinction of many species during the Pleistocene ("Pleistocene Overkill"), whereas Brodrick (1972) believed that humans were relatively rare during Paleolithic times, and thus may not have exerted a great effect on wildlife. Most agree, however, that long-term exploitation of mammals by humans has had a devastating impact. In the last 400 years, some 36 species of mammals have become extinct, and today over 100 species are threatened by extinction (Vaughan, 1986). In Africa the "big five" most highly rated prey of the western sport hunters are the lion, the leopard, the buffalo, the elephant, and the rhinoceros (Bertram, 1984). An added incentive for killing carnivores was the value of their pelts whose fine, dense underfur imparts a sensuous feel as well as warmth (Burton, 1979).

Just as humans have developed more efficient ways of killing animals, so also have hu-

mans developed sophistication about the disastrous results of overhunting (Robinson and Bolen, 1989). Both tribal and urban societies gradually restricted the efficiency of hunting with self imposed regulations. As a result, hunting gradually became more ritualized as human survival depended less on wildlife for food and fiber (Fisher *et al.*, 1969). Presently the use of wild animals by humans has been debated on both ethical and pragmatic level, and the necessity of valuing wildlife for commercial, recreational, scientific, esthetic, or spiritual reasons has been considered essential for its conservation (Robinson and Redford, 1991).

Paradoxically, even in modern urban societies, hunting is still widespread. In 1985, around 10% of the population of the United States (approximately 16.7 million people) went hunting (U.S. Fish and Wildlife Service 1987). In a simplistic way, Amory (1974) argues that reasons for that are: fun, money, and revenge. Subsistence hunting is also important in many underdeveloped regions of the world, composing the major source of food for local people (Redford and Robinson, 1991). Modern weapons are now widely available to commercial poachers (Barness, 1984). This means that, in spite of our cultural development and relative independence of wildlife resources, the impact of human hunting pressure on wildlife presently must be bigger than ever.

The way vertebrate species has been responding to this huge pressure varied from extinction (Halliday, 1980) to adaptation (Connolly, 1978), with a wide range of intermediate alterna-

tives. Hunting pressure can affect either distribution (Terborgh, 1992) and density (Bodmer *et al.*, 1994) of vertebrate populations. Wildlife social behavior is usually dynamic and sensitive to environmental pressures (Alcock, 1993). Therefore, it can also be directly or indirectly affected, resulting in mid/long term effects on population demography. Therefore, understanding how human hunting pressure affects wildlife social structure and social behavior might be essential to the management and conservation of vertebrate species.

Papers related to hunting pressure are relatively scarce. Most of them are restricted to shifts in demography of game species, and are generally "species-specific". To review the influence of hunting pressure on the social behavior of vertebrates as a whole, and not only on a small group of species, is the objective of this study.

MATERIAL AND METHODS

I reviewed the occurrence of qualitative and quantitative changes in vertebrate social behavior directly or indirectly related with human hunting pressure. The references were divided into five categories: *observation*, *experimentation*, *inference*, *inference upon observation*, and *inference upon experimentation*. *Inferences* were considered the assumptions not tested by the authors. *Inferences upon observations* were considered the assumptions based on observations but not tested by the authors. *Inferences upon experimentation* were considered the assumptions tested by the authors. *Observation* and *experimentation* were considered as described by Lehner (1979). Inferences were considered relevant because they usually expressed the author's concern about the problem. They can also contribute to the discussion and stimulate new studies on the area.

RESULTS AND DISCUSSION

The results are shown in Table I. The species were separated by their taxonomic classes. The mammals are presented in the grandorder Ungulata and in the orders Rodentia and Carnivora. The *behavior affected* is considered the behavioral component that has been affected by hunting pressure, and the *kind of change* is a brief description of the alteration reported. The methods of determination were described in the former section. Ref-

erence sources are also presented in Table I. Further discussions are on the text.

