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Moving beyond defining animal personality traits: The importance of behavioural correlations and plasticity for conservation translocation success

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ABSTRACT

Translocations using captive-reared and wild-caught animals are important and widely used conservation tools to boost dwindling endangered populations and for maintaining biodiversity, but still suffer high failure rates. Animal personality, defined as consistent inter-individual differences in behaviour, can have a critical influence on individual fitness and population dynamics. Many conservation translocations could benefit by selecting individuals with certain personality traits, but the importance of personality of the 'founders' is often not considered. The link between behavioural assessments and improving translocation success therefore needs further investigation to demonstrate that adopting behavioural assays for translocations is worthwhile and feasible. Too few studies have considered the effect of captive-rearing or novel release-site conditions on changes to pre-release behavioural structural characteristics, including such as between-trait (i.e., behavioural syndromes) or within-trait correlations (i.e., personality-plasticity correlations) among individuals. Considering that appropriate behavioural structures can usually serve as immediate adaptive responses to environmental uncertainty, we suggest that the loss of appropriate structures may give a partial explanation for why captive-reared or wild-caught animals unfamiliar with the release-site environment suffer high post-release mortality rates. We call for more comprehensive personality trait assessments to evaluate the potential negative effects on behavioural structure induced by captive rearing and an unfamiliarity to the release-site environment in future conservation studies. We suggest several specific measures that may help to reform appropriate behavioural structures during captive rearing to form part of future feasibility and pre-release stages of conservation translocations.

1. Introduction

There is now a global scientific consensus that we are currently undergoing the Sixth Mass Extinction Event (Cowie et al., 2022). Unlike previous Mass Extinction events, anthropogenic impacts on natural environments (including climate change, habitat loss and fragmentation, invasive species, and overexploitation) are the primary drivers of extinction (Dirzo et al., 2014; Ceballos et al., 2015).

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The restoration of populations driven to extinction by human activity is therefore central for biodiversity conservation initiatives, helping not only to conserve the target species, but also having the potential to restore the structure and functioning of local ecosystems (Ceballos and Ehrlich, 2002). Conservation translocation, defined as the deliberate movement of organisms from one site to another (IUCN/SSC, 2013), has long been a common strategy to restore wild populations of dwindling or extirpated species (Griffith et al., 1989; Armstrong and Seddon, 2008). Considering that all signatory parties to the Convention on Biological Diversity (CBD, www.cbd.int) have an international legislative responsibility to enhance biodiversity, translocations (either within a country or between countries) may become an increasingly required conservation technique in the future (e.g., Butt et al., 2021), especially for endangered species with limited dispersal abilities (Griffith et al., 1989; Bubac et al., 2019).

Although numerous studies have demonstrated the potential efficacy of translocation for saving species from extinction and restoring viable populations, not all translocations have been successful (Fischer and Lindenmayer, 2000; Edelblutte et al., 2022) i.e.,

