



Conservation implications of the refugee species concept and the European bison: king of the forest or refugee in a marginal habitat?

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The concept of refugee species provides a theoretical framework towards increasing the predictive power of the ‘declining population paradigm’ through identifying species which are expected to suffer from a declining population syndrome. Using a simple habitat model as a framework, refugee species are defined as those that can no longer access optimal habitat, but are confined to suboptimal habitats, with consequences of decreased fitness and density, and attendant conservation risks. Refugee species may be difficult to detect in the absence of information on prior habitat use and fitness and their observed ecology will be constrained by the habitat limits forced on them. Identification of refugee species, characterisation of pre-refugee ecology and the restoration of such species to optimal habitat is critical to their successful conservation. The concept is showcased by addressing the conundrum of a large grazing bovid, the European bison *Bison bonasus*, being managed as a forest specialist, despite its evolutionary background, dental morphology, neonatal behaviour, diet and microhabitat selection being characteristic of a grazing species inhabiting open, grass-rich habitats. It is hypothesized that a combination of increasing replacement of open steppe by forest cover after the last postglacial period and increasing human pressure forced bison into forests as a refuge habitat. This process was then reinforced through active management of bison in forests as managers committed themselves to the ‘bison as forest species’ paradigm. A research agenda to test this hypothesis using an experimental approach in the conservation management of European bison by introducing populations into diverse habitat types is suggested.

The prospects of species being trapped by threats (disease, predators, competition, loss of habitat) in suboptimal habitats and then managed in those habitats is a real risk to their conservation (Caughley 1994). Such species will have the attributes of refugees: decreased fitness and an uncertain future. Identifying such refugee species and their optimal habitats and then allowing them to recolonise optimal habitats, after removing the threats, will increase fitness, reduce risks, and should allow the persistence and natural evolution of the species (Armstrong and Seddon 2008). This concept therefore provides an opportunity to expand the theoretical basis and predictive power of conservation biology’s ‘declining population paradigm’, which Caughley (1994) described as being empirically strong but theoretically weak. In this paper we first develop the theoretical framework of the refugee species concept and outline some potential examples of refugee species. We then apply the concept to the case of European bison *Bison bonasus* to exemplify its usefulness and implications in more detail.

Refugees: species confined to suboptimal habitats

The loss of habitat is one of the fundamental drivers of extinction, as epitomised by Diamond’s (1989) ‘evil quartet’

of overkill, habitat destruction and fragmentation, impacts of introduced species and chains of extinction. Furthermore, there is general recognition (Mihoub et al. 2009) that fitness varies across a species’ distribution range (i.e. in different habitats), as embodied in the source-sink model of population performance (Pulliam and Danielson 1991). An extension of these two points is that there is a real risk that species faced with shrinking distribution (through whatever mechanism), may be confined to suboptimal habitats, where fitness is substantially lower than in better quality habitats. The worst case scenario would be where the remaining occupied habitats are of such low quality that a species will not be able to maintain populations – so-called sink habitats (Pulliam and Danielson 1991). Ecological niche theory is rich with concepts governing how habitats and landscapes influence a species’ fitness. A species’ fitness results from a composite range of processes, including resource acquisition, competition, predation and disease. It therefore reflects both the resources required for a species to fulfil its life history (Grinnell 1917), as well as the relationship of a species with other species (Elton 1927). Fitness therefore provides a currency to integrate these processes from these two somewhat different perspectives.

Fretwell’s (1972) theory of habitat selection for a single species provides a simple and useful theoretical framework

to elucidate how a species under an ideal free distribution can occur in a habitat in which fitness may be lower than in other habitats. In this model a species first occupies the habitat in which fitness is maximised (e.g. at point x, Fig. 1a) and then as a consequence of a declining fitness with increasing density within the preferred habitat, other, sub-optimal (lower fitness), habitats are occupied (sequentially optimal points y and z in Fig. 1a). When habitats with the highest fitness become unavailable, the species will be recorded at its highest densities in what were previously suboptimal habitats, with lowered fitness levels (Fig. 1b). These remaining suboptimal habitats then serve as refuge habitats in the face of the processes that rendered the previously optimal habitats unavailable. In this scenario, the realised niche of a species (as defined by Hutchinson 1957) is limited to sub-optimal habitat, and the species can be considered to be a refugee species. For species that have undergone a range decline, Caughley (1994) specifically warns against the assumption that remnant populations of once wide-spread species are found in the most favourable habitats. He suggests that a safer assumption may be that such remnant populations are actually restricted to habitat least favourable to whatever process brought about the decline in the species. It should also be noted that even relatively abundant species may be trapped in suboptimal refuge habitats, provided that there is a large area of such habitat.

