SOME EFFECTS OF HUNTING ON WILD MAMMALIAN POPULATIONS

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Abstract - Despite the importance of hunting in human evolution, in most cases the long-term effects of this activity on populations of wild animals are poorly known. Behavioural effects include chiefly an interference in spatial behaviour, e.g. a temporary abandonment or substantial increase of the previous home range and/or a significant spatial and temporal change in habitat use for security reasons. Genetic consequences may also be important, especially if trophy hunting is involved. Hunting regimes on ungulates and control of predators can greatly affect the age structure of the hunted population, with unpredictable consequences e.g. an increase of damage to coltures and the spread of disease.

Résumé - Conséquences de la chasse sur des populations de mammifères sauvages. En dépit de l'importance de la chasse dans l'évolution humaine, les effets à long terme de cette activité sur les populations animales sauvages sont, le plus souvent, mal connus. Les effets sur le comportement incluent principalement une interférence dans le comportement spatial, comme un abandon temporaire ou un accroissement substantiel du territoire d'origine et/ou un changement spatial et temporaire significatif dans l'utilisation de l'habitat pour des raisons de sécurité. Les conséquences génétiques peuvent aussi être importantes, en particulier si des trophées de chasse sont impliqués. Les régimes de chasse sur les ongulés et le contrôle des prédateurs peuvent grandement affecter la structure d'âge de la population chassée, avec des conséquences imprévisibles, comme par exemple une augmentation des dommages causés aux cultures et la diffusion de maladies.

1. Introduction

Hunting has played a fundamental role in the biological and cultural evolution of men. As a consequence of this process, the effects of hunting on wild populations of game animals have contemporaneously developed. An early example of the impact of men on wildlife can be found in Klein (1979) who, starting from the life tables of some African animal species, recognised two basic approaches in Stone Age hunters, termed respectively *attritional* (concentrated on young animals and old adults) and *catastrophic* (hunting of few young animals and many prime adults). Modern men have been, from their first appearance, responsible for strong effects on populations of wild animals; they have also been regarded as one of the main causes of animal extinctions (Davis, 1987, for a review). Despite the crucial importance of this process, poor information is currently available on the biological effects of hunting on prey populations. The results of some recent studies on this subject can provide some interesting insights. Aim of this paper is to summarise several aspects of the current knowledge on the effects of modern hunting on game animals.

2. Behavioural and physiological effects.

Some traditional hunting techniques practised in central and southern Europe make use

of dogs to search and to pursue deer, *e.g.* the Spanish *monteria*, the British *deer hunt* and the French *chasse à courre*. A similar hunt is also present in north-eastern Italy, Brescia and Udine districs. This hunt, which involves many dogs simultaneously (up to 20-30) and a long-lasting chase, exerts a remarkable interference on the hunted population, especially on its spatial behaviour. Braza (1975) reported a decrease of population size, as well as an aggregated and peripheral distribution of fallow deer *Dama dama* in an area of Spain as a consequence of a *monteria*. A similar effect may be determined just by the presence of free-ranging dogs. In a Mediterranean coastal area of central Italy two radio-tagged female roe deer *Capreolus capreolus* were pushed more than 3 km away from their normal home range (≤15 ha) by a free-ranging dog escaped for less than one day from its owner (Apollonio, unpublished).

In Denmark, roe deer have completely disappeared from forests where dogs are allowed to move freely (Jeppesen 1987a). Sweeney *et al.* (1971) reported a different impact of dog pursuing on male and female white tailed deer *Odocoileus virginianus*, because of the different behaviour of the two sexes during the chase. While males showed a long, linear run, females appeared to be strictly linked to their vital area, with runs starting and ending in the same area. Deer show a remarkable attitude to maintain their original distribution even in presence of strong human-caused interference (Dasmann & Taber, 1956; Georgii, 1980a), but the use of dogs for hunting activities has been often recorded as an important cause of harassment. Sweeney *et al.* (1971) and Naslund (1979) reported significant dispersing movements of white tailed and roe deer, respectively, from their usual home range. Jeppesen (1987b) recorded two different reactions of red deer *Cervus elaphus* in response to the use of dogs in hunting activities in Denmark: "immediate escapes" at the beginning of the disturbance (within 3.5 km, on average) and "late escapes", at the

