



The Protected Area Paradox and refugee species: The giant panda and baselines shifted towards conserving species in marginal habitats

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Abstract

Paradoxically, despite the growth in protected areas globally, many species remain threatened and continue to decline. Attempts to conserve species in suboptimal habitats (i.e., as refugee species) may in part explain this Protected Area Paradox. Refugee species yield poor conservation outcomes as they suffer lower densities and fitness. We suggest that the giant panda may serve as an iconic example, reflecting the contraction and shift in the giant panda's range, diet and habitat use over the past 3,500 years, coinciding with increasing human pressure, and now maintained by conservation efforts, this due to shifted baselines. The global bias of protected area location to less productive habitats indicates that this problem may be widespread. We urgently need efforts to identify victims of refugee species status to allow improved conservation management globally, reducing the paradoxical outcomes of our conservation efforts.

KEYWORDS

Ailuropoda melanoleuca, conservation management, fitness, giant panda, optimal habitat, protected areas, range contraction, refugee species, shifted baseline, suboptimal habitat

Paradoxically, despite the growth in marine and terrestrial protected areas globally (UNEP-WCMC, IUCN and NGS, 2018), many species remain threatened and continue to decline (e.g., Costello & Ballantine, 2015; Ripple et al., 2016). Attempts to conserve species in suboptimal habitats may in part explain this Protected Areas Paradox. Species confined to suboptimal habitats are recognized as refugee species (Kerley, Kowalczyk, & Cromsigt, 2012). They may be identified as (a) having

suffered historical range contractions, such that (b) they now occur in limited, less diverse habitats (compared to previous ranges) at (c) low densities, and with (d) anomalous resource (diet, habitat) use compared to historical records and that of close relatives (Kerley et al., 2012). Conservation efforts of refugee species yield poor outcomes as long as the species is confined to suboptimal habitats where they suffer lower densities and fitness (Kerley et al., 2012; Lea, Kerley, Hrabar, Barry, &

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Shultz, 2016; Moolman, Ferreira, Gaylard, Zimmerman, & Kerley, 2019). Importantly, the shifting baseline syndrome (Pauly, 1995) leads succeeding generations of conservation managers to misjudge as optimal the marginal habitats where the species occurs, simply because the species has persisted there. The resulting conservation management then actively traps refugee species in marginal habitats (Kerley et al., 2012). This risk was identified by Caughley (1994, 229) who pointed out that for threatened species that have suffered a range contraction, it is safer to hypothesize “that the species ends up, not in the habitat most favorable to it, but in the habitat least favorable to the agent of decline [threat].” If widespread, such conservation action focused on suboptimal habitat could be costly, both financially and in outcomes.

We argue that the giant panda *Ailuropoda melanoleuca* (David), may serve as an important example of a refugee species and hence provide important insights into a mechanism behind this Protected Area Paradox. The giant panda, the world's most iconic conservation symbol, is still highly vulnerable, with a global population of less than 2,000 individuals, despite massive investment over decades of intense conservation effort and a dedicated protected area network (Tian et al., 2019). The recent increase in giant panda numbers has led to the downlisting (from Endangered to Vulnerable) of the species (Swaigood, Wang, & Wei, 2016), but this increase reflects a 72% increase in the area censused and a 83% increase in sampling effort in the most recent census, rather than growth in the previously censused population (Kang & Li, 2019). Zhou and Pan (1997) show that a giant panda population growth rate of 3.0% per annum is achievable, but current wild populations are not performing at this level. Based on recent published findings (see below), we therefore develop a hypothesis that the underwhelming recovery rate, relative to conservation effort, may partly be the result of modern constrictions and shifts in range, habitat and resource availability. This not only limits their potential for recovery but also can lead to a narrow conception of panda ecology and their fundamental niche. This hypothesis is based on the following points.

Firstly, Han et al. (2019) demonstrate a contraction and shift in the giant panda's range, diet and habitat use that has occurred over the past 3,500 years, showing that the giant panda's predominant use of high altitude C₃ bamboo forests is in fact very recent. Thus, Han et al.'s (2019) stable isotope analyses of historical samples suggest giant pandas had a diet more characteristically ursine rather than their current highly specialized bamboo diet, and that they previously used a broader range of habitats, including warmer/moist subtropical habitats. Han et al. (2019) place this shift as mid-Holocene.

