Eur J Wildl Res
DOI 10.1007/s10344-005-0022-2

REVIEW

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Disease risks and overabundance of game species

Received: 9 August 2005 / Accepted: 26 October 2005

Abstract Different studies have evidenced the relationship between host abundance and health status of wildlife populations. Diseases that benefit from wildlife overabundance can affect not only the fitness and trophy quality of game species, but also public health, livestock health, and the conservation of endangered species. This paper reviews a number of European examples to highlight the relationship between overabundance and disease in game species, and discusses the possibilities of limiting the associated risks. Management tools to estimate overabundance are needed for legislative purposes and for the monitoring of wildlife populations, but artificial feeding interferes in the objective measurement of overabundance. Therefore, we propose a multidisciplinary approach to diagnose if a given wildlife population is overabundant. This includes not only signs such as adverse effects on the soil, vegetation or fauna (first group), poor body condition scores, low trophy scores or low reproductive performance (second group), or increased parasite burdens (third group), but also the measurement of infectious disease prevalences (the fourth group of overabundance signs). This combined assessment of overabundance ideally requires the cooperation of wildlife managers, botanists, and veterinarians. Once a given wildlife population is defined as overabundant, it is difficult to establish palliative management actions. These can consist in banning certain management tools (e.g. feeding) or increasing the hunting harvest, but both of them are difficult to implement in practice. A close monitoring of both wildlife densities and wildlife diseases, the establishment of reference values for all signs of overabundance, and the mapping of the disease and density hotspots will be needed to design adequate risk-control measures for each particular situation.

Keywords Density dependence · Galliforms · Lagomorphs · Parasites · Ungulates · Wildlife health

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Introduction: defining overabundance

According to Caughley (1981), overabundance ("overpopulation") of a given wildlife species occurs when (a) this affects human life or well-being, (b) it affects the fitness of the overabundant species, (c) it reduces the density of species with an economic or esthetic value, or (d) it causes dysfunctions in the ecosystem. The density-dependent effects of overabundance on reproductive effort and body condition have been experimentally demonstrated by Stewart et al. (2005). Other studies have highlighted the negative effects of over-grazing which can have impacts on other wildlife, vegetation and soil dynamics (Warren 1997; Augustine and DeCalesta 2003). Many other ecological consequences of overabundance are treated in a recent revision by Côté et al. (2004).

Studies provide evidence for the close relationship between host abundance and health status of wildlife populations (e.g. Anderson et al. 1981), especially in microparasites (e.g. Rossi et al. 2005) or monoxenous macroparasites (e.g. Hudson and Dobson 1997). Recent studies also show the effect of overabundance on host aggregation, another key factor in disease transmission (Barlow 1996; Vicente et al. 2004b). Both density and aggregation facilitate disease transmission due to an increase of the contact rate and thus the disease's basic reproductive rate (R_0). Density and aggregation also improve disease maintenance in a given population (Rossi et al. 2005). The effect of overabundance on host condition may also indirectly increase the risk of infection, e.g. by limiting the host's immune capacity (Fernández-Llario et al. 2004; condition b). Finally, diseases that benefit from wildlife overabundance can affect the conservation of endangered species (e.g. tuberculosis, Caron et al. 2003; condition c), cause ecosystem dysfunctions (condition d), or increase zoonotic risks (e.g. tick-borne diseases, Zeman and Januska 1999; condition a). Hence, all four of Caughley's requirements for defining overabundance can be met through disease-related mechanisms.

Nonetheless, to the best of our knowledge, there exists no specific revision on the disease risks related to wildlife overabundance. This paper reviews a number of European examples to highlight the relationship between overabundance and disease in game species, and discusses the possibilities of limiting the associated risks for public health, livestock production and wildlife conservation.

Examples in small game species

Gamebirds including grouse (Tetraonidae), quails, pheasants, and partridges (Phasianidae), doves and pigeons (Columbidae) and ducks (Anatidae), among others, are a worldwide important hunting resource. In many geographical regions, sedentary or wintering populations are managed through feeding, predator control, or the release of farm-bred birds to increase the hunting harvest. Feeding (and watering), along with the control of predators, allows the densities to rise. This increases the contact rates, specially at aggregation points such as feeders or watering sites, creating ideal conditions for disease outbreaks (e.g. Höfle et al. 2004). In addition, predator control may interfere with the sanitary role of predators that tend to prey more on diseased or parasitized individuals than on healthy ones (Hudson et al. 1992; Millán et al. 2002). Cases of chronic, emaciating diseases, such as avian tuberculosis, have been linked to these situations (Millán et al. 2004a). Finally, some diseases may be introduced through releases from intensive captive breeding facilities, where certain parasites encounter optimal environments (e.g. Millán et al. 2004b). While diseases may not be an undesirable condition from the point of view of natural population regulation (e.g. Hudson et al. 1998), artificial management of populations leads to sanitary problems if it has implications for co-existing species or for human health or for economic/cultural reasons.