end of the disturbance, to areas distant 3.8 km on average. The latter was a behaviour shown also by individuals actually not pursued by dogs and by those not directly involved in the hunt, suggesting a negative effect even greater than expected. In both cases the permanence outside their customary home ranges was 2-4 days long. Moreover, when back to their familiar areas, they tended to move continuously, in the morning trying to avoid the same areas used as a shelter the evening before, and walking randomly over wide areas. Repeated hunts forced the animals to move to the same shelter areas, which became traditional refuges at the end of all escapes. This led to an increase of home ranges (Jeppesen, 1987b). The same author reported about similar consequences of hunting pressure on roe deer. In 25 out of 26 cases the animals hunted with dogs ran 850 m away on average (1140 m in open habitats, 525 m in woodland). More than 30% of these animals were forced to temporarily abandon their home-ranges. Five out of 10 roe deer living outside the hunting area showed the same behaviour as a likely reaction to the disturbance. The animals remained in their refuge areas for a maximum of 7 hours before coming back to their previous locations. Similar results were reported by Jullien *et al.* (1991) and Brandt *et al.* (1998) for the wild boar, especially adult males, as well as Vercauteren & Hygnstrom (1998) for white tailed deer. In this case, home range sizes of resident deer did not show any substantial variation before and after the hunts, but home range centres shifted of 194 m on average, in different directions. Seven out of 19 radiotagged deer did not leave their pre-hunt home ranges, but 10 individuals moved to unhunted portions of the study area and the remaining two animals moved to areas within their home ranges where hunting was prohibited. In most cases, the deer returned to their previous home ranges within six days after the hunt. Only one individual established a new home range about 3 km away. Habitats with a rich vegetation cover were

positively selected in nearly all cases. Kufeld et al. (1988) described an identical behaviour for a related species, the mule deer *Odocoileus hemionus*. In this case females avoided hunters by spending more time in densely vegetated areas within their home ranges. Also in another study (Marshall & Whittington 1968) the increased hunting pressure was responsible for an expansion of deer movements.

Furthermore, Batcheler (1968), Douglas (1971) and Georgii (1980b) showed that a strong hunting pressure on ungulates tends to stimulate strictly nocturnal habits.

Bateson (1997) made an attempt at assessing the behavioural and physiological effects of hunting red deer with dogs. He found out that chases with dogs covered on average 19.5 km, in hunts which lasted on average just over 3 hours. Chased deer exerted themselves maximally until the end: one physiological indicator of stress (cortisol) rose rapidly in their blood and haemoglobin released by the break-up of red blood cells also appeared in the plasma in large amounts. These levels were higher in animals hunted for longer distances. In the course of the hunts muscles started to show signs of physical damage because of excessive exertion. Levels of a pain-killing hormone (β-endorphin) rose steadily with distance hunted. As prolonged stress may weaken the immune system, pursued deer could become more susceptible to disease - if they escape the hunt. Bateson's conclusions (1997) probably also apply to the fallow and especially the roe deer. In fact, while the red deer is built, to some extent, as a cursorial ungulate, with some adaptations to running, the roe deer is a wood-dwelling saltor and best adapted to evade capture by its main predators, the lynx and the wolf, with short athletic leaps and dashes or by hiding. If the prolonged exercise of the hunt may not be natural for red deer, it is even less natural for roe deer and one may assume that hunting with dogs will likely be even more damaging on this species (*cf.* Cederlund & Kjellander, 1991, but see also

Semenzato, 1996).