The main problem in determining the influence of human hunting pressure on the social behavior of game species is that it requires a large background in both the hunting pressure and the social behavior of the species. Ungulate social behavior is of particular interest for several reasons. Many species are large, occupy open areas and can be observed easily, and have therefore been well studied (Vaughan, 1986). Therefore, one could expect, without surprise, that it would be easier to find information about large social diurnal ungulates of open areas than about solitary small nocturnal rodents of tropical rain-forests, although the paca for instance is an important species for subsistence hunting in the Amazon Basin (Redford and Robinson, 1987). Furthermore, animals exposed to intense hunting become very shy in the presence of humans, what difficulties even more the study of their behavior.

The study of social behavior of crocodilians in the wild is also a hard task because they spend most of their time into the water in remote areas of difficult access to humans (Lang, 1987). However, the mound nest of some crocodilian species is relatively evident and easy to find (Martin, 1977) and can be used in aerial surveys to determine the number of reproductive females in the area (Rice *et al.*, 1992). The behavioral repertoires of female crocodilians that improve reproductive efficiency are not restricted to nest selection and construction, but include subsequent nest protection and opening, egg opening, transport of hatchlings, and parental care (Ferguson, 1985). Crawshaw (1991) compared the frequency of nest attendance of female caimans (*Caiman yacare*) between two sites: one exposed to intense hunting and another not disturbed. The observed difference in the proportion of nest attendance between the areas was considered a response to the presence of hunters. The females exposed to intense hunting were more prone to decrease or interrupt nest attendance after being disturbed. This had a marked effect on egg survivorship, by allowing increased nest predation, thereby influencing the reproductive success.

Crocodilians live in diverse habitats, from open rivers crossing a desert, like the Nile crocodile (*Crocodylus niloticus*), to flooded forests, like the black caiman (*Melanosuchus niger*) (Alcala

TABLE I
Changes in social behavior of hunted species.

Species	Behavior affected	Kind of change	Method of determination	Reference
REPTILES				
Paraguayan caiman (<i>Caiman yacare</i>)	Maternal behavior	Decrease	Observation	Crawshaw (1991)
Crocodylians	Territoriality	Increase	Inference	Magnusson (1986)
BIRDS				
Passenger-pigeon (<i>Ectopistes migratorius</i>)	Reproductive behavior	Break-down (extinction)	Inference upon observation	Halliday (1980)
Spruce budworm (<i>Choristoneura fumiferana</i>)	Reproductive behavior	Increase	Experimentation	Stewart & Aldrich (1951) and Hensley & Cope (1951)
MAMMALS: RODENTS				
Coyupus (<i>Myocastor coypus</i>)	Reproductive success	Decrease	Inference upon observation	Gosling & Baker (1987)
MAMMALS: UNGULATES				
Guanaco (<i>Lama guanicoe</i>)	Intra-specific competition for food, territory, and mates	Decrease	Inference	Franklin & Fritz (1991)
Guanaco (<i>Lama guanicoe</i>)	Young survival	Increase	Inference	Franklin & Fritz (1991)
African elephant (<i>Loxodonta africana</i>)	Immigration from hunted areas to protected areas	Increase	Observation	Barnes (1984)
Impala (<i>Aepyceros melampus</i>)	Reproductive performance	Decrease (because of an imbalance in sex ratio)	Inference upon experimentation	Ginsberg & Milner-Gulland (1994)
White-tailed deer (<i>Odocoileus virginianus</i>)	"Moving" behavior (out of original home range)	Increase	Experimentation	Marshall & Whittington (1968), Tester & Heezen (1965), and Sparrowe & Springer (1970)
White-tailed deer (<i>Odocoileus virginianus</i>)	Reproductive performance	Decrease (because of an imbalance in sex ratio)	Inference	Verne (1983)

(to be continued)

TABLE I (Continuation)

