

Forum

Parasitological Consequences of Overcrowding in Protected Areas

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Abstract: For the past several years, there has been growing interest in understanding the dynamics of parasites in ecosystems, as well as the diversity of ways in which they interfere with conservation and health preoccupations. Although it is widely recognized that many conservation practices (e.g., wildlife translocations, species removal, food supplementation) may be associated with parasite-related problems, less attention has been devoted to exploring the parasitological consequences of the overcrowding of animals in protected wildlife areas. Here, we discuss this important ecological/epidemiological problem, presenting at the same time an overview of the main questions and challenges in this field. Using empirical and theoretical examples chosen from the literature, we focus particularly on the interactions between the overcrowding of free living species and parasite population dynamics, the evolution of parasite virulence, the indirect effects on the structure of invertebrate communities, as well as the nutritional value of prey species. We argue that conservation policies should be aware more than ever of this problem, especially given the serious health risks currently posed by the spread of virulent viruses (e.g., avian influenza).

Key words: wildlife reserves, helminths, ectoparasites, virus, birds, invertebrates

Over the past decades, a great deal of attention has been devoted to understanding the ecological importance of parasites and pathogens in ecosystems (Thomas et al., 2005; Collinge and Ray, 2006; Hudson et al., 2006). A large body of theoretical and empirical work has now documented how parasites, in spite of their small size, are functionally important in ecosystems, often intervening through subtle mechanisms but having profound effects (Poulin, 1999). As a result, most conservation biologists are, for instance, aware that parasitism is one of the most significant causes of

population regulation in many species under natural conditions (Anderson and May, 1978; Anderson and Gordon, 1982; Scott, 1988; Rousset et al., 1996; Moller, 2005). Similarly, it is widely accepted that the introduction or the elimination of a parasite in an ecosystem can strongly affect the interactions between a diverse range of species in the community, both hosts and non-hosts, and hence affect biodiversity (Torchin et al., 2002; Lafferty and Kuris, 2005).

Despite these advances, it remains highly challenging for conservationists to deal with parasites and to incorporate them in most everyday situations. This is largely due to the huge diversity of ways in which parasites intervene in ecosystems. In addition, most, if not all, conservation ac-

tions may potentially have parasitological consequences. For instance, while vaccines and antibiotics appear at first glance as efficient solutions to reduce infection risks in endangered species, they may, in contrast, favor the subsequent vulnerability of individuals to infection when the population reaches a favorable size for epidemic establishment (Cleaveland et al., 2002). Similarly, while the supplementation of food can greatly help to reduce starvation and/or to enhance breeding output when food shortage is a real problem, it can also dramatically contribute to the spread of viruses, bacteria, or other parasites associated with food and/or transmitted by contagion (e.g., Wilson and Macdonald, 1967). In raccoons, for instance, when food provisioning results in the spatial concentration of hosts around food sources, the consequence is an increase in infection levels by directly transmitted nematode parasites (Wright and Gompper, 2005). The removal of particular species (e.g., competitor, predator, introduced species) can have major demographic consequences for other species, which, in turn, may favor the explosion of parasitic infections (Packer, 2003; Lafferty and Kuris, 1993; Lafferty, 2004). Finally, it is also well known that wildlife translocations that do not take into account infection risks can dramatically fail because of parasites (Cunningham, 1996; Sasal et al., 2000; Collyer and Stockwell, 2004). In addition to these phenomena that are now widely recognized, we would like here to draw attention to an underestimated phenomenon, which concerns the parasitological consequences of overcrowding in protected areas. Rather than advocating a particular view or course of action, our intention here is to use this piece as a call for future research in this area. We use mainly the case of waterbirds to illustrate our point, but the generality of our comments extends to other types of animals in protected reserves.