3. Genetical effects

Ideally, game management should not alter the sex ratio and age structure of hunted populations, as well as the genetic variability and structure within populations and species. Selective hunting for trophies has been repeatedly reported by many authors as a source of decrease in genetic variability, because of the criteria used to select individuals, mostly based on superficial morphological characters (Hartl 1996). In Central Europe this practice is widespread and it operates to obtain an extreme development of some morphological characters, such as body size and various other traits considered as a "trophy" (antlers, fangs, etc.). The number of antler points and the length of spikes in subadult individuals are thought to be amongst the most important culling criteria to reach a better quality of trophies in red deer. In particular, this is considered an important indicator for later antler development (Hartl, 1991).

Hartl et al. (1991) investigated two red deer populations originating one from another and subjected respectively to mild and intensive hunting. Although no significant association between heterozigosity and the development of various antler traits was detected, several associations between enzyme genotypes and antler traits were found, demonstrating a change in allele frequencies due to selective culling. These authors took some representative antler measurements and evaluated the genotypes of a number of stags at several enzyme *loci*. While stags homozygous for the "125" allele at the *Idh-2* locus showed a number of antler points significantly higher than carriers of other genotypes already from an age of 2 years on, stags homozygous for the "100" allele at the *Acp-2 locus* showed an interestingly different pattern. From an age of 7 years on they showed significantly larger antler dimensions than carriers of other genotypes; in 2-6 years old individuals, however, Acp-2[100/100] carriers had

an antler size lower than average. A comparison of these populations revealed a significant difference in the respective allelic frequencies at *Idh-2* and *Acp-2 loci* between the "source" population (with very little selective hunting) and the "daughter" population (with intensive selective hunting). The increment in the frequency of $Idh-2^{125}$ was too great to be explained through genetic drift alone; it was interpreted as the result of the elimination of young stags with a low number of antler points (2-5 years old). On the other hand, the frequency of $Acp-2^{100}$ was considerably lower in the intensively hunted population. Also in this case the extent was too large to be explained by genetic drift alone; the most reliable interpretation is the elimination of those stags with antlers smaller than average at the time of artificial selection against a low number of antler points, but which would become large when stags grew older. The artificial selection for a particular antler trait thus caused a remarkable effect on the genetic structure of that red deer population.

A similar approach has been used to assess the potential danger of selective hunting for the welfare of a population. The same *Idh-2* allele was used by Pemberton *et al.* (1988) for the identification of some genotypes associated with female fecundity and juvenile survival.

In the light of the correlation between allelic frequencies at *Idh-2*, the development of antlers and numerous fitness components, in the long run the effect of selective hunting for particular qualities could have unpredictable consequences for a wild population (Hartl 1996).

Hunting is often aimed at reducing the population size of predators. The genetical consequences of this practice may also be important. Frati *et al.* (2000) used allozymes and mtDNA techniques to assess and to compare the genetics of red fox *Vulpes vulpes* populations from protected areas (with no natural predator of foxes) to those sampled in areas with hunting pressure. They found a significantly much lower (actually, almost absent) genetic variability in the former in comparison to the latter; differences were independent from sample size. Thus, apparently, the effects of hunting may enhance the population viability of red foxes, which is just the opposite target of the intensive hunting campaigns against this canid.