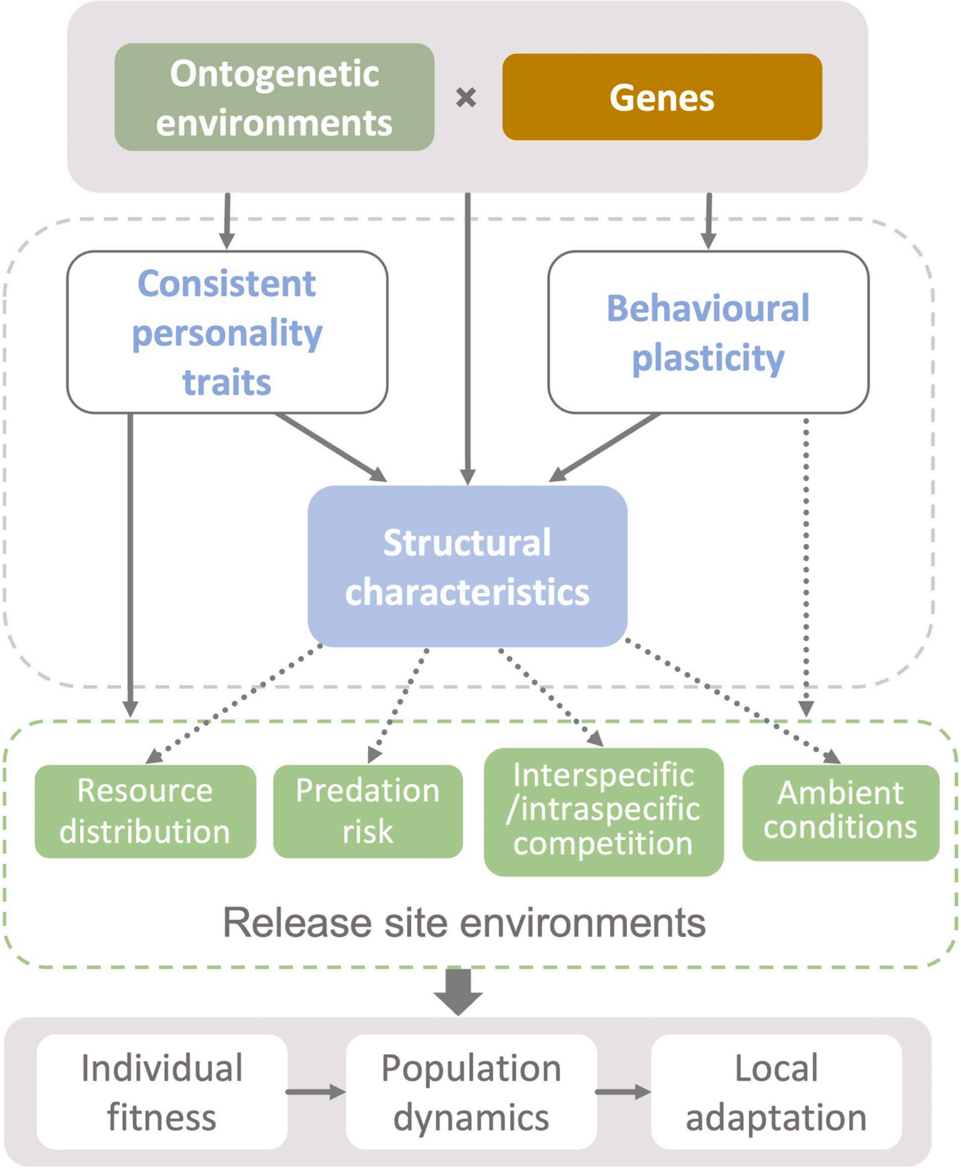

Fig. 1. How ontogenetic environments (differing from the release site environments) can influence the success of a conservation translocation. The covariance between genes and ontogenetic environments may affect not only personality traits, but also behavioural plasticity and other structural characteristics, such as behavioural correlations and personality-plasticity correlations. In addition to the consistent inter-individual differences in personality traits that have already been studied in several recent conservation studies (marked by solid arrow), those more complicated structural characteristics and plasticity (marked by dotted arrow), may also play critical roles in determining the adaptation to the release site environments (through decision-making during several fitness-relevant activities like finding food resources, predation avoidance, competition, and habitat selection) that remain to be explored in future conservation studies.

have resulted in the establishment and persistence of a new population, with success rates for threatened species varying from only 44% (Griffith et al., 1989) to 54% (Bubac et al., 2019). Furthermore, the published outcomes of many translocation projects tend to be biased toward only the successful cases (Berger-Tal et al., 2020). Thus, it is essential for conservation biologists and policymakers to ascertain the underlying factors that influence the success conservation translocations, particularly given the financial costs of such interventions relative to other conservation strategies (Armstrong and Seddon, 2008; Bernardo et al., 2011a, 2011b).

2. Integrating animal behaviour and conservation translocation

A decisive step toward meeting this challenge is the integration of animal behaviour assessment and training measures into current conservation translocation planning since these can critically affect an individuals' survival and settlement at the release site (van Heezik et al., 1999). Understanding behavioural responses to novel environmental uncertainty, i.e., an individual's decision-making under different fitness-relevant life history contexts (e.g., foraging, predator avoidance and dispersal) is essential for improving future conservation translocations (Roberts and Luther, 2023). Rearing animals in captivity can strongly affect their behavioural (Watters and Meehan, 2007) or even some behaviour-related morphological phenotypes, such as wing shape (Stojanovic, 2023). Furthermore, the more generations reared in captivity, the greater the impacts on individuals' behaviour would be (McPhee and Silverman, 2004). For example, McPhee (2004) documented decreased vigilance following predator detection by oldfield mice (*Peromyscus polionotus subgriseus*) as the number of generations in captivity increased. As a result, several pre-release/release phase tactics of translocations such as anti-predator training and environmental enrichment, along with soft release strategies have long been adopted by practitioners (Tetzlaff et al., 2019). These practices are primarily aimed to enhance the animals' behavioural capacity for adapting to their novel release site environment at the average level of the whole population (de Azevedo and Young, 2021), such as helping them to develop capabilities like escaping from previously unfamiliar predators (de Faria et al., 2020), finding wild-type foods or shelters (Mathews et al., 2005).