Species	Behavior affected	Kind of change	Method of determination	Reference
MAMMALS: UNGULATES				
Mule deer (<i>Odocoileus hemionus</i>)	"Moving" behavior (out of original home range)	Increase	Inference	Reed (1981)
Red-deer (<i>Cervus elaphus</i>)	Growth rates and fertility	Increases	Observation	Staines (1978)
Red-deer (<i>Cervus elaphus</i>)	Age of puberty natural mortality	Decrease and over-winter	Observation	Staines (1978)
Red-deer (<i>Cervus elaphus</i>)	Group size	Increase	Inference	Clutton-Brock & Albon (1989)
Red-deer (<i>Cervus elaphus</i>)	Reproductive performance	Decrease	Inference	Clutton-Brock & Albon (1989)
Roe-deer (<i>Capreolus capreolus</i>)	Fraying behavior	Decrease	Experimentation	Cumming (1974)
Moose (<i>Alces alces</i>)	Reproductive performance	Decrease	Observation	Markgren (1974)
MAMMALS: CARNIVORES				
Canids	Mating system	Changes from monogamy to polygamy	Inference	Kleiman & Brady (1978)
Canids	Proportion of breeding females	Increase	Observation	Harris & Saunders (1993)
Canids	Post-natal survival of young	Increase	Observation	Harris & Saunders (1993)
Wolf (<i>Canis lupus lycaon</i>)	Intra-specific strifes	Increase	Observation	Mech (1975)
Wolf (<i>Canis lupus lycaon</i>)	Care of young	Decrease	Observation	Mech (1975)
Jaguar (<i>Panthera onca</i>)	Ability to hunt	Decrease (due to man-inflicted wounds)	Observation	Hoogesteijn <i>et al.</i> (1993)
Grizzly-bear (<i>Ursus arctos</i>)	Dominant (<i>trophy</i>) males replacement	Increase	Observation	Wielgus & Bunnell (1994)
Grizzly-bear (<i>Ursus arctos</i>)	Infanticides	Increase	Observation	Wielgus & Bunnell (1994)
Grizzly-bear (<i>Ursus arctos</i>)	Reproductive activity (females rejected new males)	Decrease	Observation	Wielgus & Bunnell (1994)

(to be continued)

TABLE I (Continuation)

Species	Behavior affected	Kind of change	Method of determination	Reference
MAMMALS (in general)				
Mammals	Social structure	Break-down	Inference upon experimentation (on disease control)	Mollison (1987)
Mammals	Infectious contacts	Increase	Inference upon experimentation (on disease control)	Mollison (1987)

and Dy-Liacco, 1989). Many crocodylian species have been over-hunted in this Century because of their skin. This resulted in the depletion, fragmentation and even local extinction of populations (King, 1989). The territoriality of the animals appears to be related to the kind of habitat they live (Magnusson, 1986). According to Magnusson, in simple habitats such as rivers and streams animals may patrol their entire territory on a single night, but it would take much more time, and cost much more in terms of lost feeding opportunities for an animal to patrol an area of marsh with similar linear dimensions. Hunting for extended periods (10-20 years) may severely affect densities and size distributions of crocodylian populations. The few wary animals that survive may become accustomed to the exclusive use of very large areas ("superterritories"). At the cessation of hunting, reproduction should supply recruits to the breeding population, but the residents may not allow the large subadults to survive (Magnusson, 1986). Most of the intraspecific aggressive behavior observed in crocodylians both in the wild (Ayarzaguena, 1983) and in captivity (Verdade, 1992) are aggressions of adult individuals on subadults, which corroborates this hypothesis.

The passenger pigeon *Ectopistes migratorius* became extinct in 1914, largely as the result of intensive hunting by man. However, the final stages of its decline seem to have been too rapid to be accounted completely by human activity. It is suggested that social factors, like colony size and reproductive success, were related in such a way that, although the species was apparently still quite common, its breeding rate was insufficient to offset mortality (Halliday, 1980). This seems to

be an extreme case in which the interference caused by hunting pressure on the social structure and behavior could have led the species to the extinction. This should be considered when managing other species that present similar social behavior as well as reproductive strategy. The wildbeest (*Connochetes taurinus*), for instance, ranks as one of the most gregarious of all ungulates and also presents a highly pronounced reproductive seasonality in an apparent adaptation to predators (Estes, 1969 and 1976). If herd size interfere in its reproductive success, then overhunting the species, even for relatively short periods, could be disastrous.

