Short Communication

Undetected species losses, food webs, and ecological baselines: a cautionary tale from the Greater Yellowstone Ecosystem, USA

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Abstract Large protected areas are often considered natural yet outside pressures may compromise ecological integrity. This paper points to a problem in assessing ecological baselines: what if species' extirpations go undetected? I present a data set spanning 130 years that demonstrates the loss of white-tailed jack rabbits *Lepus townsendii* from two National Parks in the well studied 60,000 km^2 Greater Yellowstone Ecosystem, USA. While these extirpations have been unnoticed until now, an ecological consequence may be elevated predation on juvenile ungulates. A critical challenge we face is how to apply better the concept of shifting baselines to the restoration of functional relationships when species' losses are undetected.

Keywords Ecological baseline, extirpation, Grand Teton, *Lepus townsendii*, protected area, white-tailed jack rabbit, Yellowstone.

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Species and populations disappear, their passing often predating scientific description (Wilson, 1986) and knowledge about interactions (Berger, 1999). For well known vertebrates, especially in countries with a history of ecological research, this tends not to be the case. Mammals larger than 3-5 kg offer an example. Their demise from protected reserves is often, but not always, detected (Newmark, 1995; Brasheres *et al.*, 2001). An appreciation of historical conditions is crucial to understand functional relationships and the possibility of restoration (Arcese & Sinclair, 1997; Dayton *et al.*, 1998). The problem, however, is that when species disappear unnoticed, the utility of a baseline is greatly weakened. Here I highlight these issues by profiling previously unreported extirpations from two well-studied National Parks in the Greater Yellowstone Ecosystem, USA.

Yellowstone National Park, hereinafter Yellowstone, was established in 1872 and Grand Teton as a national monument in 1929, before elevation to Park status in 1950 (Fig. 1). Together these contiguous units, >1.2 million ha, are characterized by extensive scientific research, well developed species lists, and serve as testing grounds for restoration and potential effects of apex carnivores (Berger *et al.*, 2001; Ripple *et al.*, 2001; Pyare & Berger, 2003; Smith *et al.*, 2003). Nevertheless, when ecological conditions have not been accurately depicted, or change without detection, the concept of baselines loses utility.

A case in point involves the poorly known white-tailed jack rabbit *Lepus townsendii*. This large, once abundant, lagomorph has slipped away without notice. I chronicled *L. townsendii* disappearances by collating historical information, unpublished and published notes, and queries to professional biologists and naturalists who have (or had) worked in the Yellowstone Ecosystem for up to 5 decades (Appendix). I also checked records and queried databases of the American Museum of Natural History, the California Academy of Sciences, the Chicago Field Museum, the Burke Museum (Seattle), the Denver Museum of Nature and Science, and the Museum of South-west Biology (Albuquerque). Only the American Museum of Natural History reported *L. townsendii* from Teton County, Wyoming; samples were from 1934-35, a period consistent with their presence in the region.

Descriptions in Yellowstone between 1876 and 1926 suggested a level of abundance (e.g. 'Where ... coyotes or wolves have been killed or driven off, the hares still exist in great numbers', and 'jackrabbits with their large white tails are common ... and may also be seen almost anywhere in the open northern sections of the Park') but by the early 1990s none were detected. For Grand Teton the pattern is similar, with descriptions between 1928 and 1949 limited to 'regular occurrence' and 'commonly

