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Perspective

Translocation in relict shy-selected animal populations: Program success versus prevention of wildlife-human conflict

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ABSTRACT

Past human persecution of wildlife has acted as a major selection agent shaping many animal features including behaviour. A major component of behaviour with diverse consequences for conservation is the shyness/boldness continuum. Shyer individuals are often geographically restricted, less prone to wander out of their ecological refuges but, on the contrary, less likely to experience human-induced mortality and lead to human-wildlife conflict. In this essay we discuss how the success of translocations may interact both positively and negatively with animal personalities, based on several case studies of re-introductions and reinforcements involving remnant mammal and bird populations. Although shyness may be inconvenient to conservationists when dealing with raptor translocations in which eventual dispersal may be a desired trait in the long run, a trade-off may emerge between boldness and prevention of human-wildlife conflict when dealing with large carnivores. Some other trade-offs may also occur, such as that between boldness and desired philopatry at the initial stage of re-introductions.

1. Introduction

Rural activities have been active until today since the Neolithic revolution. Wildlife composition, abundance and richness have been shaped by direct (persecution) and indirect (habitat transformation) disturbance associated with these practices over millennia. However, in Europe human depopulation of rural areas (i.e. rural flight or rural exodus) has been occurring during the last 6–7 decades, and is still an ongoing phenomenon (https://ec.europa.eu/futurium/en/system/files/ged/eprs-briefing-633160-demographic-trends-eu-regions-final.pdf).
Depopulation of rural areas has had many ecological consequences, with both positive and negative effects depending on the animal and plant taxa considered (Hansen et al., 2002; Falcucci et al., 2007; Martínez-Abraín et al., 2020; Cimatti et al., 2021). Many species intensively persecuted in past rural economies, such as birds of prey and large and medium-sized carnivores and herbivores, are nowadays going through a period of population rebounding within Europe's human-dominated landscapes (Chapron et al., 2014; Milanesi et al., 2017; Martínez-Abraín et al., 2020). This is because most European people now live in large cities, and predators are seen as competitors or enemies much less often than in the past (Martínez-Abraín et al., 2008, 2009). Consequently, substantial conservation and management efforts have been devoted over the last few decades to fostering the demographic recovery of remnant animal populations, as well as to bringing back extirpated populations, often by means of translocations (i.e. re-introduction either using captive-bred individuals or individuals from the wild, reinforcement of endangered populations, and similar procedures involving the release of individuals in target areas). Formerly persecuted wildlife was forced to subsist in areas free of human persecution (i.e. ecological refuges), and a shy fauna was promoted by the selective removal of bolder individuals (Gaynor, 2019; Martínez-Abraín et al., 2019). That fauna is now recovering exploratory behaviours, moving out of their ecological refuges, showing less fear to human presence, and getting closer to urban areas (Silliman et al., 2018; Martínez-Abraín et al., 2019, 2020, 2021b).

The purpose of our essay is to stress the need of paying further attention to the shy-bold nature of individuals employed in translocation programs, because the success of these actions may be influenced to a

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large extent by how well we tailor the selection of individuals to be translocated to the biological needs and socio-environmental context of our programs. We first describe the shy/bold continuum in animal populations. Next we discuss the interaction between the shy/bold continuum and translocations as a management tool in conservation efforts of small populations. We then provide some case examples of this interaction affecting brown bears and birds of prey. Finally, we provide some practical recommendations for conservation practitioners to improve translocation success accounting for the shy/bold nature of translocated individuals.

2. The shy/bold continuum

An instrumental point of success in conservation translocations is not overlooking the inter-individual genetic differences in correlated behavioural traits that give rise to behavioural syndromes (i.e. animal personalities) (Conrad et al., 2011; Smith and Blumstein, 2013; Roche et al., 2016; Merrick and Koprowski, 2017; Garvey et al., 2020; Gaynor et al., 2020; Greggor et al., 2020). These syndromes are often heritable (Chervet et al., 2011; Dochtermann et al., 2019), and can have important fitness consequences (Patrick et al., 2013). One of these personality traits is the so-called shy-bold continuum that is known to be under both genetic and epigenetic control, but also influenced by cultural habituation (Oswald et al., 2013; Riyahi et al., 2015, 2017). Bold individuals a) show lower fear to humans, b) are more exploratory and c) are more aggressive (see e.g. Biro and Post, 2008). For example, the biased dispersal of bold (highly aggressive and dispersal-prone) male western bluebirds (*Sialia mexicana*) allowed them to colonize other areas by displacing less aggressive mountain bluebirds (*S. currucoides*) in the north-western United States. However, selection against aggression was favoured across consecutive generations, once the new area had been already colonized (Duckworth and Badyaev, 2007). Hence natural selection can favour the coexistence of different behavioural phenotypes within species and populations, as each can provide adaptive advantages under different environmental circumstances. However, the maintenance of these polymorphisms can only happen in large populations with broad genetic variability.