Recently, some conservation translocation case studies have highlighted the importance of quantifying the personality traits of individual animals i.e., consistent inter-individual differences in the average level of behaviour across time and contexts (Réale et al., 2007) prior to their release (systematically reviewed by Berger-Tal et al., 2016; Merrick and Koprowski, 2017; de Azevedo and Young, 2021; MacKinlay and Shaw, 2022). The relationships between post-release survival rates of individuals and personality traits can be complex (Martínez-Abraín et al., 2022). For example, survival has been demonstrated to be positively correlated with boldness in the reintroduced European mink (*Mustela lutreola*), while the relationship with exploration could be either negative or positive depending on year or location (Haage et al., 2017). These personality traits can be used as a criterion for selecting appropriate individuals for release (Bremner-Harrison et al., 2004). In fact, in addition to obtaining consistent individual differences in behavioural traits across time, animal personality may exhibit other relatively complicated structural characteristics (Sih et al., 2015), which, however, have been largely overlooked in previous conservation studies.

In this essay, we address an intriguing new possibility - that captive-rearing before release to natural environments, or even the environmental conditions of the source population of wild-caught individuals, may affect the structural characteristics of personality traits (Fig. 1), such as the decoupling of behavioural correlations, with potential negative consequences for post-release outcomes. These correlations are highly sensitive to environmental change (Bell and Sih, 2007; Adriaenssens and Johnsson, 2013; Nicolaus et al., 2022), and thus can be altered even over a small timescale within a generation. Although researchers have known that captivity experience may induce loss of variation of personality traits due to relaxed selection pressure (McDougall et al., 2006), and that promoting behavioural diversity or selecting a behaviourally diverse population for release can benefit translocations (Watters and Meehan; , 2007; Merrick and Koprowski, 2017), few have considered how captivity potentially affects the structural characteristics of personality traits and the corresponding influences on translocation success.

Our overarching perspective is that the formation of inappropriate behavioural structures of captive-reared animals can be related to immediate high post-release mortality rates. Furthermore, given that rewilding is a significant and rapidly developing approach for biodiversity conservation, in which ecosystem function is restored through the translocation of selected species, we suggest that this holds also for wild caught animals, that develop in a different environment other than the release-site. Assuming that individuals develop behavioural structures during ontogeny that are adapted to their environment, any forced movement to an environment with different selective pressures may lead to maladaptive behavioural structures and poor performance. This may include wild animals that are translocated outside their home range or natural habitat. Consequently, we advocate that it is necessary to give a more substantive consideration of how different behavioural structural characteristics might be useful in rewilding (e.g., Roberts and Luther, 2023).

In the following sections, we explain how different structural characteristics may implicitly influence the success of conservation translocations and propose several specific strategies to both investigate and alleviate the possibly negative effects from inappropriate behavioural structures on translocations. As this perspective rests on relatively limited empirical evidence, this paper is thus intended to stimulate further work to assess the above perspective, so we can begin to ascertain its relevance and applicability and help unravel underlying causal mechanisms in future conservation studies.

3. Lack of appropriate behavioural correlations due to release-site unfamiliarity

Individuals may exhibit a suite of correlated behavioural traits across multiple situations, known as behavioural syndrome (Gosling, 2011; Sih et al., 2004). Despite the lack of consensus among a series of inter- or intra-population studies regarding the response of behavioural syndromes to certain environmental conditions (Dochtermann and Dingemanse, 2013; Michelangeli et al., 2019), it is commonly accepted that the strength of such behavioural correlations is susceptible to an animals' surrounding environmental conditions, and can clearly affect the fitness gained by individuals (Smith and Blumstein, 2008; Merrick and Koprowski, 2017). Selection imposed by external abiotic and/or biotic factors can influence the formation of behavioural correlations in nature (Adriaenssens and Johnsson, 2013). For example, the presence of predators can exert selective pressure, causing stronger behavioural correlations in a population, while a low level of predation risk would weaken the relationships (Bell and Sih, 2007; Dhellemmes et al., 2020), owing to a trade-off imposed by the stressful conditions, such as between resource acquisition and safety (Bell and Sih, 2007). Where predators exist, bolder individuals tend to find food resources, while others are more willing to remain safe with their conspecifics.

