

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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## REFERENCES

- Anderson RM, Gordon DM (1982) Processes influencing the distribution of parasite numbers within host populations with special emphasis on parasite-induced host mortalities. *Parasitology* 85:373–398
- Anderson RM, May RM (1978) Regulation and stability of host-parasite population interactions. I. Regulatory mechanisms. *Journal of Animal Ecology* 47:219–247
- Arneberg P (2001) An ecological law and its macroecological consequences as revealed by studies of relationships between host densities and parasite prevalence. *Ecography* 24:352–358
- Arneberg P, Skorping A, Grenfell BT, Read AF (1998) Host densities as determinants of abundance in parasite communities. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 265:1283–1289
- Béchet A, Giroux J-F, Gauthier G (2004) The effects of disturbance on behaviour, habitat use and energy of spring staging snow geese. *Journal of Applied Ecology* 41:689–700
- Bolden EG, Robinson WL (2003) *Wildlife Ecology and Management*. Upper Saddle River, NJ: Pearson Education
- Boulinier T, Danchin E (1996) Population trend in kittiwake (*Rissa tridactyla*) colonies in relation to ectoparasite infestation. *Ibis* 138:326–334
- Bustnes JO, Galaktionov KV, Irwin SWB (2000) Potential threats to littoral biodiversity: is increased parasitism a consequence of human activity? *Oikos* 90:189–190
- Cleaveland S, Hess GR, Dobson AP, Laurenson MK, McCallum HI, Roberts MG, et al. (2002) The role of pathogens in biological conservation. In: *The Ecology of Wildlife Diseases*, Hudson PJ, Rizzoli A, Grenfell BT, Heesterbeek H, Dobson AP (editors), Oxford: Oxford University Press, pp 139–150
- Collinge SK, Ray C (2006) *Disease Ecology: Community Ecology and Pathogen Dynamics*. Oxford: Oxford University Press
- Collyer ML, Stockwell CA (2004) Experimental evidence for cost of parasitism for a threatened species, White Sands pupfish (*Cyprinodon tularosa*). *Journal of Animal Ecology* 73:821–830
- Côté IM, Poulin R (1995) Parasitism and group size in social animals: a meta-analysis. *Behavioral Ecology* 6:159–165
- Cunningham AA (1996) Disease risks of wildlife translocations. *Conservation Biology* 10:349–353
- De Castro F, Bolker BM (2005) Parasite establishment and host extinction in model communities. *Oikos* 111:501–513
- Diamond J (2002) Evolution, consequences and future of plant and animal domestication. *Nature* 418:700–707
- Dobson AP (1995a) The ecology and epidemiology of rinderpest virus in Serengeti and Ngorongoro crater conservation area. In: *Serengeti II: Research, Management and Conservation of an Ecosystem*, Sinclair ARE, Arcese P (editors), Chicago: The University of Chicago Press, pp 485–505
- Dobson AP (1995b) Rinderpest in the Serengeti ecosystem: the ecology and control of a keystone virus. In: *Proceedings of a Joint Conference American Association of Zoo Veterinarians, Wildlife Disease Association, and American Association of Wildlife Veterinarians*, Junge RE (editor), East Lansing: American Association of Zoo Veterinarians/Wildlife Disease Association/American Association of Wildlife Veterinarians, pp 518–519
- Dompka V (1996) *Human Population, Biodiversity and Protected Areas: Science and Policy Issues*. Washington, DC: American Association for the Advancement of Science
- Duffy DC (1983) The ecology of tick parasitism on densely nesting Peruvian seabirds. *Ecology* 64:110–119
- Ezenwa VO (2004) Parasite infection rates of impala (*Aepyceros melampus*) in fenced game reserves in relation to reserve characteristics. *Biological Conservation* 118:397–401
- Feare CJ (1976) Desertion and abnormal development in a colony of Sooty Terns *Sterna fuscata* infested by virus infected ticks. *Ibis* 118:112–115
- Fredensborg BL, Mouritsen KN, Poulin R (2005) Impact of trematodes on host survival and population density in the intertidal gastropod *Zeacumantus subcarinatus*. *Marine Ecology Progress Series* 290:109–117
- Fredensborg BL, Mouritsen KN, Poulin R (2006) Relating bird host distribution and spatial heterogeneity in trematode infections in an intertidal snail: from small to large scale. *Marine Biology* 149:275–283
- Fredensborg BL, Poulin R (2006) Parasitism shaping host life-history evolution: adaptive responses in a marine gastropod to infection by trematodes. *Journal of Animal Ecology* 75:44–53
- Gauthier-Clerc M, Clerquin Y, Handrich Y (1998) Hyperinfestation by ticks *Ixodes uriae*: a possible cause of death in adult of