The risk of attempting to conserve species in suboptimal habitats has been recognised (Caughley 1994, Armstrong and Seddon 2008, Braunsch et al. 2008), but may be glossed over in conservation management. With species restoration, for example, historical records or the presence of a species in a habitat is often assumed to denote the suitability of that habitat (Kerley et al. 2003, Moilanen et al. 2009). It is rare for conservation planning to select sites for protection based on fitness of the focal species, rather than some measure of occurrence (Pressey et al. 2003). Furthermore, modelling of habitat suitability frequently assumes that occupied habitat represents the best habitat for a species (Braunsch

et al. 2008). If the data for habitat suitability modelling are derived from a situation where a species is confined to a sub-optimal habitat, then the ensuing model will simply identify further areas of suboptimal habitat (Braunsch et al. 2008, Hirzel and Le Lay 2008).

The largest risk for refugee species occurs when the suboptimal habitats are identified as the conservation priority areas for the species in question (Braunsch et al. 2008). This risk is especially large when the species was limited to suboptimal habitat a long time ago, i.e. multiple generations of conservationists ago. In this case the shifting baseline syndrome comes into play (Pauly 1995). This refers to changes over time in the perception of the 'natural' baseline state of systems. Each generation accepts as a baseline the habitat a species occurs in at the start of their career. After several generations, the former sub-optimal habitat will be regarded as the species' optimal habitat. If the species is then confined to this suboptimal habitat by conservation management, the consequences will be an additional constraint on the ability to deal with whatever threatening process initially confined it to these suboptimal habitats. Furthermore, such management will lead to lower densities of the species (Fig. 1b). Provided that sufficient area is available, large populations can be achieved, but this would not be the most efficient way of achieving high numbers.

How to identify refugee species and implement conservation management

The first step in identifying refugee species is to recognise the problem or at least the probability of its existence. The identification of refugee species can be particularly tricky if there is limited information about habitat-specific fitness. We suggest two phases to identify refugee species and develop appropriate conservation management actions. The first phase is an initial assessment to identify candidate

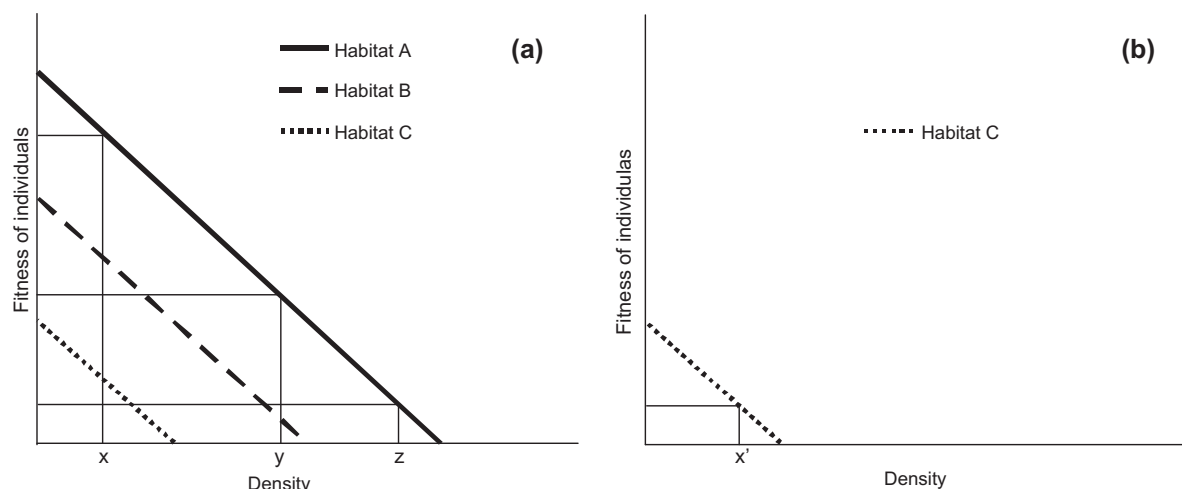


Figure 1. A diagrammatic representation of Fretwell's (1972) model of habitat selection applied to a case where preferred habitats are lost. (a) Where three habitats are available, habitat A with the highest fitness value at any specific density, will be exclusively occupied at low densities (e.g. at x), with the lesser quality habitats being occupied sequentially (i.e.: habitat B, then habitat C) as densities increase, and with associated lower fitness (e.g. at y and then z). (b) If the higher quality habitats are lost, then highest fitness will be achieved in the previously lowest quality habitat at any specific density (e.g. x'), and maximum achievable densities will be lower.