Rearing under a captive environment without selection pressures from predation and competition or wild-living within natural habitats, however, is not likely to support individuals to form adaptive behavioural correlations due to lack of the aforementioned trade-off between resource acquisition and safety. As such, released individuals may suffer from immediate high survival and/or reproduction costs due to the mismatch in behavioural decisions under different contexts (Fig. 1). For the sake of argument, let us assume a possible situation based on an exploration-aggressiveness syndrome, which has been recorded in numerous different animal taxa (Sih et al., 2004). Released individuals could be quite exploratory (e.g., selected according to exploration) but always behave timidly during conflicts (i.e., reduced aggressiveness), a scenario which has been widely supported empirically in captive-reared animal studies (e.g., Fleming et al., 1996; Künzl et al., 2003; Salonen and Peuhkuri, 2006). In this case, the released individuals may have a higher probability of finding good habitat at their release site but also might be easily outcompeted by others from either the same species or native congenerics. That is, those individuals would suffer a profound disadvantage, paying higher costs during exploration after release to the wild, but ultimately are unable to obtain the benefits. A laboratory study on three-spined sticklebacks (*Gasterosteus aceuleatus*) found that despite the absence of a bold-aggressive syndrome within the laboratory population prior to any real predator exposure, behavioural correlations appeared among the survivors following the loss of almost 50% of the sticklebacks to real predators (Bell and Sih, 2007). This implies that individuals lacking specific behavioural correlations may be more susceptible to predation in natural environments.

To our knowledge, there has been limited research on directly assessing the positive effects of behavioural correlations in conservation translocations (but see Merrick and Koprowski, 2017; Kelleher et al., 2018; West et al., 2019), even though there is increasing evidence from field and laboratory studies for the adaptive significance of such correlations (Bell and Sih, 2007; Sih et al., 2012; Michelangeli et al., 2019; Dhellemmes et al., 2020). More targeted theoretical and experimental studies on how the existence of behavioural correlations and the strength of correlations affect adaptation and population persistence should prove useful for conservation translocation practice.

4. Captive-rearing and plasticity in personality traits

Consistent behavioural differences among individuals across contexts does not necessarily equate to the loss of plasticity, and evidence now suggests that personality traits can exhibit plasticity, which may differ among individuals from the same population (Stamps and Biro, 2016). Here we consider the plasticity in personality traits as individual-level personality variations across different internal or external environmental gradients (Nussey et al., 2007; Dingemanse et al., 2010; Brommer, 2013). This has led to some concerns about studying animal personality using a behavioural reaction norm framework (BRN), which includes information on how an individual behaves on average (i.e., "personality"), how its behaviour changes (i.e., "plasticity") and also how the above two components covary across time or contexts (Dingemanse et al., 2010). Numerous empirical studies of different animal taxa have found consistent individual differences in plasticity of personality (e.g., Morand-Ferron et al., 2011; Dingemanse and Wolf, 2013; Mitchell and Biro, 2017).

Such plasticity can have important fitness consequences in the wild, such as benefitting individuals in terms of survival (Toscano, 2017), and mating success (Barou-Dagues et al., 2020). Conversely, behavioural plasticity could also be detrimental to population persistence in circumstances where individuals gather inaccurate environmental information (Dore et al., 2018), e.g., while translocating animals to a new environment (Reed et al., 2010). This is because, in such cases, individuals might face extreme or novel environmental stochasticity, and previously reliable cues that act as indicators of adaptive plastic responses become less-informative, or even misleading, causing behaviour-environment mismatching (Schlaepfer et al., 2002; Ghalambor et al., 2007). Plasticity in personality traits can therefore play contradictory roles in adaptation, and failing to develop locally adaptive plasticity during the feasibility phase might partially explain a relatively low success rate of local population establishments following release in some conservation translocations.