These examples in birds are in contrast with the lack of information of overabundance–disease links in lagomorphs, such as rabbits and hares. Despite the fact that some diseases, such as EBHS (European brown hare syndrome), pseudotuberculosis (yersiniosis), or tularemia are more frequent in dense populations (e.g. Frölich et al. 2003, Pikula et al. 2004), this group of game species seems to be less affected by overabundance-related disease problems. In the particular case of the European wild rabbit (*Oryctolagus cuniculus*), it has even been suggested that high densities may benefit herd immunity against viral diseases (e.g. Story et al. 2004).

Examples in wild ungulates

The consumption of lean meat from large game animals has probably contributed to human evolution since pre-history (Mann 2000; Rivals et al. 2004). Nowadays, wild ungulates, including Cervidae, Bovidae and Suidae, are still important game species all over Europe. But problems can arise when human intervention interferes in the natural regulation of these wildlife populations, eliminating their predators, translocating individuals or favouring some species in excess (Gortázar et al. 2000). In fact, the most obvious cases of relationships between overabundance and diseases occur among wild ungulates. The European wild boar (*Sus scrofa*) is a good example. This species is increasing its range, reaching levels previously unrecorded (Geisser and Reyer 2004). This has contributed to the spread of many diseases, including classical swine fever, Aujeszky´s disease, Porcine Circovirus type 2, and bovine tuberculosis, among others (see Table 1 and references therein).

Figure 1 uses the seroprevalence of antibodies against Aujeszky's disease virus in Spanish wild boar populations to highlight how density and management factors favouring aggregation (such as fencing and feeding) interact to create optimal epidemiological conditions for high disease prevalences. It has also been shown that the increased density and spatial aggregation of wild boars in fenced hunting estates increases the risk of getting in contact with multiple disease agents (Ruiz-Fons et al. 2006). These situations are good examples of how overabundance affects animal health.

The existence of wildlife reservoirs complicates the control of bovine tuberculosis (bTB), an important re-emerging zoonotic disease that causes major economic losses and constrains international trade of animals and their products (Wedlock et al. 2002). Major problems with wildlife TB occur in areas with a high density of susceptible host species, such as the possum (*Trichosurus vulpecula*) in New Zealand (Roberts 1996), the buffalo (*Syncerus caffer*) in South Africa (De Vos et al. 2001), and the badger (*Meles meles*) in the UK and Ireland (Cheeseman et al. 1989). Recent examples from central and southern Spain illustrate different aspects of TB epidemiology in overabundant wild boar populations. From November 1999 to February 2004, data from more than 2,000 red deer and wild boar harvested by hunters in 76 different hunting estates were obtained. Where wild boar coexist with deer, 84% of populations were TB-positive whereas only 75% were TB-positive when wild boar were present in the absence of deer. Prevalence ranged up to 100% in local populations of wild boar (mean estate prevalence 42%, Vicente et al. 2006). The isolation of TB strains from these estates strongly suggests that the *Mycobacterium tuberculosis* complex is able to survive in these high-density wildlife populations in the absence of livestock hosts (Gortázar et al. 2005).

Deer (Cervidae) are the species that have most frequently been studied regarding the issue of overabundance (Warren 1997). Problems arise specially in non-hunted, protected or periurban areas (Lees 2004), and are more evident in gregarious species, such as the fallow deer than in less gregarious ones (e.g. Santín-Durán et al. 2004).