3. Translocations and shyness

Translocations are one of the major management tools used for ex-situ conservation of extirpated and rebounding relict animal populations, once the level of human persecution or other anthropogenic disturbances have become negligible. Translocations must follow the recommendations of the IUCN conservation translocation specialist group, which take into account the levels of genetic variability to prevent the problems associated with small populations, such as demographic stochasticity or inbreeding depression (Caughley, 1994; Ralls et al., 2017). The role of behaviour has also been taken into account in translocations (Martin, 1998; Sutherland, 1998; Blumstein and Fernández-Juridic, 2010; Berger-Tal, 2011), mostly regarding the need of preventing boldness in captive-bred individuals (via selection or habituation), so that released individuals are capable of finding food and protecting themselves against predators (see e.g. Griffin et al., 2000; Azevedo and Young, 2006; Blumstein et al., 2019). However, not all programs pay enough attention to behavioural matters and thus high mortality of captive-bred individuals immediately after release occurs in many re-introductions (see e.g. Tavecchia et al., 2009). The unintended selection or/and habituation of bolder individuals during captive-rearing may be partially responsible of it (McDougall et al., 2006). One way of preventing this problem is making use of wild-caught individuals whenever possible and performing wild-wild translocations. However, wild-wild translocations are not always possible, and are not free from having problems such as unintendedly introducing shy wild-caught individuals, where wild-caught bold individuals would be more appropriate to achieve success or vice-versa. In principle translocations should select a large number of individuals for re-introduction (Merrick and Koprowski, 2017) as a precautionary measure to prevent skewing the selection of individuals in relation to personality just by chance. However, this may not be always possible either. On occasion the manager has to draw on small shy-selected populations as a source of wild individuals for translocation. A complex interaction between translocation success and the behavioural composition of released individuals may thus emerge. Here we analyse some case studies of this interaction as a way of example, including the trade-offs that conservation practitioners may face when including concern for the shy/bold nature of the translocated individuals in their agendas.

4. Translocation of brown bears and birds of prey as case studies

The restocking of brown bears (*Ursus arctos*) in the French and Spanish Pyrenees with wild individuals from Slovenia seems appropriate a priori considering that bears come from a growing population of >1000 individuals that is located close to the large Carpathian population, with ca. 7600 individuals (https://www.iucnredlist.org/species/41688/144339998#assessment-information). Most likely this population has a broader behavioural variability than the Pyrenean one, which only had 5 remaining individuals when the first translocations were scheduled. Moreover, the composition of the whole Iberian brown bear population (ca. 400 individuals) is most likely skewed towards the shier end of the shy/bold spectrum, after many centuries of unintended selection against bolder individuals by direct human persecution (see Swenson, 1999; Zedrosser et al., 2013). Reinforcing the Iberian population with bolder bears seems initially the right thing to do, because they are more exploratory, what could foster bear dispersal out of their historical ecological refuges. However, bolder individuals are not only more exploratory but are also supposed to show less fear to humans (Geffroy et al., 2015). In the bear example increased boldness could lead to have bears approaching livestock, farms, people and villages more often. Restocking bolder bears in a social context where humans are used to shy bears may lead to increased human-wildlife conflict (Bombieri et al., 2021). This has been the case in the French Pyrenees and the Alps (see e.g. Breintenmoser, 1998; Tenan et al., 2016). Hence, we face the trade-off between achieving greater bear dispersal (via increased boldness) and avoiding conflict with humans (via preserving shyness). The wildlife manager hence has two options at hand in this case. Either releasing only shy bears to prevent human-bear conflict (despite range expansion may be low) or releasing enough individuals to recover the whole array of personalities, which in principle may be a better option to foster range expansion. In the latter case selective removal of some extremely bold individuals that may eventually generate serious conflict with humans might have to be performed. In any case, the choice to release shy or behaviourally diverse bears will depend on the socioeconomic context.