For captive-reared animals, living together in an artificial environment for a relatively long-term (i.e., a selection relaxed and predator-free, homogeneous environment with abundant food resources) may affect their capacity to gather information and to cope with environmental uncertainty. For example, they might form inappropriate syndrome structures or may be unable to form any significant fitness-relevant adaptive plasticity at all, hindering adaptation to their new wild environment immediately following release (Crates et al., 2023). A lack of environmental heterogeneity in captive environments can negatively impact cognitive development (Reading et al., 2013), leading to impaired predator responses, as shown by studies of captive-reared fish (Salvanes et al., 2013), mammals (McPhee, 2004), marsupials (Jolly et al., 2018), and birds (White et al., 2012; McCune et al., 2019). Captive animals often do not have opportunities to learn from wild conspecifics (Courtney-Jones et al., 2017), which can impact sociality and functional responses to vocalizations (Freeberg, 1996; Rose and Croft, 2015). Because different vocalizations are under selection in not only anti-predator responses, but also breeding ecology, territoriality and recognition of different individuals (Lindström, 1999). Other empirical studies have also shown that population-level habitat changes e.g., changes from natural to more urban environments

(Scales et al., 2011), or changes to selection regimes e.g., recent changes in selection pressures in modern dog breeds (Hansen-Wheat et al., 2019) can indeed cause behavioural correlation breakdown (Bell and Sih, 2007).

Considering that the adaptivity of plasticity largely depends on the novelty of the new release-site environment relative to the captive environment, and the ability of individuals to accurately track and even predict environmental changes (Sih, 2011; Snell-Rood et al., 2018), stable captive environments thus seem unlikely to support individuals to develop adaptive plasticity. Conversely, captive conditions may drive individuals to exhibit even higher behavioural plasticity, due to the relatively low cost in adjusting behaviours under weak selective pressures (Sih, 2013; Hewes et al., 2017; Westrick et al., 2019; Tranquillo et al., 2023). In this case, it may be possible that the plasticity developed in captive environments would generate a behavioural mismatch and become maladaptive following release to a quite different environment (e.g., through inappropriate syndromes). It is also important to acknowledge that in some cases, limited plasticity or personality trait correlations may not be adaptive because they are the product of intrinsic constraints (Duckworth, 2010; Dochtermann and Dingemanse, 2013) such as time or functional constraints for limited plasticity, or genetic constraints for personality-trait correlations (Duckworth et al., 2018). In these instances, remodeling of behavioural phenotypes may simply not be possible and/or it may be difficult to select individuals for translocation based on their behavioural properties.

Regardless, we suggest that obtaining a relatively high level of plasticity in personality traits should do more good than harm, since it also provides the potential for those animals to reform appropriate behavioural structures within a short time period through certain training prior to being released. For example, a recent empirical study of a reintroduced mesopredator species verified that plasticity of different personality traits is associated with several fitness-relevant aspects of post-release performances such as travelling distance and time-length of den sharing (Wilson et al., 2022), thereby contributing toward the overall success of the translocations. Furthermore, variation in plasticity among individuals may also play a critical role in promoting translocation success, because plasticity differences among individuals can enable those released individuals to adopt diverse response strategies for dealing with complex and changeable release-site environments, benefiting founding population stability and persistence (Dingemanse and Wolf, 2013). Although empirical evidence about how captive-rearing affects plasticity differences is hitherto quite rare, we suppose that captive-rearing for generations might play a negative role in general. It is well-known that captive breeding can lead to a loss of genetic diversity (Francuski et al., 2014; Aguiar et al., 2018), possibly due to the lack of fluctuating selection pressures in nature (Quinn et al., 2009; Mouchet et al., 2021; Johnson et al., 2023). More research should be conducted to enhance our understanding of the relative importance of the different dimensions of the impacts of plasticity.

In practice, using captive-reared or wild-caught animals with consistent individual differences in plasticity as a source for conservation translocation can potentially be effective for population reestablishment, depending on how best to assess and develop behavioural plasticity e.g., through designing appropriate pre-release behavioural assessments and training for helping animals to reform fitness-relevant behavioural structures (see Section 6 below). Recent empirical studies conducted of wild populations have shown that behavioural structural characteristics can still be changeable depending on individuals' local experiences and/or ecological conditions (Garamszegi et al., 2015; Nicolaus et al., 2022). This does not necessarily mean that individuals can immediately adjust their behaviours accordingly under dramatic environmental changes. Therefore, it might be more cost-coefficient to conduct behavioural structures remodeling via plasticity during captivity before release.