refugee species that need further detailed examination. The assessment in the first phase should follow three 'rules of thumb' to assign candidate refugee species status as those species which 1) have undergone severe declines in their historical geographic range and hence habitat use, 2) maintain slow population growth rates and/or low densities despite conservation efforts, and 3) appear to be anomalous in their current habitat (as indicated by knowledge of habitat use of closely related species). If species fit these rules of thumb, they should enter the more detailed examination of the second phase. This should contain at least two steps; 1) a thorough analysis of the species' evolutionary history, ecology and biogeography, focusing on changes in distribution patterns, habitat and resources use. This serves as the basis for the development of hypotheses as to how the species became a refugee species and what would be the optimal combination of resources and habitats for the species (Hirzel and Le Lay 2008). 2) Then test these hypotheses experimentally by reintroducing populations into the hypothesized optimal (and suboptimal to serve as controls) habitats and monitor their habitat-specific fitness, in line with Armstrong and Seddon's (2008) systematic framework for reintroducing species. It is worth recalling Caughley's (1994) warning that refugee species may not show normal patterns of resource use. Thus, not only should patterns of habitat use be examined critically, but attention should be paid to identifying resource use patterns and behaviours which may be artefacts of the confinement of a species to sub-optimal habitat.

We demonstrate the functionality of this step-by-step framework by identifying some examples of candidate refugee species following the three 'rules of thumb' of the first phase, and then, for one of those species, perform the thorough analysis of phase 2 and develop hypotheses and tests of these hypotheses.

Phase 1: identifying candidate refugee species

The five examples of candidate refugee species listed in Table 1 have the hallmarks of potential refugee species. Each is at risk unless optimal habitat is provided. For the aurochs this is too late. The timely recognition of the refugee status of the Lord Howe woodhen and intervention to allow access to optimal habitats (by removal of the threat in the optimal habitat – Caughley 1994) strongly support the relevance of this concept to conservation. We suggest that there may be many more cases of potential refugee species that are currently not recognised. The global bias to higher elevations and steeper slopes in the location of protected areas (Joppa and Pfaff 2009), suggests that many lowland species that are represented in these protected areas may be refugee species. Furthermore, we expect that this will become increasingly common as global change alters environments but species are trapped as refugees in what were previously optimal locations.

We use the European bison, which is traditionally conserved in forest habitats, to exemplify and further explore the refugee species concept. The European bison was

Table 1. Examples of candidate refugee species, the habitats to which they are/were confined, and the phase 1 evidence for refugee status of these species. These lines of evidence suggest that all five examples should be included in a phase 2 analysis.

Candidate species	Refugee habitat	Evidence for refugee status		
		Distribution	Population performance	Anomaly
Lowland anoa <i>Bubalus depressicornis</i>	Closed forest habitats in Sulawesi	Assumed to have had a much wider distribution?	Occurs in very low numbers within a very restricted geographic range	Muzzle morphology is typical of grazing ungulates of open habitats (Mendoza and Palmqvist 2008)
Knysna elephant population <i>Loxodonta africana</i>	Confined to Afromontane forests on the south-east coast of South Africa since the early 1900s	Decline in geographic range and habitat diversity over last 300 yr	Population continues to decline despite a century of protection. Population suffers from dietary limits to reproduction (Seydack et al. 2000)	The species is typical of open savanna habitat
Takahe <i>Porphyrio mantelli</i> , a type of rail	Montane habitat in the Murcheson mountains, New Zealand	A relict population that was previously much more widely distributed	Poor population performance (Lawton 1993)	?
The Lord Howe woodhen <i>Tricholimnas sylvestris</i>	Mountain plateaus on Lord Howe Island in the south-west Pacific	Fully displaced from their preferred coastal plain habitats by 1920 due to predation by feral pigs	Refugee status recognized in time and after eradication of the pigs and re-introduction of birds from captive programs, the birds could recover in their original habitat (Caughley 1994)	?
Aurochs <i>Bos primigenius</i>	Confined to Wiskicka and Jaktorów forests in Poland, from the 13th century	Very strong decline of geographic range during first part of Holocene	Extinct in 1627 despite protection and supplementary feeding (Van Vuure 2005)	Fossil records indicates that it previously used open habitats (Hall 2008). Isotope analyses shows use of open grass-rich habitats (Drucker and Bocherens 2009)

historically widely distributed across the European continent but hunting pressure, combined with on-going displacement by a growing human population, led to a decline of the species across its range, particularly from the Middle Ages, and in western Europe (Fig. 2; Benecke 2005). The European bison is an iconic species of eastern European forests (Samojlik 2005), especially the Białowieża Primeval Forest, where the species survived until the beginning of 20th century and where it was reintroduced after it had gone extinct in the wild (Pucek 2004). It has therefore suffered a severe reduction in range and is largely confined to forest habitat. Historically the population occurred at very low densities when not intensively supplemented with forage (see later). Finally, large sized bovids, usually grazers, are typically not forest-habitat species (Hofmann 1989, Kappelman et al. 1997), not least because of the limited occurrence of grass in such habitats. The European bison consequently appears to be an anomalous species in its current habitat and fulfils the requirements of phase 1 in the identification of a refugee species. We explore the phase 2 process with this species below.