Protected areas often encompass a very small portion of the total surface area potentially suitable (Dompka, 1996). In addition, even when they appear relatively large in terms of surface, the true optimal size of protected areas remains a relative parameter as it mainly depends on the number/type of species present. During the hunting season or reproductive periods, for instance, the confinement of birds inside protected areas can be extreme, with densities reaching values of several tens of thousand birds in only a few hectares (Tamisier and Dehorter, 1999; Béchet et al., 2004). The local increase in the number of hosts can have dramatic consequences for the spread of parasites in the whole population (Scott, 1988; Ezenwa, 2004). Both theoretical arguments (Anderson and May, 1978; Roberts et al.,

2002) and empirical evidence (Arneberg et al., 1998; Morand and Poulin, 1998; Arneberg, 2001; Nunn et al., 2003) are in total agreement: local host density is a major determinant of infection levels and the number of parasite species supported by a host population. In addition, as illustrated by recent mathematical developments (Hochberg et al., 2000), demographic differences across geographical landscapes can produce selection mosaics in interacting species, with virulent parasites being most likely to be found in habitats where host population density is the highest. As long as protected areas remain synonymous with high animal concentrations, their potential role in amplifying pathogen demography will persist. The use of treatments or vaccine, if any, in protected areas is likely to lead to the selection of resistance. The idea that protected areas may then constitute production units of “pathogen resistant ecosystems” is a complex problem at the interface between conservation and public health.

Not only do protected areas favor high population densities, they also usually have a positive effect on species richness (Bolden and Robinson, 2003). Because of this, they are also likely to trigger disease outbreaks by pushing parasites and hosts closer together. In extreme cases, this type of phenomenon favors the emergence of new diseases since increased interspecific contacts, and/or the elimination of the preferred host species, may result in parasites “jumping” to new host species. To our knowledge, conservation policies have not attached any real importance to this ecological/epidemiological problem in the context of wildlife reserves. These considerations, however, appear more than ever relevant in light of the serious health problems currently posed by the spread of highly pathogenic strains of avian influenza A viruses. Wild waterfowls are considered the natural reservoir of these viruses. Since infected birds mainly shed the virus in their feces, and given that it can survive in water for long periods (Stallknecht et al., 1990), attention should be paid to how overcrowding in protected areas lends itself to the spread of these diseases. Increased host densities are also likely to increase ectoparasite transmission (see review in Côté and Poulin, 1995). High ectoparasite loads have been shown to cause nest desertion and chick mortality in a range of bird species (Feare, 1976; King et al., 1977; Duffy, 1983). There is also clear evidence of the impact of ectoparasites on reproductive success and avian population dynamics (Boulinier and Danchin, 1996; Gauthier-Clerc et al., 1998).

In addition to influencing the dynamic of directly transmitted parasites, there is also much evidence that local

concentrations of vertebrates significantly determine spatial and temporal variation in the prevalences and species composition of parasites with complex life cycles. Waterbirds are definitive hosts of a broad spectrum of parasites including flukes (Digenea), tapeworms (Cestoda), roundworms (Nematoda), and thorny-headed worms (Acanthocephala). Many invertebrates such as mollusks (snails, bivalves), crustaceans, and also fish commonly act as first and second intermediate hosts for these parasites. Several studies have found a positive relationship between the distribution of waterbirds and prevalences of parasitic worms in invertebrate species (e.g., Matthews et al., 1985; Bustnes et al., 2000; Skirnisson et al., 2004) as well as in fish intermediate hosts (Marcogliese et al., 2001). Trematode parasites of snails typically attain higher densities in salt-marsh reserves than in degraded areas (Lafferty and Gerber, 2002). The parasites detrimentally affect these invertebrates, for instance, by castrating them and/or by reducing their resistance to fluctuations in abiotic conditions. The regular and massive release of infective stages resulting from waterbird concentrations can therefore have dramatic consequences for invertebrate communities through direct or indirect effects on their populations (i.e., interference with interspecific competition). For example, in populations of the periwinkle, *Littorina littorea*, a first intermediate host of trematodes, Lauckner (1987) observed cases of “zero growth” due to high rates of parasite-induced castration. Similarly, in the New Zealand mud snail *Zeacumantus subcarinatus*, the prevalence of trematode infections varies among localities in parallel with local abundance of bird definitive hosts, and trematode prevalence has proven to be the key regulating factor of local snail densities (Fredensborg et al., 2005, 2006). For definitive hosts as well, a high rate of infection by parasitic helminths may be detrimental. For instance, epizootics have been reported among bird hosts heavily infected with trematodes (Lauckner, 1985) and, in extreme cases, tapeworm or nematode infections have even been associated with mass mortality events (e.g., seabirds: Muzaffar and Jones, 2004). Although further evidence would be welcome, all these phenomena are expected to be amplified in protected areas.