Birds of prey are another common target of translocation projects. Examples of likely benefits of restocking shy-selected remnant raptor populations using bolder individuals from other populations are the Mediterranean osprey (*Pandion haliaetus*) populations, and the small cinereous vulture (*Aegypius monachus*) population nesting in Majorca Island.

5. Shy-selected populations with currently low genetic variability

Martínez-Abraín (2018) suggested that using chicks from northern European osprey populations to reintroduce or reinforce populations inhabiting touristic areas of southern Europe could be practical for conservation purposes. The current habit of Mediterranean ospreys of nesting on rock pinnacles in marine cliffs is commonly perceived as an idiosyncratic trait worth preserving. However, it is possible that Mediterranean ospreys currently nest in cliffs because the bolder individuals that nested on trees in the past were killed due to high human persecution (unlike northern populations that have been much less heavily persecuted over the last centuries) (see Jiménez et al., 2019). Trees would make osprey more vulnerable to predators than cliffs because predators can easily climb trees and trees can be cut down. As a result, the genotype of bold individuals that nested on trees could have been eliminated. Reintroducing bolder northern individuals in the Mediterranean could be beneficial for osprey, as it would allow them to coexist with the large number of tourists performing recreational activities along Mediterranean coasts. Osprey breeding success in Corsica is lower in its highly visited MPAs than in control areas (Monti et al., 2018), indicating fear of humans that affects their reproductive success. Thus, if southern European osprey were bolder than they are now (i.e. if northern individuals were introduced), they could withstand people presence better and increase their breeding success. Bolder osprey could then shift to tree nesting. In fact, some spontaneous shifts from cliffs to trees located close to summer residential areas have already been observed in the osprey population of Majorca without population reinforcement (J. Muntaner, pers. com.). Such recovery of former behavioural patterns would be expected in populations that did not decline to the point of losing all genetic variability along the bold-shy continuum, and secondarily via social copying of bolder individuals by shier individuals. A process that can feed-back positively especially in social species (Oro, 2020). The preservation of osprey cliff nesting per se could thus be a wrong conservation target.

Similar reasoning applies regarding the relict cinereous vulture population breeding in the island of Majorca. These vultures nest on pine trees growing directly in the cliffs facing the sea, instead of nesting on the holm oak (*Quercus ilex*) forest patches in the island sierras, as they usually do in mainland Spain. The choice of this nesting microhabitat has been considered for decades an idiosyncratic trait that deserves preservation, rather than the ghost of severe past human persecution (Silliman et al., 2018; Martínez-Abraín et al., 2019), as we think it is the case. The reinforcement of the remaining population with individuals from outside the Balearic Islands carried out by conservation practitioners during the last few decades may have brought back a broader behavioural variability to the population that hopefully will be able to move soon out of the cliffs and grow at a faster rate in the large pine and holm oaks forests in the island. Indeed, some shifts have already been observed, such as the reproduction on pine trees of some individuals outside (but close to) marine cliffs, and near paths highly frequented by hikers (J. Muntaner, pers. com.). This innovation is likely a positive consequence of the reinforcements with birds from the continent.

6. Population growth without dispersal

Conservation problems may arise because small shy-selected populations may not have much remaining behavioural genetic variability and may not receive new genetic input from outside. By 1987 there were less than 400 bearded vultures (*Gypaetus barbatus*) left in the Spanish and French Pyrenees, whereas 937–1119 individuals were estimated in 2016 (Margalida, 2020). This is a successful conservation story, but subsequently negative effects of growing population density on juvenile survival, fecundity and adult survival have been identified (i.e. 30–35% of the breeding population are polyandrous trios in which fecundity drops; Margalida, 2020). The growth of this bearded vulture population most likely has happened by reproduction among shy individuals. Bolder (more prospective) individuals venturing outside the Pyrenees in the past likely had a low survival probability due to direct and indirect human persecution (see an example with fish in Biro and Post, 2008). Numbers of bearded vultures are growing now, but dispersal out of the high mountain ranges is barely taking place. On the contrary, an ongoing captive-breeding program in southern Spain that includes parental birds with genes from larger Asian populations have a higher pre-adult dispersal (Margalida et al., 2013), presumably allowing them to colonize new areas more quickly. This most likely will not be the case for the currently re-introduced population of bearded vultures in the Cantabrian Mountains (NW Spain), based only on shy individuals from the Pyrenees.