As recommended by Wilson et al. (2022), individuals with different degrees of plasticity could be used for translocations at different stages. These authors suggest that more behaviourally-rigid individuals should be selected for initial translocations to reduce predation risk and other forms of mortality caused by hyper-dispersal following release. Individuals with greater plasticity are better suited for subsequent release cohorts following the initial translocation of individuals that exhibit less behavioural plasticity, because they may increase the translocation success by further enhancing the behavioural diversity of the newly released population (Wilson et al., 2022). Nevertheless, there is widespread acknowledgement that dispersal tendency by animals can also be associated with both the individual personality or the population average personality traits such as boldness and sociability (Cote et al., 2010, 2011). Similarly, home range movements and the degree of site fidelity can be personality-dependent (Minderman et al., 2010; Harrison et al., 2015). Thus, assessing the diversity of spatial movement behavioural types from source populations (either captive or wild-caught) in combination with plasticity, might have important implications for planned conservation translocations (Harrison et al., 2015).

5. Absence of plasticity-personality correlations

Increasingly, empirical studies are now investigating hypotheses about the relationships between personality traits and certain aspects of the plasticity of those traits (Stamps and Biro, 2016). Personality-related differences in behavioural plasticity have been detected in laboratory and field studies from a broad array of taxa (e.g., Dingemanse et al., 2012a; Betini and Norris, 2012; Found and St. Clair, 2017; Jolles et al., 2019). Mathot et al. (2012) stated that theoretically, plasticity-personality correlations may be related to the adaptive strategies for coping with environmental uncertainty, i.e., only the adaptive plasticity can enable individuals to benefit from accurate responses to environmental change. In this instance, the existence of plasticity-personality correlations may also play a role in affecting the success of conservation translocations.

Although there has been little direct evidence for assessing the effect of personality-plasticity correlation on translocation success, increasing behavioural studies have indicated such correlations can be fitness-relevant (Mathot et al., 2012). For example, a laboratory study of Rainbow trout (*Onchorhyncus mykiss*) showed that the benefits gained through changing in behaviour (i.e., plasticity) were directly related to boldness (Frost et al., 2007). Betini and Norris (2011) indicated that the interaction between male personality and plasticity was significantly related to the number of offspring fledged in tree swallows (*Tachycineta bicolor*), and that nonaggressive males would have high reproductive success if they were plastic. Therefore, we suggest that the lack of certain personality-plasticity relationships in either captive or wild-caught individuals may impact their adaptation to the unfamiliar release site environments. For example, let us assume some individuals, that are bold-explorers but without a high level of behavioural plasticity (e.g., Jolles et al., 2019), are selected unintentionally for translocation, due to the fact that bold individuals would be more likely to enter the trap and then be captured (Merrick and Koprowski, 2017). Although these individuals might be able to detect environment change quickly, they would be unable to adjust their behavioural traits accordingly to improve their fitness. In the meantime, they would need to pay the relatively high costs of exploration e.g., energy costs or predation risks during moving around the unfamiliar release-site environment, further contributing toward the failure of the translocation.

While adjusting behaviour, animals need to collect information on environmental change to determine their responses. The efficacy of different information sampling tactics might be environment dependent (Mathot et al., 2012). For instance, when resources are widely dispersed and environmental cues for animals are conspicuous, individuals moving through the environment more quickly (i.e., higher activity and/or exploration) should be more effective in sampling. In captive-rearing environments however, conditions usually remain almost unchanged with abundant food resources and a lack of predation risk. Even if some of the captive conditions are changed unintentionally, the relatively limited extent of the captive area of activity may enable all of the individuals to obtain the same information about any environment changes, and therefore exhibit uniform behavioural responses at the population level. In this scenario, captive-reared animals may be unable to form a relationship between personality and plasticity, which may in turn affect their adaptation to the natural release-site environment (Dingemanse et al., 2010; Mathot and Dingemanse, 2015).

6. Conservation implications

1) Appropriate and comprehensive pre-release assessments for different personality traits.