Phase 2: is the European bison a refugee species?

We assessed available information on European bison evolution, ecology and behaviour to address the prevalent hypothesis that it is a forest specialist and to consider the alternative that bison are adapted to more open habitats and hence are currently refugees in a suboptimal forest habitat.

Evolutionary history of *Bison bonasus* and implications for habitat preference

The evolutionary background of a species provides useful insights to understanding current resource and habitat use. The genus *Bison* emerged on the open Eurasian steppe by the mid-Pliocene, the ancestral steppe bison *B. priscus* spreading over the Bering land bridge during the mid-Pleistocene, with subsequent exchanges between Eurasia and North America. The modern forms of *B. bison* (North America)



Figure 2. Known distribution of European bison based on fossil and historical records (Geptner et al. 1961, Benecke 2005). Solid line – Mid-Holocene (7000–5000 yr BP), dashed line – Pre-Roman-Middle Ages (1000 BC–1500 AD). Dots reflect the 19th–20th century relict population locations, with extinction dates prior to restoration.

and *B. bonasus* appeared after the Last Glacial Maxima when *B. priscus* disappeared (McDonald 1981, Shapiro et al. 2004, Benecke 2005). The origins of *B. bonasus* are under debate (Verkaar et al. 2004), but the occurrence of fully fertile hybrids between *B. bonasus* and *B. bison* emphasise the closeness of these two species (Kraśnińska and Kraśniński 2007). On this time scale, bison species have typically been associated with open habitats (McDonald 1981), and some local extinctions have been attributed to the development of forest habitats (Wilson et al. 2009). There is no evidence for forest specialization in ancestral bison (McDonald 1981).

Current evidence for *Bison bonasus* as forest habitat specialist

In circumstances when it is not possible to study the ecology of a species in habitats of interest, Sarrazin and Barbault (1996) suggest that it is appropriate to use information on closely-related species. Hence, we can gain useful insights from studies on American bison. The American *B. b. bison* (plains bison) and *B. b. athabasca* (wood bison) historically ranged over much of North America, with the latter occurring further north (McDonald 1981, Sanderson et al. 2008). The American bison achieves its highest densities in grassland habitats (McDonald 1981). The wood bison, although typical of forested landscapes, uses these in a coarse-grained manner, spending most of its foraging effort in open grassy habitats (Bergman et al. 2001, Fortin et al. 2003). Fortin et al. (2003) also show that larger meadows are more important than smaller meadows. This suggests that the wood bison, like the plains bison, is a grassland rather than a forest species. What evidence is there that its European counterpart is different? This question is complicated by the lack of opportunity to collect data on European bison on open landscapes and the fact that free-ranging bison herds are heavily managed through supplementary feeding. However, studies on morphology, diet and behaviour support the open habitat side of the argument, as summarised below.

Mendoza and Palmqvist (2008) showed that cranio-dental morphology of ungulates can be used to discriminate between species typical of open (grassland) habitats vs closed (forested) habitats, as well as between grazing and browsing species. Importantly, Mendoza and Palmqvist (2008) emphasize that habitat is the primary driver of the overall patterns that they detected. Although classified as a forest species, the cranio-dental morphology of the European bison is typical of open habitat, grazing species. They note that these findings are supported by data on its diet (see below) which is dominated by herbaceous plants and grass. Also the digestive system of the European bison indicate its morphophysiological adaptation to grazing (Hofmann 1989). Thus the forest habitat that bison are currently confined to does not reflect its feeding morphology and digestive physiology.

Studies on the diet of European bison need to be interpreted with caution, given the restriction on access to foraging areas due to their confinement to forest habitats, as well as the provision of supplementary fodder (mostly hay and silage). In addition, almost all studies on the diet of this species originate from a single area, Białowieża forest. This also holds true for historical, pre-extinction studies (Kraśnińska

and Kraśniński 2007). Prior to the extinction of the Białowieża population Wróblewski (1927, after Kraśnińska and Kraśniński 2007), showed that the bison diet comprised 80% grass. Numerous recent studies agree that they are largely grazers, with a significant component of forbs and grass in the diet (67–97%, Borowski and Kossak 1972, Caboń-Raczyńska et al. 1987, Gębczyńska et al. 1991). Bison also feed on browse, acorns and tree bark (Kraśnińska and Kraśniński 2007, Kowalczyk et al. 2011). Significantly, when bison in forest habitats are provided with supplementary hay, their consumption of browse declines, despite the relatively higher availability of browse (Kowalczyk et al. 2011). We can therefore conclude that it is primarily a grazer.