4. Demographic implications
Besides behavioural and genetical effects, hunted populations can suffer from a shooting unbalanced in terms of sex and age classes. As a consequence, the structure of a population may be greatly altered. Different hunting regimes can affect the demographic structure of the hunted population in different ways (*e.g.* Tosi & Spagnesi 1985, for Alpine chamois *Rupicapra rupicapra*; Mccullough 1987, for American deer *Odocoileus* spp). In Poland, Milkowski and Wojcik (1984) found out that, in the decade from 1970 to 1980, a heavy hunting pressure on the adult cohort of a wild boar population lowered the mean age of that population and, thus, its reproductive rate. A local concentration of females, subadults and piglets in large mixed groups determined a markedly greater impact on coltures, while mean body weight significantly decreased. Comparable information was reported by Gaillard *et al.* (1987) for a study area in France. As to carnivores, Cavallini (1994) described the age structure of the fox population in Pisa Province (Western Central Italy). This author calculated an average rate of 0.46 killed specimens/100 ha, close to the European mean value. The relatively small percentage of subadults in his sample (lower than the European average) and a fair longevity represented by 9 age classes, suggested a scarce mortality rate for that population. Hence, the effects of hunting seemed to be fairly small, probably due to the relatively mild and temporally restricted hunting pressure (Cavallini, 1994). On the contrary, the substantially higher percentage of subadults found in USA (*e.g.* Ables, 1975) may be referred to a longer early hunting season, where young foxes

are killed before their first winter. Parigi & Lovari (unpublished) found a strong impact on the age class composition of an intensively hunted fox population in Central Italy. About 78% of the sampled foxes (N=122) were under 1 year of age; the maximum age class assessed by tooth wear was 4 years old (Fig.1). As life expectation in wild foxes can reach 9 years (Macdonald & Barrett, 1993), the situation reported above (with a mean age estimate of 1.4 years) was strongly abnormal. Nearly all foxes had been shot in drive hunts with dogs; biased sampling towards the youngest age classes was unlikely, in particular to such a great extent. Therefore, Parigi & Lovari's (unpublished) sample probably reflected the local population structure, with some approximation. Young foxes tend to disperse and dispersal movements can be substantial (e.g. up to several tens of kilometres in just one year). Thus, a population structure abnormally biased towards the younger age classes may favour the spread of disease such as rabies and mange (Fico, pers. comm.).

Conversely, Fico et al. (unpublished) have described the age composition of an unhunted wolf population in Central Eastern Italy. In this sample (N=59) nearly all causes of mor-
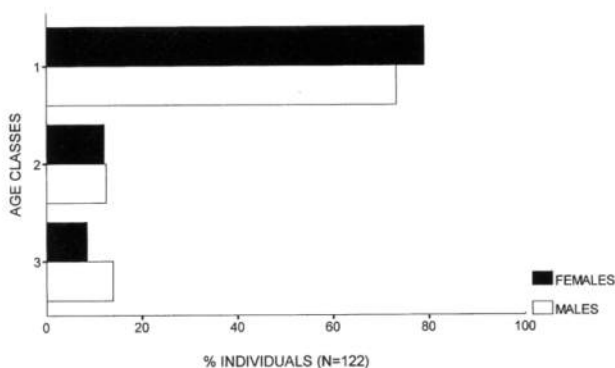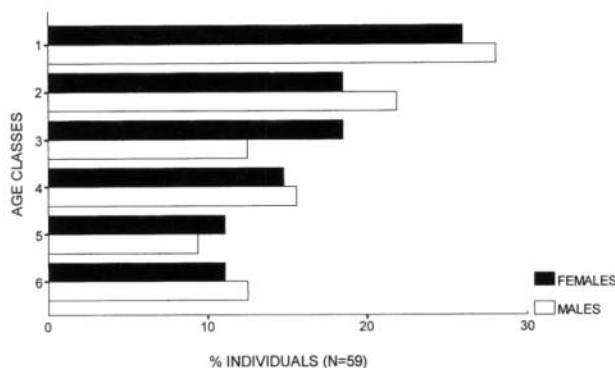

Fig. 1 - Age structure of a fox population under heavy hunting pressure, Central Italy. Age classes are expressed in months: 1 (12); 2 (13-24); 3 (≥ 25). Parigi & Lovari, unpublished data.