Results from translocation studies already applying behavioural training have been mixed, ranging from improved survival to having no effect, or even being detrimental to success (Tetzlaff et al., 2019). This may be due to previous training attempts being ineffective in reforming behavioural structures or simply were not of sufficient duration to permit certain behavioural structures to reform. We suggest that some criteria for behavioural structure can be used to identify whether the trained animals are suitable for release. To achieve this, designing cost-efficient behavioural tests that are easy to conduct across a range of fitness-relevant situations during training is essential and would have to be species- and/or context-specific, and the criteria used should be considered on a case-by-case basis. For instance, when predation risk and competition are relatively high at the release-site, forming certain bold-aggressive syndromes after behavioural training can be used as an optional criterion. Plasticity-personality correlations can also be used as criteria when the release-site environments are highly stochastic. With the help of these criteria, practitioners therefore can assess the efficacy of different training tactics (e.g., more targeted approaches, or in reducing the financial costs of training). However, this would assume that practitioners and researchers have the capacity to assess accurately what the selective pressures of the new environment are, whilst also implying that by training animals in a certain way, behavioural syndromes can be remodeled in a way that would lead to a subset of behavioural phenotypes being selected. We acknowledge that, in practice, this may be extremely challenging to undertake, and by selecting the same behavioural types that are deemed more suitable could lead to other conservation problems such as founder effects, or loss of genetic diversity. The feasibility of this approach would also depend on the mechanisms underpinning individual behavioural variation. A more pragmatic approach would be to aim for translocating as much as behavioural diversity as possible because different behavioural types may occupy different niches and make new populations more resilient to environmental change (Dall et al., 2012; Wolf and Weissing, 2012).

Appropriate and comprehensive pre-release phase behavioural estimates should play a fundamental role in reducing the potential impacts of inappropriate behavioural structures. To date, conservation translocation studies that consider animal personality typically focus on a single trait or different traits separately (de Azevedo and Young, 2021), and provide little guidance as to how behavioural correlations or other structures influence the success of translocation programs. Future translocation studies could work on accounting for the bridge between behavioural structures and local adaptation in a broader range of contexts (see the dotted arrows shown in Fig. 1), which could prove useful in promoting conservation success.

Repeated measures of different behaviour traits are crucial for any assessment of inter-individual variation, which is the core criteria for determining the existence of animal personality (Réale et al., 2007). However, the repeatability of a behavioural trait has only been assessed in approximately half of the studies that consider animal personality (MacKinlay and Shaw, 2022). Besides repeated behavioural tests, reasonable statistical analyses are also vital for assessing personality traits and relevant structures. For example, behavioural syndrome has often been assessed by calculating the phenotypic correlations between behavioural traits following an "individual gambit" (Brommer, 2013). However, given the strength and direction of the correlations between traits may differ between the among- and within-individual levels, Dingemanse et al. (2012b) suggested that behavioural syndrome should only refer to the among-individual component of phenotypic correlations. Without eliminating the within-individual component, phenotypic correlations may inaccurately estimate among-individual correlations, resulting in misleading conclusions on behavioural syndromes (Moiron et al., 2020).

2) More comprehensive and better targeted pre-release phase training.

Translocation practitioners may need to conduct more comprehensive and better targeted pre-release phase behaviour training of individuals before release, to enhance the success rate, building on well-established training and enrichment techniques already developed by practitioners (see Tetzlaff et al., 2019). Specifically, other than choosing individuals with certain personality traits (reviewed in Merrick and Koprowski, 2017; de Azevedo and Young, 2021; MacKinlay and Shaw, 2022) or plasticity (Wilson et al., 2022), it is necessary to enable captive-reared animals establish some degree of the ecologically relevant behavioural structures before release. In fact, some classic behavioural training tactics are likely to unconsciously promote the establishment of such behavioural structures to some extent. For instance, conservationists often put animals into large, structure-complex outdoor pens for some time before transfer and release to the wild either at the proposed release site (i.e., soft-release) or not (e.g., Urbanek et al., 2010). Constructing outdoor pens at the proposed released site is a proven effective practice by which individuals can develop and improve different fitness-relevant behavioural skills and cognitive abilities (Reading et al., 2013), and improve their physical condition prior to release (e.g., Mathews et al., 2005). We suggest that putting animals in semi-natural conditions at the proposed released site can enable them to cope better with a heterogenous environment with relatively high uncertainty, which may drive individuals to reform appropriate structural characteristics to adapt to the release-site environment. This would further help improve the likelihood of population establishment and the overall success of the translocation.