Following our hypothesis, we argue that, rather than an evolutionary specialization on a specific resource, these shifts reflect a retreat to ecologically suboptimal refuges in the face of habitat loss and other human threats, similar to the “retreat of the elephants” from most of China (Elvin, 2008). The current population uses a small portion of its historical range in south-western China and its distribution, habitat and diet was previously much broader, contracting with growing human pressure (Han et al., 2019; Pan et al., 2014; Swaisgood et al., 2016; Yang et al., 2017). Genetic evidence of strong population divergences in giant panda 2,800 years ago (Zhao et al., 2013) provides further support for these fragmentations.

Secondly, this hypothesis is based on the observation that the giant panda gut microbiota is carnivore-like, with no evidence of the development of a gut microbiota that is adapted to the bamboo-dominated diet (Xue et al., 2015). Xue et al. (2015) point out that this apparently maladaptive gut microbiota may explain the poor digestive efficiency of bamboo by giant panda, as well as their susceptibility to enteric diseases. An analysis of the causes of mortality in giant panda (Qiu & Mainka, 1993) shows that gastro-intestinal disease (37% of deaths) was the most common cause of death in captive and wild giant panda, with high levels of malnutrition as a cause of death (33%) in wild giant pandas. These patterns indicate dietary problems are common in this species.

Tellingly, in an important multidisciplinary review of the prospects of persistence of giant panda, Wei et al. (2014, 10) pose the question “Moreover, what factors drive the persistence of giant panda populations only in isolated mountain range refuges?” A likely explanation is a retreat from anthropogenic land use change and disturbance. Giant panda are averse to human activities, as shown by the occurrence of grazing by domestic livestock, infrastructure and farming all being important and negative variables in models of giant panda habitat use (Qiu et al., 2019). This therefore supports the view that giant panda would retreat from areas occupied by humans, one of the criteria for refugee species (Kerley et al., 2012).

The fact that these recent changes in the giant panda's range and resource use patterns coincide with increasing human pressure, and that this resource use is anomalous to that of the rest of the Ursidae family, which use a diversity of habitats and are omnivores, further supports the hypothesis that the giant panda is a refugee species, sensu Kerley et al. (2012). Based on the criteria to identify refugee species (Kerley et al., 2012), other endangered mammals that co-occur with giant panda, such as the red panda (*Ailurus fulgens*) and the Yunnan snub-nosed monkey (*Rhinopithecus bieti*), were recently identified as

refugee species (Nüchel, Bøcher, Xiao, Zhu, & Svenning, 2018). In the first application of the refugee species concept to plants, Jensen, Ma, and Svenning (2020) show that the gymnosperms of China are refugee species, being restricted to steep slopes by human pressure. The highlands of China therefore harbor the highest concentration of currently recognized refugee species globally, this likely related to the fact that China is both rich in biodiversity and the world's most populated country.

The implications of the hypothesized refugee species status for the giant panda are that we need to reassess the current focus of limiting populations to reserves in high altitude forests, and perhaps even reassess the idea of panda as a “bamboo specialist.” For the giant panda,

archaeological evidence can identify alternative suitable reserve areas, and experimental introductions of giant panda into such alternative habitats will serve to test this refugee status hypothesis. A less risky test of this hypothesis would be diet choice experiments with captive giant pandas. Although this has not been explicitly done, Mainka, Guanlu, and Mao (1989) showed that captive giant panda consumed all of the “panda gruel” (a mixture of cereal, eggs, meat, and bonemeal), but left substantial amounts of bamboo provided. This indicates preference for the gruel over bamboo. In addition, given that successfully breeding captive populations of giant panda have diets heavily supplemented with non-bamboo items (up to 83% of the diet being various “panda gruels” as described above—Dierenfeld, Qiu, Mainka, &