As in the case of the wild boar, mycobacterial diseases are among the most frequently cited problems in dense deer

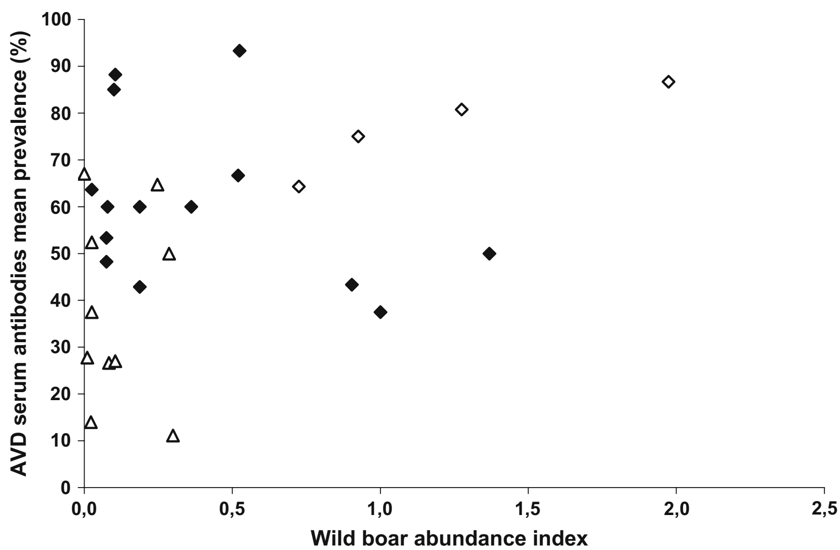
Table 1 European examples of infectious and parasitic wildlife diseases that benefit from risk factors often linked with overabundance

Disease problem	Host species	Country	Remarks	References
Tick-borne encephalitis	Roe deer and other ungulates	Czech Republic	Prevalences increase with increasing hunting harvest	Zeman and Benes 2004
Aujeszky's disease	Wild boar	Spain	Clear effect of density and management factors on prevalences	Vicente et al. 2005
Classical swine fever	Wild boar	Several European countries	Review highlighting the effect of density on disease persistence	Rossi et al. 2005
Porcine Circovirus 2	Wild boar	Spain	Clear effect of density and management factors on prevalences	Vicente et al. 2004b
Bovine tuberculosis	Red deer, wild boar	Spain	Aggregation at feeders and waterholes increases risks	Vicente et al. 2006
Paratuberculosis (Johne´s disease)	Red deer and other ungulates	Italy, Austria	Abundant domestic livestock (cattle, goats, sheep)	Nebbia et al. 2000; Deutz et al. 2005
Avian tuberculosis	Red-legged partridge	Spain	Aggregation and interspecific contacts at feeders are suspected risk factors	Millán et al. 2004a
Lyme borreliosis	Roe deer and other ungulates	Czech Republic, France, Sweden	Wild ungulate densities correlate with LB prevalence and with tick density	Pichon et al. 1999; Zeman and Januska 1999; Jensen et al. 2000
Gastrointestinal nematodes	Roe, red and fallow deer	Spain	Prevalence increases with host density	Drozdz et al. 1992; Sugar 1991; Santín-Durán et al. 2004
Lungworms	Roe deer, Spanish ibex	France, Spain	Prevalence increases with host density	Hugonnet and Cabaret 1987; Acevedo et al. 2005
Sarcoptic mange	Spanish ibex, Barbary sheep	Spain	Overabundance suspected as risk factor	González-Candela et al. 2004; León-Vizcaino et al. 1999

populations. Wherever deer are farmed, bovine TB, avian TB, and Johne´s disease (paratuberculosis), cause serious concerns (Mackintosh et al. 2004). Mycobacterial diseases have also been found in wild deer, normally when they concentrate at feeding sites (Miller et al. 2003), when high deer and livestock densities coincide (Nebbia et al. 2000), or when management factors such as fencing and feeding or even the ban of hunting (protected areas) promote deer overabundance (Vicente et al. 2005b). Increases in tick populations and in tick-borne diseases are just one of many other examples regarding the implication for herd health in high-density populations (e.g. Stafford et al. 2003, Table 1).

The introduction of exotic species can further complicate the situation (Richardson and Demarais 1992). Intense recreational use (Lutz and Kierdorf 1997) or modern infrastructures (Szabo et al. 2003) can cause wildlife habitat loss. In these cases, when high host densities coincide with limited food availability, high parasite abundances can be expected due to a loss of fitness and an increased aggregation. This was apparently the case in the sarcoptic mange (*Sarcoptes scabiei*) outbreaks in the Spanish ibex (*Capra pyrenaica*) populations of Cazorla (southern Spain, León-Vizcaino et al. 1999). In contrast, aggregation alone does not always cause higher parasitism. For example, the use of

Fig. 1 Mean seroprevalence of antibodies against Aujeszky's disease virus, plotted against abundance indexes (mean number of droppings every 100 m in 4-km transects) in 28 wild boar populations from south-central Spain (Vicente et al. 2005). Δ, open; ♦, fenced; ◇, intensively managed



feedplots did not increase gastrointestinal parasitism in white-tailed deer in the southern US (Schultz et al. 1994).