The assessment of habitat use by European bison suffers the same constraints as that for diet. Several studies agree that bison use open habitats heavily and preferentially (Kraśnińska et al. 1987, Daleszczyk et al. 2007, Kraśnińska and Kraśniński 2007, Kowalczyk 2010). Their ranging behaviour in Białowieża is a function of the availability of open habitat (Kraśnińska et al. 2000, Daleszczyk et al. 2007). Recent data from GPS-tracked bison from multiple, similarly-sized herds confirms this pattern (22 ± 2 km² in areas with high % of meadows versus 68 ± 27 km² otherwise, Mann–Whitney U-test, $p < 0.01$, Kowalczyk unpubl.). Additionally, bison core areas are strongly concentrated on open habitat patches (Kowalczyk 2010). In the Carpathian Mountains, Kuemmerle et al. (2010) showed that bison prefer ‘managed’ grassland areas.

If forests are suboptimal habitats for bison, following Fretwell’s (1972) model, their densities should be low there. Indeed, the first historical data on bison numbers in the Białowieża Forest from 1783, showed only 284 bison inhabiting the forest, i.e. 0.2 ind. 9km⁻² of the area. So, after nearly 400 yr of intensive royal protection bison numbers were low. The subsequent increase was related to intensive winter feeding and forest management (mowing of valleys and creation of foraging meadows) strongly improving foraging condition and bison survival (Samojlik 2005, Kraśnińska and Kraśniński 2007).

Finally, the neonatal behaviour of European bison is atypical of forest ungulates in which the neonate is normally hidden for a period immediately after birth (Lent 1974). European bison calves adopt a ‘following strategy’ with their mothers, as do calves of American bison, behaviour more typical of open habitat species (Lent 1974, Daleszczyk 2004). Hence, in this respect as well, *B. bonasus* has not developed a typical forest habitat adaptation.

How did the European bison come to be associated with forest habitats?

It is clear that the evolutionary background of the genus *Bison*, the natural history of its closest current relative, the American bison, and the combined knowledge we have on its morphology, behaviour, resource use and habitat selection all indicate that the European bison is more typical of an open habitat species than a forest species. So what led it to being confined to forest habitats and being perceived by many as a forest species? We suggest that this may be a combination of three processes, as set out below.

The European bison appeared in the paleontological record after the Last Glacial Maximum (LGM), and has persisted through to modern times. Consequently, as a species it experienced the postglacial development of forested ecosystems in Europe from the earlier postglacial steppe (Schwark et al. 2002). Data are limited but a possible scenario is that this species was originally spread across the postglacial steppe habitat (as was its ancestral species *B. priscus*), and was increasingly restricted to open habitat patches as forests developed. Intriguingly, there is also the possibility that bison were in part instrumental in maintaining these open habitat patches, as hypothesized by Vera (2000) and Svenning (2002). This role was later taken up by agricultural activities (Vera 2000, Svenning 2002) which consequently displaced bison from the remaining open patches.

This leads us to the second process that might have confined bison to forests, human predation risk and competition. Bison have been heavily preyed upon by humans for as long as records are available (Pucek et al. 2004). A strategy to reduce predation risk is avoiding predators or decreasing vulnerability through habitat selection (Ripple and Beschta 2004). American wood bison reduce predation risk through increased use of forest habitat (Fortin et al. 2009). Data on human predation risks in forests versus open habitats is limited, although detection of bison is much lower in forested than open habitat. Recent analyses show that bison prefer areas with low human presence (Kuemmerle et al. 2010). It is therefore plausible that the historical association of European bison with forest habitats reflects a classic case (Caughley 1994) of threat avoidance, not habitat preference. The increased loss of natural landscapes as human populations increased would have reinforced this behaviour. A similar process of confinement to forests of wild bovids by increasing human pressure has been shown by Drucker and Bocherens (2009). This 'threat avoidance hypothesis' explains that bison use forest under predation risk. However, they would have to use alternative habitats for optimal resource access. Hence, the optimal landscape for bison exposed to predation would compromise of a mixture of forest habitat to reduce predation risk and grassland habitat to fulfil dietary resource needs, where use of forest should decline with declining predation risk. This prediction is supported by the fact that, with increased protection, bison are increasingly recorded in open grassland and agricultural croplands around the traditional forest habitat (Table 2), despite the provision of forage in the forest habitat to reduce such wandering (Kraśnińska and Kraśniński 2007).

The two processes described above may have slowly confined bison to more forested areas over the past few thousand years. At this time scale, a third process becomes as important, the previously-mentioned shifting baseline syndrome (Pauly 1995). Both the above processes allowed plenty of time for the perception of bison's natural history to shift from that of an open habitat species to that of a closed forest species. As a result this last paradigm has been accepted by most people; conservation managers, scientists and the public, alike. So, for centuries bison have been actively confined to forests by humans. Clear evidence of this shifting baseline syndrome is that the European bison are often displayed as an iconic species of eastern European forests (Samojlik 2005), and that active management in the Białowieża Primeval Forest has

confined bison in forest habitat over at least the last 600 yr by supplying hay in the central forest parts (Samojlik 2005, Kraśnińska and Kraśniński 2007). In more recent times, bison that move out of the forest are actively relocated back into the forest or culled (Kraśnińska and Kraśniński 2007). Moreover, in terms of its current conservation management, the IUCN Species Action Plan specifically states 'deciduous forest types are the most suitable habitats for European bison' (chapter 10.1, Pucek et al. 2004). Indeed, most recent and current plans only considered forested landscapes and habitats for re-introduction (Table 2, Decker et al. 2010).