7. Shy bearded vultures and supplementary feeding stations

The fact that immature bearded vultures in the Pyrenees are tightly linked to a few major supplementary feeding stations does not contribute to dispersal either. Perhaps limiting supplementary feeding temporarily could foster dispersal out of the Pyrenees even of shy individuals, although any measure taken in that direction would not be free of uncertainty. Cases of raptor dispersal incidentally forced by food scarcity are known, probably due to the existence of sufficient latent behavioural variability in the focal populations. For example, griffon vultures (*Gyps fulvus*) dispersed widely after a food availability crisis caused by the bovine spongiform encephalopathy epidemics in Europe (Martínez-Abraín et al., 2011; Oro et al., 2012). Red kites (*Milvus milvus*) also dispersed notably after the closing of a major landfill in Majorca (Muntaner, 2014), with positive fitness outcomes in both cases, caused by the finding of new high-quality habitat.

Examples are also known of populations that were ecological refugees in the past due to human persecution but preserved enough behavioural variability to move to other habitats and expand geographically when persecution stopped. That is the case of booted eagles (*Aquila pennata*) in Majorca. This population has been historically characterized by the fact of nesting in cliffs despite the high availability of trees, the preferred nesting habitat of the species in the European continent (Jiménez et al., 2019). A fact that has been interpreted recently as an indication of shy-selection by past human persecution, because cliffs are safer than trees regarding perturbation by humans (Martínez-Abraín et al., 2010, 2021a). Specifically, in 2020 86.5% of the breeding pairs still nested on cliffs, but 13.5% already nested on trees, out of a sample of 37 territories (C. Viada, pers. com.).

8. Higher colonization potential versus higher risk of mortality?

The reinforcement of relict raptor populations with bold individuals can speed up the process of colonization (Silva et al., 2021), and hence be positive for the reinforcement project. A higher exploratory momentum and lower fear to make risky decisions when faced with novel situations (i.e. reduced neofobia) is positive as a rule, because it entails that individuals can make use of novel resources (i.e. breeding closer to humans, on new nesting substrata, using new food resources). But it could also have some negative consequences, such as increasing the risk of mortality due to interaction with humans and their infrastructures (Bremner-Harrison et al., 2004). However, the evidence available does not seem to point in that direction. Some studies have found that bold individuals (Tasmanian devils *Sarcophilus harrisii* and freshwater turtles, *Emydoidea blandingii*) survive better in the wild (Sinn et al., 2014, Allard et al., 2019). More importantly, a recent meta-analysis found that bold individuals survive better across taxa of vertebrates and invertebrates (Moiron et al., 2020), and hence that individuals expressing risky behaviours do not suffer higher mortality, despite some studies find no clear effects of boldness on survival (e.g. Lopes et al., 2017 studying captive-bred blue-fronted Amazon parrots, *Amazona aestiva*). On the other hand, increased boldness could limit philopatry in cases in which this is desired, thus compromising the success of hacking programs in which the goal is the establishment of an extirpated population in a particular site. In this regard Bamber et al. (2020) suggested to release shy individuals (red squirrels, *Sciurus vulgaris*) at the initial stages of a re-introduction, and to make use of bolder individuals later on to foster dispersal.

9. Some room for culture

The bold/shy behavioural continuum is seemingly under both genetic and epigenetic control (Riyahi et al., 2015; Miranda, 2017),

Table 1
Examples of translocation programs that have been implemented or could be implemented in the future for the conservation of endangered bird and mammal populations in the Iberian Peninsula, specifying the biological problem to be solved (conservation target) and some recommendations to conservation practitioners to achieve those conservation targets even when trade-offs operate.