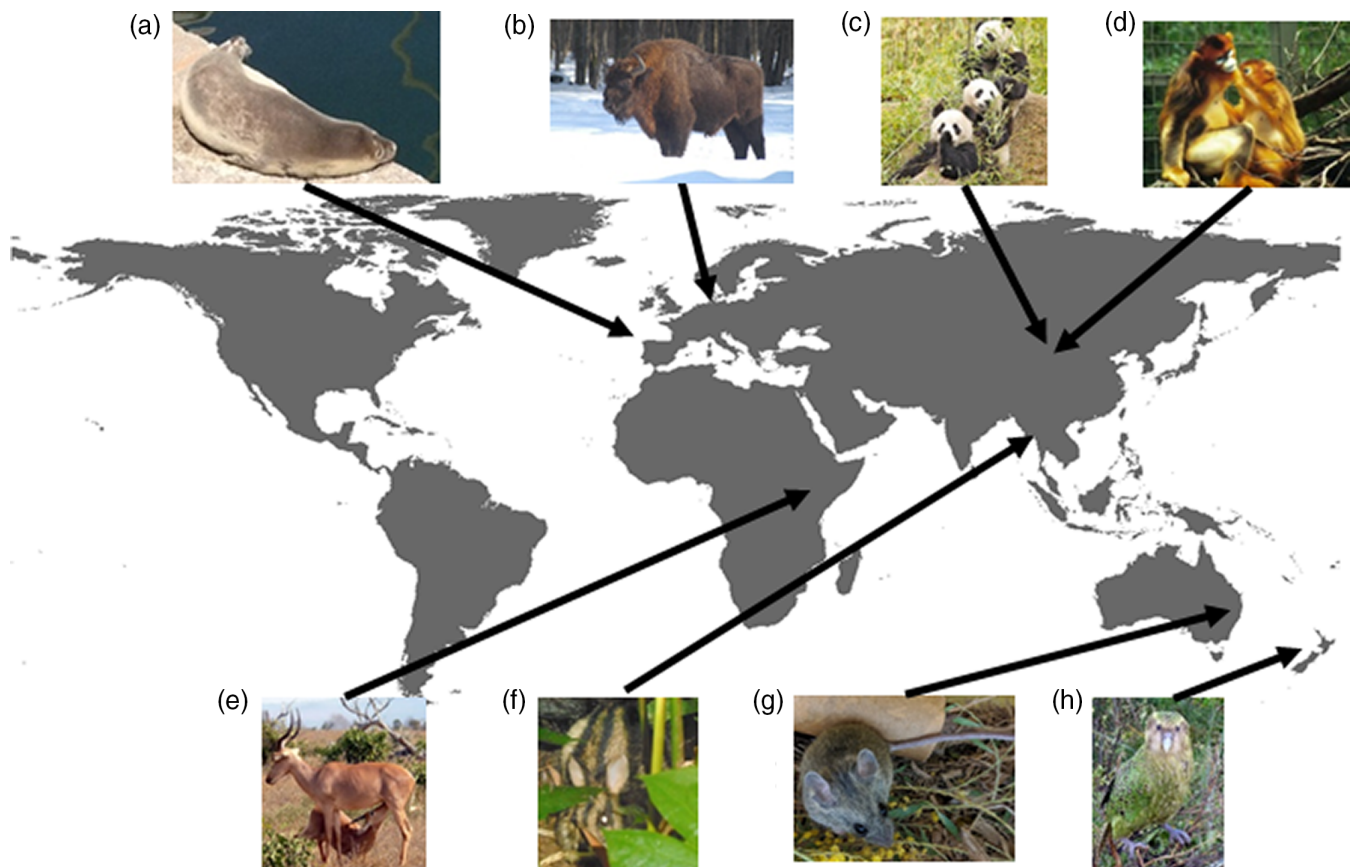


FIGURE 1 A global overview of currently identified animal refugee species, where conservation management confines species to suboptimal habitat (a) Mediterranean monk seal, (b) European bison, (c) giant panda—this study, (d) snub-nosed monkeys (five species), (e) hirola, (f) Annamite striped rabbit, (g) New England mouse, (h) kakapo. Refugee status can also occur at the population level, such cases (see Table 1) representing partial refuges, where management maintains populations in suboptimal habitat. See Table 1 for scientific names and sources. Photo credits: European bison: G Kerley; Mediterranean Monk seal: By Matumbamilo, CC BY-SA 3.0, <https://commons.wikimedia.org/w/index.php?curid=47286572>; Giant panda: By Chi King, CC BY 2.0, <https://creativecommons.org/licenses/by/2.0/>; Hirola: By JRProbert—Own work, CC BY-SA 4.0, <https://commons.wikimedia.org/w/index.php?curid=46570654>; Snub-nosed monkey: By Eva Hejda <http://fotos.naturspot.de/>, CC BY-SA 2.0 de, <https://commons.wikimedia.org/w/index.php?curid=239671>; Kakapo: By Department of Conservation—<https://www.flickr.com/photos/docnz/4015891720/>, CC BY 2.0, <https://commons.wikimedia.org/w/index.php?curid=48081940>; Annamite striped rabbit: from <https://www.savethesaola.org/annamite-striped-rabbit/>, photo courtesy of A. Tilker; New England mouse: photo courtesy of K. Smith

TABLE 1 Recognized faunal refugee species (related to Figure 1) and partial refugee species (species with populations recognized as in refugee species circumstances) documented to date