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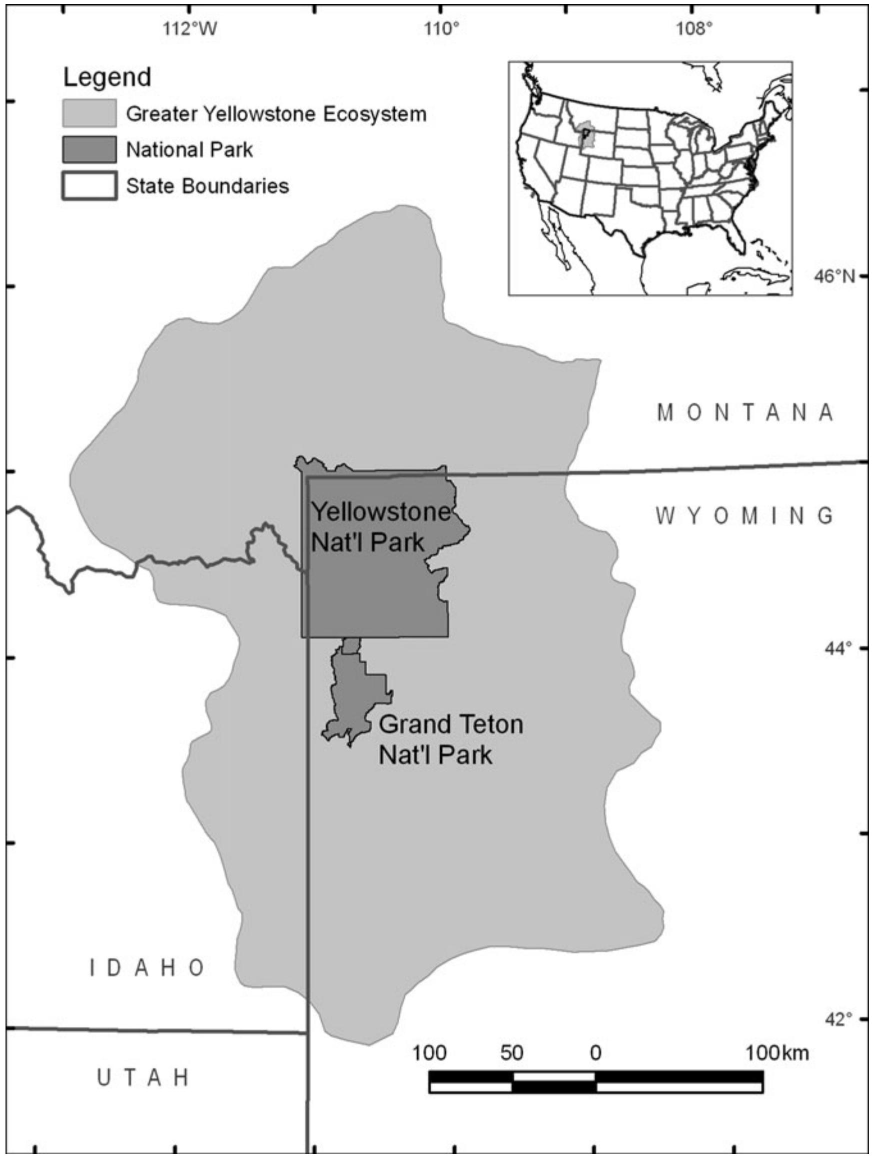

Fig. 1 The study area, indicating the Greater Yellowstone Ecosystem and Yellowstone and Grand Teton National Parks. The inset indicates the position of the Greater Yellowstone Ecosystem in North America.

in the vicinity', but few thereafter (Appendix). Hence, despite the spectacular scientific attention to coyotes *Canis latrans*, wolves *Canis lupus*, and their prey in the open habitats of Yellowstone and Grand Teton, not a single sighting of *L. townsendii* could be confirmed since 1991 in the former and only three since 1978 in the latter.

The intimation that *L. townsendii* have disappeared begs an obvious question; is a metric other than human observation superior for detection, particularly because tracks, faeces, and individuals become less obvious at low densities? Hence, I relied on a nutritional bioassay using the diets of coyotes as a marker for *L. townsendii* presence. Based on scat analyses conducted both in Teton and Yellowstone spanning up to 70 years (Murie, 1935; Murie, 1940), the amount of hare hair has declined. Faecal collections for 1931-1935 (n = 2,415) in the general region of what is currently Grand Teton contained *c.* 10% hare (Murie, 1935; based on extrapolations in Weaver, 1977); for 1973-1975, *c.* 1% (n = 1,500; Weaver, 1977) and for 1998-1999, 0% (n = 339; Wigglesworth *et al.*, 2001). The evidence points to simultaneous attrition in both parks coupled with little to no recolonization.