Species	Type of translocation	Conservation target	Recommendations regarding source population and trade-offs	References to be consulted
Brown bear	Reinforcement	Dispersal out of ecological refuges	Bold females would foster movement out of refuges; however bolder bears released in shy-selected populations could be a source of human wildlife conflict. The latter factor prevails above the former.	Palomero et al. (2021)
Bearded vulture	Wild-wild reinforcement	Dispersal out of ecological refuges	Individuals from shy-selected populations may not achieve dispersal (see text for comparison between types of individuals and dispersal rates in the Cazorla and Picos de Europa translocation programs).	Margalida et al. (2013)
Cinereous vulture (Majorca)	Wild-wild reinforcement	To allow dispersal out of refuges in marine cliffs	Promote the use of birds from large non-inland populations to increase the probability of bringing bold genes to the island population. Preservation of the idiosyncratic reproduction of cinereous vultures in marine cliffs could not be a right conservation target as this is likely a consequence of past persecution. Nesting on the abundant pine and holm oak tree "inland" formations would be the conservation target to be achieved at the long run.	Martínez-Abraín et al. (2019)
Osprey	Wild-wild reinforcement	To allow human-wildlife coexistence in highly touristic southern European coastal areas	Promote the use of bolder individuals from northern European populations. This may foster the nesting of ospreys on trees but cliff-nesting is not a right conservation target to preserve as it is a consequence of the ghost of persecution past.	Martínez-Abraín (2018)
Crested coot	Wild-wild reinforcement	To prevent high mortality immediately after release	Promote the use of offspring from pairs coming from captive-breeding that have survived in the wild for more than one year and have reproduced.	Tavecchia et al. (2009)
Capercaillie (Western Europe)	Wild-wild reinforcement	To prevent low recruitment rates	Promote the translocation of birds from larger northern populations having larger probabilities of containing bolder individuals. Although southern European capercaillies form a distinct genetic subpopulation it is necessary to weight whether it is realistic to conserve the subspecies or if it is more advisable to aim for the conservation of the species regardless of the its subspecific nature. Captive-breeding programs have not succeeded so far.	Bajc et al. (2011) Frankham et al. (2011) Fernández-Olalla et al. (2012) Ralls et al. (2017)

suggesting that there is a role for both genetics and environment to generate heritable variability and plasticity. Boldness can be also achieved culturally via learning and habituation (Whittaker and Knight, 1998; Herrero et al., 2005; Wheat and Wilmers, 2016). This type of boldness (cultural) is most likely easier and faster to manage than that linked to the genetic component requiring selection. However, a relevant issue here is the likely interaction between genetic boldness and culturally-acquired boldness. Cultural habituation to harmless human presence by genetically bold individuals should be easier to be achieved than in the case of genetically shy individuals which are known to be less behaviourally variable (Verdolin and Harper, 2013). Yet even in the latter case, it is not impossible, especially when dealing with food availability or other main resources (Enders et al., 2019; Found, 2019). In this sense humans could play a major role promoting boldness in shy-selected populations, for good or for bad. An example is the case of shy-selected grey wolf and brown bear populations whose loss of fear to humans can be promoted unintendedly by the inappropriate use of garbage containers or other sources of alternative food (see Swenson, 1999; Palomero et al., 2021). Garbage management could also be key for the prevention of cultural loss of fear to humans by shy-selected grey wolves in populations where they are known to make extensive use of carrion and garbage (Mech and Boitani, 2003).

In remnant populations (supposedly composed, in whole or to a great extent, by shy individuals) in which reinforcement with bolder individuals is not wanted, it is likely that some behavioural changes may take place over time, perhaps helped by some environmental management such as the management of trophic resources. However, the risk of population extirpation needs to be evaluated on a case by case basis, and if it is high then the management of shy/bold phenotypes should be incorporated, together with other extended management techniques such as predator avoidance or environmental enrichment.

10. Concluding remarks

We think that rebounding relict animal populations that cope with favourable socio-environmental conditions, but despite this do not disperse outside their ecological refuges, could be affected by the ghost of past human selection in favour of shier individuals. This non-random genetic distribution (likely with little variability left in small populations) needs to be accounted for by conservation practitioners as a priority in their conservation agendas, because desired long-term levels of dispersal of translocated individuals could be hampered if individuals selected for translocations come from ecological refuges. From this perspective, the preservation of individuals of threatened species that show unequivocal bolder behaviours (such as nesting or foraging close to human settlements or infrastructure or withstanding the presence of people on nests) (Arroyo et al., 2011; Gómez-Serrano, 2021), could become especially relevant for the conservation of many species in an increasingly humanized world. However, the balance between promoting boldness and preserving shyness is less obvious when harm to people is one of the possible outcomes of increased boldness, or when interactions with humans or infrastructures lead to higher mortality rates. We summarize in Table 1 some recommendations for conservation practitioners dealing with the species and populations analysed in this essay, plus some other case studies in which we have been involved directly or indirectly in our work, including how to proceed with the trade-offs that practitioners can face.

Effects of boldness on survival of reintroduced individuals vary greatly depending on the taxa involved and that heterogeneity of success occurs in space and time. For sure there are no universal recipes, and each re-introduction/reinforcement program needs to be evaluated on a case by case basis and within an adaptive management framework, in relation to the shy-bold continuum. However, paying attention to among-individual differences in behaviour could increase the success of many ongoing and future translocations projects, as well as help us understand why many programs have failed to reach their goals in the past.

Declaration of competing interest

The authors have no conflict of interests to declare.

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