Refugee species		Sources
European bison	<i>Bison bonasus</i>	Kerley et al. (2012)
Black snub-nosed monkey	<i>Rhinopithecus bieti</i>	Nüchel et al. (2018)
Grey snub-nosed monkey	<i>Rhinopithecus brelichi</i>	Nüchel et al. (2018)
Golden snub-nosed monkey	<i>Rhinopithecus roxellana</i>	Nüchel et al. (2018)
Myanmar snub-nosed monkey	<i>Rhinopithecus strykeri</i>	Nüchel et al. (2018)
Tonkin snub-nosed monkey	<i>Rhinopithecus avunculus</i>	Nüchel et al. (2018)
Mediterranean monk seal	<i>Monachus monachus</i>	González (2015)
Hirola	<i>Beatragsus hunteri</i>	Ali et al. (2018)
Kakapo	<i>Strigops habroptilus</i>	Lentini, Stirnemann, Stojanovic, Worthy, and Stein (2018)
Annamite striped rabbit	<i>Nesolagus timmins</i>	Tilker et al. (2018)
New Holland mouse	<i>Pseudomys novaehollandiae</i>	Abicair, Manning, Ford, Newport, and Banks (2020)
Partial refugee species		
Cape mountain zebra	<i>Equus zebra zebra</i>	Lea et al. (2016)
African elephant	<i>Loxodonta africana</i>	Moolman et al. (2019)
American bison	<i>Bison bison</i>	Plumb and McMullen (2018)
San Clemente Bell's sparrow	<i>Artemisiospiza belli clementeae</i>	Meiman, DeLeon, and Bridges (2020)

Liu, 1995), captive populations provide a robust opportunity to assess the relationship between reliance on bamboo in the diet and population performance. Unfortunately, the latest synthesis on successful breeding of giant panda in captivity (Martin-Wintle et al., 2019) does not refer to diet management to improve reproduction. Revising its conservation approach is in line with the currently called-for adaptive management approach for the species (Swaisgood, Wang, & Wei, 2018), and may enhance giant panda density and fitness, without which there is a prospect that the giant panda may ultimately only persist as the logo of a conservation NGO.

Perhaps more importantly, the giant panda, as a globally recognized conservation icon, may provide a key insight as to mechanism behind the global trends in poor conservation outcomes. One possible explanation for the Protected Area Paradox lies in the bias of the location of protected areas to less productive habitats that are less attractive to humans. The global bias of conservation areas to “high and steep” habitats (Joppa & Pfaff, 2009) suggests this phenomenon is widespread. We predict that many of the species in such protected areas are refugee species, due to similar mechanisms described above and resulting in similar consequences that we have highlighted for the giant panda. Indeed, the list of confirmed refugee species is growing, transcending phylogenetic, geographic and ecological boundaries (Figure 1,

Table 1). Refugee status also occurs at population level (i.e., partial refugees—Table 1), where management confines populations to poor habitat (e.g., Cape mountain zebra *Equus zebra*, Lea et al., 2016).

We urgently need efforts to identify victims of refugee species status to allow improved conservation management (Kerley et al., 2012). The first, and perhaps biggest, challenge is to overcome the shifted baselines of conservation managers and scientists. Monsarrat, Novellie, Rushworth, and Kerley (2019) recently showed that neglecting historical range data underestimates conservation opportunities, ecological niches and habitat usage for species, and that this is relatively common (34% of their admittedly small sample of 34 large mammal species) and biased towards carnivores. These shifted baselines hinder the critical assessment of current conservation efforts, and the exploration of alternative approaches, this through the identification of optimal habitats and testing hypotheses around refugee species status, following the process outlined by Kerley et al. (2012). We also accept that there may be special cases of species where optimal habitat no longer exists, but this needs to be quantified so that it can be included in conservation planning for these species or for management of their existing habitat. It is noteworthy that for all of the refugee species identified to date, alternative, apparently more optimal habitat, has been identified (see Figure 1 and Table 1 for these species

and cited sources). The outcome of this proposed research agenda will therefore be the identification of more effective protected areas for the conservation of these species, thereby reducing the paradoxical outcomes of our conservation efforts. Testing the Protected Area Paradox hypothesis we outlined in this paper using the giant panda will allow it to again assume its iconic role in inspiring conservation and promoting more effective protected area policy and implementation globally.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

1 | AUTHOR CONTRIBUTIONS

All authors developed the concept and located published resources; Graham I. H. Kerley wrote the draft; all authors contributed to writing and agreed to submission.

2 | DATA AVAILABILITY STATEMENT

No unpublished data were used in this study.

3 | ETHICS STATEMENT

No animals were used in this study.

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