- King Penguin, a long-lived seabird. *Colonial Waterbirds* 21:229–233
- Hochberg ME, Gomulkiewicz R, Holt RD, Thompson JN (2000) Weak sinks could cradle mutualistic symbioses—strong sources should harbour parasitic symbioses. *Journal of Evolutionary Biology* 13:213–222
- Hudson PJ, Dobson AP, Lafferty KD (2006) Is a healthy ecosystem one that is rich in parasite? *Trends in Ecology and Evolution* 21:381–385
- King KA, Blankinship CR, Paul RT, Rice RCA (1977) Ticks as a factor in the 1975 nesting failure of Texas Brown pelicans. *Wilson Bulletin* 89:157–158
- Krause J, Ruxton GD (2002) *Living in Groups*. New York: Oxford University Press
- Lafferty KD (1992) Foraging on prey that are modified by parasites. *American Naturalist* 140:854–867
- Lafferty KD (1993a) Effects of parasitic castration on growth, reproduction and population dynamics of the marine snail *Cerithidea californica*. *Marine Ecology Progress Series* 96:229–237
- Lafferty KD (1993b) The marine snail *Cerithidea californica*, matures at smaller sizes where parasitism is high. *Oikos* 68:3–11
- Lafferty KD (2004) Fishing for lobster indirectly increases epidemics in sea urchins. *Ecological Applications* 14:1566–1573
- Lafferty KD, Dobson AP, Kuris AM (2006) Parasites dominate food web links. *Proceeding of the National Academy of Science USA* 30:11211–11216
- Lafferty KD, Gerber LR (2002) Good medicine for conservation biology: the intersection of epidemiology and conservation theory. *Conservation Biology* 16:593–604
- Lafferty KD, Kuris AM (1993) Mass mortality of abalone *Haliotis cracherodii* on the California Channel Islands: tests of epidemiological hypotheses. *Marine Ecology Progress Series* 96:239–248
- Lafferty KD, Kuris AM (2005) Parasitism and environmental disturbances. In: *Parasitism and Ecosystems*, Thomas F, Renaud F, Guégan JF (editors), Oxford: Oxford University Press, pp 113–123
- Lafferty KD, Kushner D (2000) Population regulation of the purple sea urchin, *Strongylocentrotus purpuratus*, at the California Channel Islands. In: *Fifth California Islands Symposium, Vol 99-0038*, Brown DR, Mitchell KL, Chang HW (editors), Santa Barbara, CA: Minerals Management Service, pp 379–381
- Laukner G (1985) Diseases of Aves (marine birds). In: *Diseases of Marine Animals*, Kinne O (editor), Chichester, UK/New York: John & Sons, pp 627–643
- Laukner G (1987) Ecological effects of larval trematode infestations on littoral invertebrate populations. *International Journal for Parasitology* 17:391–398
- Lindstöm ER, Andren H, Angeltam P, Cederlund G, Hornfeldt B, Jaderberg L, et al. (1994) Disease reveals the predator: sarcoptic mange, red fox predation and prey populations. *Ecology* 75:1042–1049
- Marcogliese DJ, Compagna S, Bergeron E, McLaughlin JD (2001) Population biology of eyefluks in fish from a large fluvial ecosystem: the importance of gulls and habitat characteristics. *Canadian Journal of Zoology* 79:1102–1113
- Matthews PM, Montgomery WI, Hanna REB (1985) Infestation of littorinids by larval digenea around a small fishing port. *Parasitology* 90:277–287
- Moller AP (2005) Parasitism and the regulation of host populations. In: *Parasitism and Ecosystems*, Thomas F, Renaud F, Guégan JF (editors), Oxford: Oxford University Press, pp 43–53
- Morand S, Poulin R (1998) Density, body mass and parasite species richness of terrestrial mammals. *Evolutionary Ecology* 12:717–727
- Muzaffar SB, Jones IL (2004) Parasites and diseases of the auks (Alcidae) of the world and their ecology—a review. *Marine Ornithology* 32:121–146
- Nunn CL, Altizer S, Jones KE, Sechrest W (2003) Comparative tests of parasite species richness in primates. *American Naturalist* 162:597–614
- Packer C, Holt RD, Hudson PJ, Lafferty KD, Dobson AP (2003) Keeping the herds healthy and alert: implications of predator control for infectious disease. *Ecology Letters* 6:797–802
- Plowright W (1982) The effects of rinderpest and rinderpest control on wildlife in Africa. *Symposia of the Zoological Society of London* 50:1–28
- Poulin R (1999) The functional importance of parasites in animal communities. *International Journal for Parasitology* 29:915–920
- Roberts MG, Dobson AP, Arneberg P, de Leo GA, Kreczek RC, Manfredi MT, et al. (2002) Parasite community ecology and biodiversity. In: *The Ecology of Wildlife Diseases*, Hudson PJ, Rizzoli A, Grenfell BT, Heesterbeek H, Dobson AP (editors), Oxford: Oxford University Press, pp 63–82
- Rousset F, Thomas F, De Meeüs T, Renaud F (1996) Inference of parasite-induced host mortality from distributions of parasite loads. *Ecology* 77:2203–2211
- Sasal P, Durand P, Faliex E, Morand S (2000) Experimental approach to the importance of parasitism in biological conservation. *Marine Ecology Progress Series* 198:293–302
- Scott ME (1988) The impact of infection and disease on animal populations: implications for conservation biology. *Conservation Biology* 2:40–56
- Skirnisson K, Galaktionov K, Kozinsky EV (2004) Factors influencing the distribution of digenetic trematode infections in a mudsnail (*Hydrobia ventrosa*) population inhabiting salt marsh ponds in Iceland. *Journal of Parasitology* 90:50–59
- Stallknecht DE, Shane SM, Kearney MT, Zwank PJ (1990) Persistence of avian influenza viruses in water. *Avian Diseases* 34:406–411
- Tamisier A, Dehorter O (1999) *Camargue, Canards et Foulques*. Nîmes, France: C.O. GARD
- Thomas F, Renaud F, Guégan JF (2005) *Parasitism and Ecosystems*. Oxford: Oxford University Press
- Torchin ME, Lafferty KD, Kuris AM (2002) Parasites and marine invasions. *Parasitology* 124:S137–S151
- Wilson JE, Macdonald JW (1967) Salmonella infection in wild birds. *British Veterinary Journal* 123:212–219
- Wright AN, Gompper ME (2005) Altered parasite assemblages in raccoons in response to manipulated resource availability. *Oecologia* 144:148–156