Removal studies of birds like those conducted by Stewart and Aldrich (1951) and Hensley and Cope (1951) with spruce budworm (*Choristoneura fumiferana*) in spruce-fir forest have demonstrated a surprising capacity of the bird population to replace reproductive active individuals by a surplus population present in the area. According to these authors, this surplus acted as a reserve supply to fill in or replenish gaps when an area was depleted. Thus, the removal of the territorial individuals by shooting permitted the non-territorial individuals to get access to a territory. Since the territory was the limit factor for reproduction, removing territorial individuals has increased the number of reproductive active animals in a certain period of time. On the other hand, tentative eradication of coypu (*Myocastor coypus*) in East Anglia, England, showed that there may be a density dependent reduction in reproductive success in declined populations (Gosling and Baker, 1987), similarly to what was described above to the passenger pigeon.

The South American guanaco (*Lama guanicoe*) wild populations have dramatically declined over the past century. Despite their expressive reduced numbers throughout their former range, guanacos continue to be an important and viable asset to local and regional economies in South America (Franklin and Fritz, 1991). In an attempt to establish a scientific management system for the species, the authors assume that harvesting "surplus males" from male groups would most likely decrease intraspecific competition for food, territorial space, and mates, as well as reduce any interference of nonterritorial males with territorial stability and the rearing of young (*chulengos*). According to these authors, harvesting guanacos unselectively would be impractical for a sustained yield program because of the rigid separation of males in male groups and females in family groups. Removing territorial males would disband family groups, orphaned *chulengos* would be created, and unweaned *chulengos* would be separated from their mothers. However, male guanacos spend 3-4 years in all-male groups where they assess size and fighting ability via chest-rams and playfighting, presumably improving fighting skills that may ultimately affect reproductive success (Wilson and Franklin, 1985). Thus, this period could be considered as a learning period for young and subadult males that could be affected by selective hunting pressure on male groups, and could result in a future decrease in the reproductive performance of males.

The former habitats of African elephants (*Loxodonta africana*) have been destroyed and their populations depleted because of their ivory. Thus, some national parks have been set up specifically to protect the species. When a national park is created, mortality is reduced because poaching is controlled and access to water is guaranteed. The higher survival rates cause an increase in the population within the park that usually results in a great impact on the environment by overgrazing and killing the trees in search of food (Eltringham, 1979). At the same time, continuing human harassment outside drives elephants into the protected area of the park. Elephants have density-dependent mechanisms which regulate the population size. At high population densities there is an increase in the age of puberty, an increase in the interval between births, an earlier age of

menopause and an increase in infant mortality. But under artificial conditions these mechanisms act too slowly. At high elephant densities, more trees and shrubs are killed by their feeding than can be replaced by natural regeneration. This results in a conversion of the habitat from woodland or bushland to grassland (Barness, 1984). In despite of some controversy, population control by culling has been considered in order to keep the population in a safe level (Eltringham, 1979). The species has a complex matriarchal social system from which male elephants are excluded at puberty (Moss, 1988). Female elephants need to live in groups, and their longevity has created conditions favorable for the evolution of complex social interactions among herd members (Dublin, 1983). According to Dublin, dominant females may reduce the reproductive success of lower-ranking females either by outcompeting them for resources necessary for reproduction or by direct behavioral intervention. The elimination of dominant females by ivory poaching or culling may breakup the complex social structure of the groups, permitting subordinate females to breed. However, evidence from other mammals that live in matriarchs suggests that this often lead to the aggregation of neighboring groups into large herds (Clutton-Brock and Albon, 1989).