Thus, there is considerable support for the hypothesis that the European bison is a refugee in a marginal habitat. This hypothesis has implications for the long term conservation of the species and is testable through a number of predictions it leads to, the next step in phase 2.

Testing our hypothesis

We have highlighted an alternative view of the ecology, with major conservation management implications, for the European bison through the development of a hypothesis of a species trapped in sub-optimal habitat by a combination of post-glacial succession and anthropogenic pressures (originally hunting, now management). An obvious first step is to test this hypothesis.

A clear prediction of the hypothesis is that European bison would originally have been grazers, with an increased browse component in the diet as forests increased postglacially and their subsequent anthropogenic confinement to forests. This prediction can be tested using isotope analysis of paleontological, archaeological and historical bison material, and relating this to grass/browse isotope profiles (Vogel 1978, Post 2002). Drucker and Bocherens (2009) were able to track the confinement of aurochs to forest habitat as agriculture emerged using this approach. An additional opportunity to explore movement patterns using strontium isotopes (Koch et al. 1995) may also address the question as to whether increasing forest cover forced bison to move greater distances between grassland resources. These isotope studies should be complemented by diet selection studies of extant bison, ideally in the absence of artificial forage, without limits to their access to forage availability and in a variety of habitats. An extension of the above is also that European bison prefer to forage in open grassland habitat. This prediction needs to be tested with fine resolution data on habitat use and availability, so that such preferences can be properly assessed. This hypothesis can only be tested if there is enough variation in habitat in areas where bison occur. At present this is not the case, due to the focus of reintroductions into forest habitat and the active confinement or culling of bison that attempt to leave this habitat.

If bison populations suffered increasing loss of optimal open habitat as a consequence of postglacial forest establishment, the prediction is that the population would have declined as a function of increasing forest cover. This prediction can be tested through the analysis of changes in heterozygosity using ancient DNA in relation to vegetation change. This approach has already been successful in demonstrating a decline in *B. priscus* population size in Beringea during the

Table 2. Management approaches and characteristics of free-ranging (unfenced) European bison populations in Belarus, Lithuania, Poland, Russia and the Ukraine at the end of 2009 (Raczyński 2009 and A. Bunevich, V. Smagol, L. Balčiauskas and T. Sipko pers. comm.).

Country	Location	Habitat introduced to	Habitat use	Number of bison	Winter feeding ^a	Culling ^a	Status ^b
Belarus	Belovezhskaya Pushcha	Forest	Forest and meadows	403	+	+	I
	Borisovskii Forest	Forest	Forest, marshes and farmland	35	–	sporadic	S
	Volozhinskii Leskhov	Forest	Forest, shrubland and meadows	76	+	sporadic	I
	Osipovichskii Leskhov	Forest	Forest and farmland	138	+	sporadic	I
	Pripyatskii National Park	Forest	Forest and marshland	94	+	sporadic	S
	Poleskii Zapovednik	Forest	Forest and meadows	72	+	sporadic	I
	Kolkhoz Ozery	Forest	Forest	119	+	sporadic	I
	Naidyanskii Forest	Forest	Forest and farmland	23	+	–	I
	Lyaskovich Forest	Forest	Forest and farmland	18	+	–	S
Lithuania	Panevėžys-Pašilių Stumbrynas	Forest	Forest and farmland	61	–	sporadic	I
Poland	Białowieża Forest	Forest	Forest, meadows and farmland	451	+	+	I
	Bieszczady Mountains	Forest mosaic	Forest and meadows (mountains)	303	+	sporadic	I
	Borki Forest	Forest	Forest	86	+	+	I
Russia	Knyszyn Forest	Forest	Forest and farmland	84	+	sporadic	I
	West-Pomeranian Forests	Forest	Forest and farmland	67	+	–	I
	Ust-Kubinskoe Game Management Area	Forest	Forest	36	+	–	I
	Sknyatinskoe Game Management Area	Forest	Forest	32	–	+	S
	Velikoozerskoe Forest and Game Management Area	Forest	Forest	19	+	–	I
	Orlovskoe Poles'e National Park	Forest	Forest	203	+	–	I
	Fominskii Zakaznik	Forest	Meadows and forests	–	–	?	E
	Arkhyzskii Area (Teberdinsky Reserve)	Forest	Meadows and forest (mountains)	15	–	?	D
	Tseiskii Zakaznik	Forest	Forest and meadow (mountains)	55	–	–	S
Ukraine	Muromskii Zakaznik	Forest	Forest	23	–	–	I
	Petrovskoe Game Management Area	Forest	Forest	13	+	–	I
	Cherga	Forest	Forest and meadows	47	+	–	S
	Karachevskii Zakaznik	Migration from Orlovskoe Poles'e	Forest and open areas	8	–	–	–
	Taldomskoe Roor	Migration from Sknyatinskoe	Forest and abandoned farmland	10	–	–	–
	Danivska	Forest	Forest and farmland	–	–	+	E
	Konotopska	Forest	Forest	41	?	?	S
	Tsumanska	Forest	Forest and meadows	21	+	?	D
	Lopatynska	Forest	Forest and farmland	24	?	?	I
Ukraine	Majdanska	Forest	Forest and meadows	7	?	?	D
	Nadvornjanska	Forest	Forest and farmland	–	–	poached	E
	Bykovynska	Forest	Forest	46	?	?	D
	Uladiivska	Forest	Forest and farmland	83	?	?	S
	Zalisska	Forest	Forest	20	+	?	S