A final possibility concerns the parasite-induced consequences of overcrowding on the trophic potential of the habitat. Indeed, parasites, by definition, divert resources from their hosts. For this reason, although parasitized prey are often easy to capture (Lafferty, 1992), they may be less profitable than unparasitized ones for predators, especially when parasitic loads are high. In addition to the reduction

of profitability associated with infection, a global decrease of prey body size (in all individuals, infected or not) is expected in highly parasitized areas as the result of parasite pressures selecting for early sexual maturity (Lafferty, 1993a, b; Fredensborg and Poulin, 2006). The loss of trophic potential in areas characterized by high parasite prevalences is not documented at the moment but is undoubtedly substantial (but see Plowright, 1982; Dobson, 1995ab; Lafferty and Kushner, 2000, for counterexamples). Famous case studies, for instance, the rinderpest virus in East Africa or the epizootic of sarcoptic mange in Scandinavia (Lindstöm et al., 1994), have also taught us that the impact of parasites on food webs may, because of cascade effects, result in profound disequilibria at the ecosystem level, especially when it indirectly changes herbivore demography and, thus, plant communities. In addition, De Castro and Bolker (2005) as well as Lafferty et al. (2006) recently highlighted that, in contrast to the classic belief, parasites disproportionately dominate food webs in ecosystems. Predators often ingest parasites when feeding, and such links have a large effect on food web connectance (percentage of possible links realized). Similarly, while top predators serve disproportionately as hosts, species at the mid-trophic levels have the highest combined vulnerability to natural enemies (parasites and predators). These phenomena need to be taken into account to properly assess the vulnerability of species according to their trophic level, as well as the stability and the structure of food webs in general (Lafferty et al., 2006).

A promising way of studying the interactions between parasites and overcrowding would be to manipulate variables influencing host densities in large experimental areas and to measure the resulting parasitological consequences. Alternatively, several studies have illustrated that grouping (as a behavioral trait) varies between populations, and/or can also be selected for in certain species (see Krause and Ruxton, 2002). Such situations could be used to explore the parasitic consequences of overcrowding. Species comparisons may also allow far-reaching conclusions regarding the relationships between social organization and ecological parameters like levels of parasitism. Animals that regularly and naturally congregate at extremely high densities on small areas (e.g., pinnipeds, penguins, or shorebirds) provide fruitful biological situations for such considerations. Indeed, because social congregation on islands is somewhat analogous to protected areas in terms of isolation, though it results from thousands of years of evolution, these species might help to predict long-term ecological

and parasitological consequences of overcrowding. Another interesting situation is provided by domesticated species. In many cases, the wild ancestor and its geographic range have been identified, its relation to the domestic breed has been determined by genetic and chromosomal studies, its changes under domestication have been delineated, and the approximate time and place of its domestication have been identified (see Diamond, 2002, for review). Correlations between historical and parasitological data should help to understand the evolutionary consequences of infectious diseases in isolated populations.

While reserves are in many cases an effective means of protecting wildlife from threats, they can, in certain circumstances, enhance the spread of infectious diseases. The parasitological consequences of host overcrowding in protected areas are probably inescapable, although more studies would be welcome at the moment to quantify such phenomena. Should conservation managers be happy or unhappy when wildlife reserves are packed full of species/individuals compared to outside areas? The parasitological consequences of such disequilibria should be considered as an important point in discussions concerning the optimal characteristics of protected areas.

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