Can vets contribute to diagnose overabundance?

Management tools to estimate overabundance are needed for legislative purposes and for the monitoring of wildlife populations. But measuring overabundance is difficult and does probably require a multidisciplinary approach. Overabundance can be measured directly in terms of population density and also indirectly by measuring the consequences for the habitat (e.g. effects on natural vegetation, Augustine and DeCalesta 2003) or on the animal's fitness (e.g. trophy scores, fat levels or reproduction, Stewart et al. 2005, and parasites, Eve and Kellogg 1977).

In natural populations (i.e. without feeding, fencing and releasing), a comparison of a given population density with those already reported in the literature (considering also the habitat, the population cycles and the management goals and biodiversity objectives) is a useful first step that can help to diagnose an overabundance situation. However, overabundance in wildlife may occur without most of the associated signs because of management interventions such as supplementary feeding. This is because supplementary feeding can, to a certain extent, limit the detrimental effects of abundant ungulates on natural vegetation and crops (Calenge et al. 2004) and allow wildlife to maintain almost optimal body condition and trophy scores despite living in high densities (e.g. Fierro et al. 2002; Vicente et al. 2004a). Thus, artificial feeding interferes in the objective measurement of overabundance.

Therefore, we propose a multidisciplinary approach to decide if a given wildlife population is overabundant, which aims to quantify the impact in terms of the effects on body condition, reproduction, parasite burdens, infectious disease and the indirect effects on vegetation and soil dynamics (dysfunctions in the ecosystem). If a high-density population also shows other signs, such as adverse effects on the soil, vegetation or fauna (first group of signs), poor body condition scores, low trophy scores or low reproductive performance (second group), frequently also with increased parasite burdens (third group), overabundance must be suspected. This also includes the measurement of infectious disease prevalence (the fourth group of overabundance signs), along with the three aforementioned variables. For example, a food-supplemented ungulate population may well have acceptable trophy scores, fat levels and reproductive performance, and even a relatively low impact on natural vegetation (except in the proximities of waterholes or feeders; Brits et al. 2002), while maintaining a high prevalence of bovine TB or any other relevant disease. In our opinion, only a combined assessment of all four groups of indicators guarantees the correct identification of overabundance. This combined assessment of overabundance ideally requires the cooperation of wildlife managers, botanists, and veterinarians.

Overabundance is frequently defined by comparison of a given situation with other known ones. A population is overabundant if density estimates clearly exceed references from other populations of the same species under similar habitat conditions, and if any of the four groups of overabundance signs exceeds the limits observed in other known cases or is perceived to cause detrimental effects on the species itself, the environment or animal and human health. Hence, there is a need to define reference values for each of these signs of overabundance (e.g. Eve and Kellogg 1977; Fierro et al. 2002; Sauerwein et al. 2004; Vicente et al. 2005, 2006). A useful alternative in regions or species with little references in the literature is to monitor the changes of the defined signs in time. For example, yearling carcass weights have been used to study population density–physical condition relationships in deer (Keyser et al. 2005), and changes in the prevalence of diseases can sometimes be recorded rather easily (Rodwell et al. 2001) to assess increasing or decreasing trends, and to eventually take appropriate management actions.

Two groups of overabundance signs, the effects on soil and vegetation (e.g. Morellet et al. 2001) and the effects on parasite loads (e.g. Acevedo et al. 2005), are available in non-invasive studies. These indirect indicators are especially relevant for the monitoring of overabundance in periurban or protected areas, where hunting is limited. Unfortunately, studies on the impact on natural vegetation require a good basic knowledge on the local habitat characteristics, and there is still debate on the usefulness of fecal parasite counts as an index of parasitic burden in wildlife (Fernandez-de-Mera 2003; Seivwright et al. 2004). Exceptionally, techniques based on the physiological response of wild animals to stress or ecological pressures (for example, to numeric overabundance) may supply new non-invasive monitoring tools (Huber et al. 2003).