^a + = does occur; – = does not occur; ? = no data.

^b I = increasing; S = stable; D = declining; E = extinct.

mid-Pleistocene (Shapiro et al. 2004). Furthermore, such studies of ancient DNA would also add to our understanding of just how much genetic variability this species has lost, particularly during the 20th century bottleneck of extinction in the wild.

If European bison are refugees in forests, we predict that fitness may be enhanced in populations that have higher access to grassland habitats. This can be tested through a meta-analysis of bison population performance and other indicators of fitness such as growth rates, body condition, etc. in populations that have access to varying combina-

tions of forest/grassland habitat. Since bison mostly occur in forest habitats, an obvious condition for this test would be to establish European bison populations in grassland and/or grassland-woodland habitats as an explicit application of adaptive management (Caughley 1994) to test the above predictions. Hence, we strongly advocate that one of the most important agenda points to take conservation of European bison a step further is to develop an experimental re-introduction program. In such a program bison should be re-introduced across Europe under different climatic conditions and in areas that differ in the proportions of grassland

and forest. Ideally, such an experiment should be well replicated. Each experimental re-introduction should be monitored for habitat and diet selection and the fitness parameters mentioned earlier. Interestingly, recent and ongoing socio-political changes of the European rural landscape might offer the ideal window of opportunity for such a program and at the same time aid European biodiversity conservation (Henle et al. 2008). Across Europe extensively managed pastoral farms are declining and this abandonment of pastoral management practices has been identified as a key threat to grazed pasture or grassland habitats, including many habitats listed on the EU habitat directive (Ostermann 1998, Cremene et al. 2005). Kuemmerle et al. (2008) show that in parts of eastern Europe abandonment of farmland after the collapse of the socialist system is widespread and in some regions may exceed 20% of the area of farmland used in socialist times. These abandoned farmlands typically offer a mix of grassland, shrub and woodland habitat. Re-introduction of European bison on such abandoned farmland might be a win-win situation for the conservation of European bison and these grassland habitats, which the bison may help maintain. That this is not an unrealistic proposal, e.g. due to the lack of such lands, is shown by the fact that across Europe cattle and other livestock are being introduced on abandoned agricultural land for ecological restoration purposes (Van Uytvanck et al. 2008).

The alternative of failing to recognise the refugee status of bison is that they will continue to be confined to forests. The background to this management approach and the implications are explored below.

Historic and current bison management paradigm and its implications

In response to declining bison populations in eastern Europe, various political figures (typically royalty) put measures in place to protect their hunting interests from at least the 1500s. These included the protection of bison-supporting areas such as the Białowieża Forest in Poland as hunting reserves, and the provision of supplementary winter forage in these areas (Samojlik 2005). Royal protection collapsed during World War 1, and the Białowieża bison were wiped out by 1919 (Pucek 2004). The last remaining free-ranging population of European bison persisted until 1927 in the Caucasus Mountains (Pucek et al. 2004). A coordinated captive breeding program was initiated in 1929, with a founder stock of only 12 bison (Pucek et al. 2004). This was successful and in 1952 the first bison were released back into the wild in Białowieża Forest. Additional captive and free-ranging populations have been established across Europe, and by 2009, the global population was 4231 bison, of which 66% are free ranging (unfenced), distributed in 33 free ranging populations (note that a further three reintroduced populations have gone extinct) in eastern Europe (Table 2, Raczyński 2009). We extracted information on the location of unfenced, free-ranging bison from the European bison pedigree book (Raczyński 2009) and added information on the habitat used by bison and management measures (supplementary feeding, culling, and status) by consulting local managers. All free-ranging populations were originally