Trophy hunting and game ranching of African ungulates, in special the impala (*Aepyceros melampus*), differ significantly from natural predation, with trophy hunting showing extreme selection for adult males and game hunting leading to disproportionate harvests of young males (Ginsberg and Milner-Gulland, 1994). According to these authors, both theory and experimental data suggest that male ungulates are limited in absolute ability to inseminate females. They argue that the interaction between sperm limitation and harvests with highly male-biased sex ratios can lead to greatly reduced number of young born and population collapse.

Movement data obtained on radio-tagged white-tailed deer (*Odocoileus virginianus*) during managed hunts reveal that the daytime movement patterns are different from daytime movements prior to and following the hunts. Generally, deer movement increases as hunting pressure increases. An absence of understory vegetation may stimulate deer to move as hunting pressure increases

(Marshall and Whittington, 1968). Similar reactions were observed in the drive census of the species (Tester and Heezen, 1965), and can be expected for mule deer exposed to hunting pressure (Reed, 1981). Moving away from their original home-range may not be considered as a social behavior. However, when animals move from a place to another, in order to avoid hunters, they probably increase the population density in the new site. This may affect density-dependent factors of the population in the area (Fowler, 1987). In terms of social behavior, there is an increase in the frequency of social encounters which can affect the social behavior – at least quantitatively – and the social structure of both the original and the new groups or populations.

Polygynous mammals offspring sex ratio seems to be affected by maternal capacity for reproductive investment (Sunquist and Eisenberg, 1993). According to Verme (1983), a male-biased birth rate usually occurs in white-tailed deer populations under the following conditions: where the bulk of the breeding stock consisted of pubertal doe fawns and yearlings, in herds of low density or scattered distribution, among animals nutritionally deprived during the rut, and in instances of extremely density leading to intraspecific strife. Conversely, according to this author, more female births would prevail in stable or increasing populations on good range, or alternatively, where seasonal food restrictions caused infertility or heavy neonatal mortality leading to compensatory fecundity in the ensuing breeding season. Based on that, the authors suggests that biologists should consider such differences among herds and manage them accordingly when establishing bucks-only and/or antless deer harvest quotas under a particular set of circumstances to avoid a future breakdown in the reproductive activity of the population as a result of a disproportion in its sex ratio.

Staines (1978) noted that red-deer (*Cervus elephus*) under low population density, caused by hunting, presents higher growth rates of young and fertility of adults. He also noted that the age of puberty decreases, as well as the over-winter natural mortality. This seems to be related to a decrease in the intraspecific competition in hunted populations. Clutton-Brock and Albon (1989) inferred that selective culling of older hinds, in or-

der to minimize natural mortality, may lead to the aggregation of neighboring groups into large herds, by the removal of matriarchs. The optimal group size is variable in a population and can change in response to ecological factors and environmental disturbances, in order to yield maximum individual fitness (Caraco and Wolf, 1975 and Sibly, 1983). On the other hand, increasing group size in red-deer populations exposed to over-hunting is likely to be associated with a reduction in reproductive performance, besides making culling harder (Clutton-Brock and Albon (1989)).

Many cervids scrape their antlers against young trees and remove bark from the stems. In roe deer (*Capreolus capreolus*) this behavior is called fraying. This can result in damage in a commercial forest plantation, so attempts have been made to control deer population in affected areas in Scotland (Cumming, 1974). Results from a shooting experiment, conducted by Cumming, suggests that fraying could be reduced most effectively by shooting non-territorial bucks. The reason seems to be that fraying is related to a redirected activity, or mock fighting, by low ranked young bucks, and not to scent marking of territorial bucks. Indiscriminate shooting would be inefficient and might actually increase fraying because the competition to replace territories could result in an increase in the frequency of mock fighting.