Fig. 2 - Age structure of an unhunted wolf population, Central Italy. Age classes are expressed in months: 1 (0-12); 2 (13-24); 3(25-36); 4 (37-48); 5 (49-60); 6 (≥ 61). Fico, Lovari & Burrini, unpublished data.

tality were induced by man, mainly (about 50%) by road casualties, but not by hunting. Young wolves (less than 1 year old) built up 27.1% of the population, the bulk of which (88%) was constituted by 2-5 years old individuals. Up to six age classes were recorded (Fig.2). The unaffected age structure of this population can be explained as the likely non-selective effect of causes of mortality, although man-related.

5. Conclusions

Wildlife management is "the science and the art of changing the characteristics and interactions of habitats, wild animal populations and men in order to achieve specific human goals by means of the wildlife resource" (Giles, 1971). A great responsibility is laid on man any time he manipulates the populations of wild animals. Awareness of the effects of these manipulations has grown in recent years, but far too many management operations are still prompted by short-term policies, often ignorant of long-term effects on wildlife. These operations often act on animal populations in an anti-Darwinian sense, *e.g.* trophy hunting (Lovari, in press), and must not be encouraged.

Aknowledgements

REFERENCES

ABLES E.D. (1975) - Ecology of the red fox in North America. In: Fox M.W. (ed.), *The wild canids. Their systematics, behavioral ecology and evolution.* New York, Van Nostrand Reinhold Co.: 216-236.

BATCHELER C.L. (1968) - Compensatory response to artificially controlled mammal populations. *Proceedings of the New Zealand Ecological Society* 15:25-30.

BATESON P.P.G. (1997) - *The behavioural and physiological effects of culling red deer.* Report to the Council of the National Trust, University Publication Centre, Cambridge.

BRANDT S., VASSANT J. & JULLIEN J.M. (1998) - Domaine vital diurne des sangliers en forêt de Chateauvillain - Arc en Barrois. *Bull. Mens. Off. Nat. Chasse* 162: 29-36.

BRAZA F. (1975) - Censo del gamo *Dama dama* en Doñana. *Naturalia Hispanica* 3: 1-27.

CAVALLINI P. (1994) - *Variazioni nella biologia della volpe* Vulpes vulpes (L.). Doctoral thesis, Univ. of Siena, Siena, Italy.

CEDERLUND G. & KJELLANDER P. (1991) - Effects of chasing by hunting dogs on roe deer. Trans. *Congr. Int. Union Game Biol.* 20: 363-370.

DASMANN R.F. & TABER R.D. (1956) - Behaviour of Columbian black tailed deer with reference to population ecology. *J. Mammalogy* 37: 143-164.

DAVIS S.J.M. (1987) - *The archaeology of animals.* Batsford, London.

DOUGLAS M.J.W. (1971) - Behaviour responses of red deer and chamois to cessation of hunting. *New Zeal. Journal of Science* 14: 507-518.

FRATI F., LOVARI S. & HARTL G.B. (2000) - Does protection from hunting favour genetic uniformity in the red fox? Z.f. Saügetierkunde 65: 76-83.

GAILLARD J.M., VASSANT J. & KLEIN F. (1987) - Quelques caractéristiques de la dynamique des populations de sanglier en milieu chassé. *Gibier Faune Sauvage* 4: 31-47.

GEORGII B. (1980a) - Einflüsse menschlicher Störungen auf Standortwahl und Aktivitätsmunster weiblicher Rothirsche.

GEORGII B. (1980b) - Home range patterns of female red deer (*Cervus elaphus*) in the Alps. *Oecologia* 47:278-285.

GILES R.H. (1971) - The Approach. In: Giles R.H. (ed.), *Wildlife Management Techniques*, Wildlife Society, Washington D.C., U.S.A.: 1-4.

HARTL G.B. (1991) - The influence of game

management on allelic variation in large mammals of central Europe. In: Randi E., M. Spagnesi (eds.), Proceedings of the meeting: "Genetica e Conservazione della Fauna". *Suppl. Ric. Biol. Selvaggina* 18: 95-108.