Lacking a sense of historical conditions it will always be difficult to decide whether current systems function ecologically like past ones. Consequently, what might be adduced can only come about by analogy using surrogate models although it is not obvious which leporid might be more appropriate, black-tailed jack rabbits

Lepus californicus or snowshoe hares *Lepus americana*. Elsewhere, rabbits play key roles in boreal, desert and high altitude landscapes, and black-tailed jack rabbits drive the dynamics of coyote populations (Knowlton & Stoddart, 1992). This predator-prey relationship has important ecological effects because predation on domestic ungulates increases when hare densities drop (Stoddart *et al.*, 2001). If *L. townsendii* once filled similar niches in more mesic or climatically more extreme regions such as the Greater Yellowstone area then their loss could have had a striking influence upon food webs.

As is common in many rangelands, large carnivores have been relentlessly persecuted, with unknown community-wide effects (Berger, 2006). In Grand Teton, however, coyotes remove a high proportion of young elk *Cervus elaphus* and pronghorn *Antilocapra americana* (Smith & Anderson, 1996; Berger, 2007). Whereas historical relationships are uncertain, coyotes are catholic feeders and switch between energetically-beneficial prey (Gese *et al.*, 1995). It is possible that the localized extirpations of *L. townsendii* prompted independent but high levels of predation on pronghorn fawns in both Grand Teton (Berger, 2007) and Yellowstone (Smith *et al.*, 2003). Similar patterns have been noted on Montana's National Bison Range and South Dakota's Wind Cave National Park, both relatively small fenced areas managed for high ungulate biomass where lagomorphs are rare (Byers, 1997; Sievers, 2004; J. Berger, unpubl. data) and coincident grazing impacts on vegetation large.

While the loss of *L. townsendii* from Grand Teton and Yellowstone, and reductions elsewhere, are likely to facilitate increased predation on ungulate neonates, at least in localized settings, prey-predator relationships are dynamic across space and time. If the loss of wolves promotes coyote numbers, then a top-down effect on fawn survival may be prominent (Berger, 2007). Still, the role of potentially important bottom-up drivers, such as *L. townsendii*, requires clarification, something that will not occur when species are extirpated and, moreover, when their loss is unknown.

The reintroduction of carnivores has been pivotal in attempts to restore ecological integrity (Smith *et al.*, 2003) but rarely have small or medium sized mammals been reintroduced with a goal beyond that of population recovery. The supplementation of native wild hare *Oryctolagus cuniculus* into Spain's Doñana National Park with an aim of offering a food base for Iberian lynx *Lynx pardina* is an obvious exception (Moreno *et al.*, 2004).

A similar but more dramatic manipulative approach to food webs from below is diversionary feeding. For example, in India's Sanjay Ghandi National Park, where leopards killed 19 people during 3 months, exotic pigs and rabbits were targeted for introduction as prey alternatives to humans (Soondas, 2004). In Alaska the relocation of train- or road-killed moose concentrated 12 t of carcasses to lure brown bears from sites with newborn calves (Orians, 1997). These sorts of lateral or bottom-driven approaches are intended to achieve a specific management goal atypical of biological conservation. The case of *L. townsendii* in both Grand Teton and Yellowstone differs.

If the prospects for successful reintroduction of species of lower trophic levels were bright, then adoption of bottom-up as well as top-down approaches could serve multiple purposes. Firstly, a reintroduction may result in the establishment of dynamic ecological processes that were intact prior to extirpation. Secondly, from perspectives that involve ecological health and wildlife conservation, the public as well as managers of protected areas may find it easier to garner endorsement if it were clear that a species loss had serious ecological costs. In this case, it will be prudent to consider reintroduction of *L. townsendii* to Grand Teton and Yellowstone National Parks (Berger *et al.*, 2006). At a broader level the problems of species disappearance in the two parks in the Greater Yellowstone Ecosystem is not likely to be a unique episode restricted to this well studied region. A critical challenge we face is therefore how to apply better the concept of shifting baselines to the restoration of functional relationships when species' losses are undetected.

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Appendix

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Biographical sketch

Joel Berger has researched questions involving food webs and the ecological role of carnivores in the greater Yellowstone and polar regions, Alaska, the Russian Far East, and southern Africa. His current work concentrates on the development of conservation strategies to protect long distance migration and wide ranging movements in terrestrial mammals both in Mongolia and western North America.