Heavy hunting pressure on bull moose (*Alces alces*) can lead to a pronounced male-biased sex-ratio. The reproductive ability of certain European moose population decreased markedly when there were more than two females per adult male (Markgren, 1974). According to this author, the moose is "conditionally polygamous", as the bulls stays with one cow for several days until her estrus is over and then he goes searching for other females in a receptive stage. Comparing different densities between European and Alaskan populations, the author infers that changes in sex-ratio associated with population decline, both caused by hunting pressure, may result in the decrease of the population reproductive activity.

Wild canids such as wolves, foxes, coyotes, and dingoes had a great impact in human culture. Their control, in some situations, still represent some of the most complex wildlife management

problems with considerable amounts of money being spent, usually without success. The costs and benefits of control and/or alternative management strategies are rarely evaluated, nor do we know why canid depredations on livestock can be significant in some areas but negligible in others. The impact of control operations on canid populations is also poorly understood, with few effective methods to monitor changes in population size (Harris and Saunders, 1993). According to these authors, population perturbations invariably result in an increased productivity by an increase in the proportion of the females breeding and the post-natal survival of young. Also according to Connolly (1978), coyote population density is not affected by human harvesting because of compensatory changes in reproduction. Kleiman and Brady (1978) argue that polygamy may be common in persecuted canid populations, although it can be occasionally observed in undisturbed species. However, according to Mech (1977), as wolf numbers decline, pup starvation become apparent, followed by lower pup production, and then by increased intraspecific strife. According to this author, at higher densities, adult pack wolves were the most secure members of the population, but as the population declines, they become the least secure because of intraspecific strife.

According to Hoogesteijn *et al.* (1993), deforestation, rudimentary cattle herd management, and poaching of the jaguar and its preys in the Venezuelan Llanos predispose this species to prey on cattle. According to these authors 53 to 75% of jaguars killed while preying on cattle exhibited man-inflicted wounds, diminishing the cat's ability to hunt normally. Besides forcing the animals to prey on easier prey, these man-inflicted wounds could prevent territorial animals from defending their territory satisfactorily. This could stimulate non-territorial animals to displace injured ones, which could result in an increase of the fights in the population.

Wielgus and Bunnell (1994) report that increased hunting mortality of older adult brown bears (*Ursus arctus*) coincides with an influx of younger immigrant males. According to these authors, this results in infant kills by such males, in order to bring females into estrus, and in the rejection of such males by the adult females, which

results in the decrease of the reproductive rate and the population decline.

One of the most crucial, and controversial, problems in the wildlife management is the evaluation of strategies for eliminating endemic diseases that can be transmitted to humans and/or livestock by wildlife, such as fox rabies and tuberculosis in badgers. Mathematical results on this need to be treated with caution, as they depend heavily on the assumptions made as to how infectivity would change under the strategies considered (Mollison, 1987). According to this author, reducing population density by killing a certain proportion of the population could actually increase infectivity if the social structure of the population is disrupted.

Capybaras, peccaries, and primates are largely hunted for subsistence and commercial purposes in the Neotropics (Ojasti, 1991; Kaplan and Kopschke, 1992; and Mittermeir, 1991). Capybaras are the largest surviving rodents. Although the number of individuals participating in a group varies widely, accounts of their social lives indicate that they are gregarious (MacDonald, 1981 and Alho *et al.*, 1989). Although some groups produce many young, these are rarely recruited as adults into their parental group (Herrera and MacDonald, 1987). Replacement of the dominant male can cause a notably loss in the social structure in capybara groups (Schaller and Crawshaw, 1981). Peccaries are social animals that live in herds or groups throughout their lives. No temporary seasonal groups occur according to sex and age, as happens among many ungulates where male bands and harems are common at certain seasons. The most common changes in herd size occur because of deaths or births, but occasionally animals move out of a herd or new animals join (Sowls, 1974). Anecdotal reports from hunters in Arizona indicate that herd size has been decreasing in the last years possibly as a consequence of hunting pressure (Sowls, 1984). Primates perform a wide range of different kinds of social behavior. Some of their interactions with other members of their groups are altruistic or cooperative, while other interactions are competitive or aggressive (Silk, 1987). According to Rudran (1973), the replacement of the leader male can lead to social changes in one-male troops of purple-faced langurs (*Presbytes senex senex*). Although there is no

scientific report about, shooting dominant individuals from populations of capybaras, peccaries, and primates can result in temporary social structure breakdown and shifts in the social behavior of the animals.