re-introduced into forest habitat (Kraśińska and Kraśiński 2007), but over half (69%, 27) have expanded their range to include open habitats (Table 2). However, the use of open habitats by free-ranging bison is regarded as a management problem, rather than a condition for species conservation, because typically this means the use of agricultural lands. To prevent bison from using agricultural lands and to reduce the impact of the bison on economically valuable forest species (Kraśińska and Kraśiński 2007) most free-ranging populations of European bison are supplementary fed (Table 2; 65%, 20 of 27 populations for which data were available). Numbers of bison are increasing in only 58% of these populations, with only six of these populations having more than 100 bison (Table 2). Paradoxically for a species with such low numbers, many populations for which data are available (54% of 26 populations) are subjected to culling (Table 2). This policy of culling contrasts strongly with the management of other large mammals which have undergone similar population declines as the bison and for which populations are increasing in response to conservation management, such as white rhinoceros *Ceratotherium simum*, black rhinoceros *Diceros bicornis* and Cape mountain zebra *Equus zebra zebra* (Emslie 2008, IUCN SSC African Rhino Specialist Group 2008, Hrabar and Kerley 2009). For these species conservation management focuses on expanding habitat availability to allow populations to grow (Morgan et al. 2009), rather than maintaining low numbers in limited areas. The need for culling of the Białowieża bison population is therefore an effect of limited habitat availability (Kraśińska and Kraśiński 2007) and is additional to observed density-dependent effects (Myserud et al. 2007). The absence of robust estimates of carrying capacity (Kraśińska and Kraśiński 2007), suggests that this policy is not informed by science and reflects managers' opinions of an excessive number of animals.

Consequences of managing bison in forests

The most obvious consequence of bison being confined to forest habitat is that the area of potential habitat is limited. This is exacerbated by the suggested lower densities that can be achieved in forest habitat. As a consequence it is likely that European bison will remain trapped in the zone of the 'small population paradigm', in which the species is vulnerable to all the risks that such limited population size conveys (Caughley 1994). This effect will be particularly strong given that bison went through a population bottleneck of only twelve individuals, with an even lower effective population size. As a consequence there is a high degree of inbreeding and very low genetic variability (Pucek et al. 2004, Tokarska et al. 2009). Wołk and Kraśińska (2004) hypothesized that an observed decline in body condition of the Białowieża bison and increase in disease and parasites (Demiaszkiewicz and Lachowicz 2007) may be an expression of problems associated with inbreeding, or a consequence of the artificial aggregations of bison around feeding areas in winter (Radwan et al. 2010). Every effort should be made to allow the European bison population to increase, ideally to levels where the contribution of heterozygosity through mutation exceeds loss due to genetic drift and inbreeding. This is unlikely under the current approach of capping populations within forest habitats.

The consequences of supplementary feeding bison in winter is not well understood, but may include increased pathogen and parasite transmission (Wołk and Krasnińska 2004, Radwan et al. 2010), the development of unusual behaviours reflecting increased group sizes, and possibly the further fragmentation of populations within forests as individual dispersal is restricted by adherence to traditional hay feeding sites (Kowalczyk unpubl.). In addition, it might influence the basic physiology of bison in ways that are currently unclear. Temperate ungulates typically have to survive severe winter conditions with low food availability. Adaptations to this include reducing energy expenditure through lowering metabolic rate (Arnold et al. 2004), changing their foraging behaviour, reducing food intake and increasing gut passage time of low quality food, and as a result they lose a substantial proportion of their body fat in winter (Parker et al. 2009). In contrast, European bison are typically fed high-quality food (hay, silage, beetroots) in feeding stations during winter. As a result, their movement is limited to the feeding sites (Kowalczyk et al. 2011) and they lose hardly any body weight. This suggests that management has been acting against the natural selection pressures of the winter season for centuries (at least the past 600 yr). The physiological and demographic consequences of this are unclear but probably profound.

Conclusion

The concept of refugee species provides a useful framework for assessing risks to such species. Furthermore, the utility of this is demonstrated in the case of the European bison, for which we conclude that in the absence of good evidence for adaptation to a forest habitat, a body of evidence for adaptation and preference for open habitats, and in the light of the postulated scenario of bison responding to postglacial changes and predator avoidance; that it is indeed a refugee species. Specifically, using habitat-specific fitness to assess habitat quality will strengthen conservation planning and management for particular species. Learning to recognise, understand and manage refugee species will be a key part of future conservation actions, specifically identifying species that are not recognized as occurring in suboptimal habitat, such as the European bison.

The refugee species concept also delivers a theoretical framework for the 'declining population paradigm' and provides some badly needed predictive ability that Caughley (1994) identified as a major weakness of this field of conservation biology. As such, we believe that exploring and applying the concept across a wide range of ecosystems, including marine and freshwater systems, to test its validity can have an important impact on the field.

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