Managing overabundance

For all the reasons given above, overabundance is not desirable. Nature has its own mechanisms to limit overabundance in wildlife populations, including diseases, predators and food limitation (Okarma et al. 1995; Hudson et al. 1998; Aguirre et al. 1999; Albon et al. 2002). The effectiveness of these mechanisms in regulating wildlife populations depends on the species considered, the geographical region, and the degree of human intervention (or non-intervention) in a given population. Overabundance is much more frequent (or has been better studied) among ungulates than, for example, in lagomorphs (excepting introduced populations, e.g. Saunders et al. 2002). Abiotic factors such as drought or long periods of snow-lie can cause high mortality due to starvation and increased disease risk as animals are weakened and become aggregated on increasingly reduced areas of preferred habitat (e.g. Lawrence et al. 2004; Gazzola et al. 2005). But human interference can limit the effects of these natural mechanisms of population control, for example, feeding wildlife (Putman and Staines 2004), providing water (Borralho et al. 1999), controlling predators (Frey et al. 2003), or even treating against parasites (Rajkovic-Janje et al. 2004) and vaccinating (e.g. against

Aujeszky's disease in Spanish wild boars to improve hunting harvest). These interfering factors can interact with each other as suggested for predation, diseases and artificial feeding (e.g. Packer et al. 2003; Buenestado et al. 2004; Millán et al. 2004a). Hence, overabundance tends to be mostly a problem of ungulates in temperate, non-extreme climates with intense artificial management.

Once a given wildlife population is defined as overabundant, and even if there is specific evidence for disease problems, it is difficult to establish corrective management actions. If artificial feeding is one of the suspected causes, as occurs for TB in deer and wild boar, banning this practice is an option (Miller et al. 2003). However, this will be most difficult to attain in areas where feeding is used to bait animals for hunting, if the feeding ban causes significant (visible) mortality in areas open to the public (Putman and Staines 2004), or where feeding is used to provide a diversion from agricultural crops (e.g. Calenge et al. 2004, but see Geisser and Reyer 2004). Feeding may even have positive consequences on certain disease risks, as it may improve the animal's immune response weakened by such factors as stress, old age or droughts (De Vos et al. 2001), and as many parasites and disease agents benefit from an undernutrition of their hosts (Prat and De Souza 2003, Cunningham-Rundles et al. 2005). Moreover, other management tools that can contribute to overabundance, such as the provision of water at more or less artificial waterholes, or high-wire fencing, are even less easy to avoid due to different ecological, social and legal constraints.

Alternatively, increased hunting can reduce wildlife numbers and their negative effects (Geisser and Reyer 2004), but this again is difficult in certain areas such as national parks, or in regions where the management goal is set at quantity rather than quality of a game species, as in most central and southern Spanish hunting estates. One future direction is to convince hunters and wildlife managers of the benefits of management for quality, with lower densities and less detrimental consequences on habitat, wildlife and animal and human health. Eventually, government game agencies will have to establish higher hunting quotas for those estates where overabundance is diagnosed, and set up mechanisms to confirm that these extraction goals are achieved. It is evident that, in the absence of predators, hunting is the main mechanism for population regulation in forest ungulates (Gaillard et al. 1987).

A second alternative consists in the rehabilitation of the ecological situations existing previously to human intervention (the complex coexistence of natural regulatory forces), for example re-introducing large predators that formerly inhabited the area (White and Garrott 2005). But this generates social conflicts that can easily outbalance the advocated benefits of this management decision (Blanco et al. 1992).

As wild populations are increasingly managed, and urban or protected areas are also increasing in those regions where wildlife is of great socio-economic value, new sanitary problems due to overabundance can be expected in the future. A close monitoring of both wildlife densities and wildlife diseases, the establishment of reference values for all signs of overabundance, and the mapping of the disease and density hotspots will be needed to design adequate risk-control measures for each particular situation.

Acknowledgements This text summarises a lecture at the XXVIIth IUGB Congress in Hannover. This is a contribution to projects PREG-05-19, Junta de Comunidades de Castilla-La Mancha and RTA03-074-C2 INIA and FEDER, and to the agreements between FG-UCLM and Grupo Santander, beween Principado de Asturias and CSIC, and between Yolanda Fierro and the UCLM. F. Ruiz-Fons has a FPU research fellowship from Ministerio de Educación y Ciencia. Two anonymous referees substantially improved the first manuscript.

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