The social behavior of a species is a complex resultant of different environmental pressures like food and predators (Krebs and Davies, 1993). The fitness benefits of sociality are related to the improving of the following factors: detection of enemies, foraging efficiency, defense, and care of offspring. On the other hand, the fitness costs of sociality are related to the increase of the various aspects of intra-specific competition and dissemination of diseases (Alexander, 1974). Most of these factors can be affected by the social structure breakdown usually caused by hunting pressure. Experiments in captivity have demonstrated that the social behavior of rodents can change very fast in response to environmental changes (Strecker and Emlen, 1953; Strecker, 1954 and Southwick, 1955a and 1955b). Although pacas (*Cuniculus paca*) are remarkable solitary rodents, Smythe (1991), using some very creative management tricks, is rearing a second-generation "social" pacas in captivity.

There is some controversy about the real role of humans as predators in some specific environments such as rain-forests. Bailey *et al.* (1989) argue that rain-forests could never have supported human populations by relying solely on hunting and gathering, but some agricultural activity is necessary. On the other hand, Colinvaux and Bush (1991) consider this ecosystem as an ample support for humans to live by foraging, hunting and fishing using simple missile weapons. The disciplinary boundaries between the natural and the social sciences have caused humans and their activities to be viewed as somehow separate from other animals. Studies of sympatric predators have suggested that species may partition their use of habitat and prey species in response to competition between the predators themselves. This may no longer be the case in the Neotropics when humans hunt in areas occupied by pumas and jaguars. As a result, where pumas and jaguars are sympatric with humans hunting for subsistence, the population of big cats may decline as a direct consequence of competition with humans (Jorgenson and Redford, 1993).

Inferences and observations are important to the development of wildlife management and conservation but science advances most rapidly by manipulative experiments. In wildlife management, manipulations are performed most commonly by managers to achieve a management objective rather to answer a question. Hence, most management treatments are not designed as experiments (McNab, 1983). Manipulative experiments might help us to understand better the complex implications of hunting pressure on the social behavior of vertebrates, although such studies would not be an easy task with rare or shy species.

CONCLUSIONS

Hunting pressure is essentially an interaction between both human and hunted species. Therefore, it is dynamic both in terms of space and time. Vertebrates respond to human hunting pressure in many different ways, depending on the susceptibility of the species. The one-side extreme example is the coyote, whose population densities apparently are not affected by hunting (Connoly, 1978). The other-side extreme example can be considered the passenger pigeon, that became extinct after a breakdown in the reproductive success of declining (although still common) populations (Halliday, 1980). Many intermediate situations are possible, and more likely.

Human hunting pressure can affect not only a species demography but also its social behavior. Parental care, territoriality, reproductive behavior, group-size, fraying behavior, mating system, and intraspecific competition can change in response to the exploitation of individuals of a population. Hunting can be considered as a disturbance that can lead the animals to move out of their original home-rangers. This can breakup the social structure and can cause long-term effects on the demography of hunted as well as nearby populations, amplifying the impact of hunting. Species depending on large herds or aggregations to breed successfully may decline markedly when exposed to overhunting, even for few years. On the other hand, harvest can be compensated in territorial species by a "surplus population" of non-territorial individuals. Furthermore, an increase in the reproductive activity, as a response to hunting pressure, can compensate its effects in some species. Understanding the implications of hunting

pressure on the social behavior of vertebrates might be decisive in the establishment of wildlife management and conservation programs as well as to the establishment of disease control and eradication of damaging species. Manipulative experiments might help us to model such complex interactions.

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