HARTL G. B. (1996) - Population genetics and game management. In: Lorenzini R. *Aspetti genetici nella gestione della fauna selvatica.* Veterinaria Italiana Monogr. 19: 89-101.

HARTL G.B., LANG G., KLEIN F. & WILLING R. (1991) - Relationships between allozymes, heterozygosity and morpho-logical characters in red deer *Cervus elaphus* and the influence of selective hunting on allele frequency distributions. *Heredity* 66: 343-350.

JEPPESEN J.L. (1987a) - The disturbing effects of orienteering and hunting on roe deer *Capreolus capreolus. Dan. Rev. Game Biol.* 13: 1-24.

JEPPESEN J.L. (1987b) - Impact of human disturbance on home range, movements and activity of red deer *Cervus elaphus* in a Danish environment. *Dan. Rev. Game Biol.* 13: 1-38.

JULLIEN J.M., BRANDT S., VASSANT J. & CHANTECAILLE S. (1991) - Des sangliers chassés en battue en forêt démaniale de Chateauvillain - Arc en Barrois: leurs stratégies pour échapper aux chasseurs et aux chiens. *Bull. Mens. Off. Nat. Chasse* 162: 29-36.

KLEIN R.G. (1979) - Stone Age exploitation of animals in southern Africa. *American scientist* 67: 151-160.

KUFELD R.C., BOWDEN D.C., SCHRUPP D.L. (1988) - Influence of hunting on move-ments of female mule deer. *J. Range Manage.* 41: 70-72.

LOVARI S. (in press) - Conservation and hun-ting: a viable formula? In: Franco N. (ed.), *World Atlas of Caprinae.* International Council for Hunting and Game Conservation, Paris and Madrid.

MACDONALD D.W. & BARRETT P. (1993) - *Mammals of Britain and Europe.* Collins, London.

McCULLOUGH D.R. (1987) - The theory and management of *Odocoileus* popula-tions. In: *Biology and management of the Cervidae.* Research Symp. Nat. Zool. Park, Smithsonian Institution Press, Washington D.C., U.S.A. Pp.: 535-549.

MARSHALL A.D. & WHITTINGTON R.W. (1968) - A telemetric study of deer home ranges and behaviour of deer during managed hunts. *Proceedings of the Southeastern Association of Game and Fish Commissioners* 22: 30-46.

MILKOWSKI L. & WOJCIK J.M. (1984) - Structure of wild boar harvest in the Bialowieza Primeval Forest. *Acta Theriologica* 28-29: 337-347.

NASLUND B. (1979) - Rörelse och aktivitet-sregistering av rådiur som utsatts för simule-rande fritidsaktiviteter. *Naturvårdsverket Rapport* SVN pm 1147.

PEMBERTON J.M., ALBON S.D., GUINNES F.E., CLUTTON-BROCK T.H. & BERRY R.J. (1988) - Genetic variability and juvenile survival in red deer. *Evolution* 42: 921-934.

SEMENZATO R. (1996) - *Relazione tecnica [caccia al capriolo con cani].* Osservatorio Faunistico di Pordenone, Pordenone, Italy.: 1-19.

SWEENEY J.R., MARCHINTON R.L. & SWEENEY J.M. (1971) - Responses of radio-monitored white-tailed deer cha-sed by hunting dogs. J. *Wildl. Manage.* 35: 707-716.

TOSI G. & SPAGNESI M. (1985) - Valutazione quantitativa e pianificazione della gestione venatoria in popolamenti di camosci. In: *Atti Simp. Inter. Cheratocongiuntivite Infettiva del Camoscio,* Vercelli-Varallo Sesia. Pp.: 171-177.

VERCAUTEREN K.C. & HYGNSTROM S.E. (1998) - Effects of agricultural activities and hunting on home ranges of female white-tailed deer. *J. Wildl. Manage.* 62: 280-285.