To help establishing appropriate structural characteristics further, more targeted training tactics can be adopted, such as occasionally setting food restrictions to force competition among individuals, and presentation of predator cues at the release site. Aversive experiences may be included in some contexts e.g., exposed individuals to controlled predators (Edwards et al., 2021). These tactics can not only help to promote the competitive ability at the population level (Manlick et al., 2017) and predator-recognition ability (Greggor et al., 2019), but also enable captive-reared or wild caught animals to adapt to a changeable and competitive environment with predation risks, which can play a role in driving the formation of behavioural correlations. For example, empirical evidence has revealed that predation pressure affects the behavioural correlations in different lemon shark (*Negaprion brevirostris*) populations (Dhellemmes et al., 2020), and where competitive contests are common or important, individuals should be more likely to exhibit clear-cut behavioural syndromes (Sih and Bell, 2008). Furthermore, given that environmental conditions at proposed release sites are generally heterogeneous, practitioners should also provide relative changeable food resources for the animals to help them form adaptive plasticity before release. This training tactic can also provide diverse experiences to the released animals (Watters and Meehan, 2007) and may help them to develop the adaptive associative learning capacity (Morand-Ferron 2017) for better adaptation to the post-release environment through plasticity. However, it is important to acknowledge that there are different forms of plasticity, both irreversible and reversible, and hence remodelling of e.g., syndromes can happen at different periods in the lifetime of an individual, including after the translocation.

To further promote the developing of certain matched plasticity-personality correlations, practitioners can also alternatively choose to hide or not to hide the supplied novel food items (e.g., wild-type foods, Mathews et al., 2005) in the holding pen depending on the release-site environment. When utilized resources are clumped and environmental cues are less conspicuous at the release-site (e.g., scattered trees in savanna-like landscapes (Tews et al., 2004)), individuals exploring more slowly but thoroughly, and those that have a higher degree of plasticity in adjusting their behaviour in response to changes in resource distributions (Mathot et al., 2012), should be more beneficial for achieving translocation success. Any supplied novel food items thus should be placed more cryptically (e.g., hiding foods under unpredictable covers) at randomly selected sites in the holding pen during training, enabling slow explorers to develop adaptive behavioural responses (i.e., relative high plasticity). In other instances, with resources widely dispersed and conspicuous (e.g., in large and continuous natural grasslands (Kang et al., 2007)), the supplied novel foods should be directly placed at randomly selected sites but not hidden. In this case, fast explorers can be trained to develop a higher plasticity instead, increasing their capacity to adapt post-release through quickly perceiving changes in the release-site environment (Mathot et al., 2012).

Finally, although there has been debate about the use of predator-proof fencing strategies due to the purported low cost-efficiency and lack of empirical data on their effectiveness (Bombaci et al., 2018), we suggest that it can be used more often in future translocations, because it may again serve to promote behavioural correlations and adaptive plasticity for captive-reared animals. That is, in a relatively large, fenced reserve, individuals need to cope with various abiotic factors and biotic interactions that are near-natural, possibly driving the formation of behavioural correlations on one hand (Sih and Bell, 2008). On the other hand, those individuals might be widely dispersed throughout the reserve, and thus unable to acquire the abiotic and/or biotic environmental variation information simultaneously, enabling individuals that have a more efficient sampling tactic to benefit from greater plasticity in adjusting their behaviour to environmental heterogeneity (Mathot et al., 2012). Further empirical studies should consider these issues for more definite answers.

7. Conclusion

In this essay, we make the point that translocation research needs to look beyond defining personality traits, and examine behavioural syndromes and behavioural plasticity, including the interaction between plasticity and personality. We highlight the potential detrimental effects of captive-rearing environments on several personality-related behavioural structures of the released animals that also hold relevance for wild-caught individuals that are the focus of rewilding programmes. We suggest that the absence of appropriate structures may partially explain why captive-reared or wild caught animals unfamiliar with the release site suffer a high post-release mortality rate, resulting ultimately in the failure of the translocation. More research is required to investigate whether behavioural syndromes, rather than just individual personality traits can influence translocation, and to identify the direct links between syndromes and translocation. We encourage more direct or taxon-specific exploration to determine whether behavioural syndromes are more likely to break down in captivity for certain taxa or contexts, which can then be used to inform management. For example, studies have revealed that captive enrichment is very effective for numerous fish species (Näslund and Johnsson, 2016) but more research is needed to determine whether this could be a function of behavioural syndromes. Similarly, research has shown that juvenile fish respond more favourably to enrichment techniques than adults (Johnsson et al., 2014) and therefore more laboratory experiments could address behavioural syndrome establishment across different age classes.

Whilst we hope that this can serve as a ‘call to arms’ to start studying these behavioural processes, we acknowledge that most translocation programs may not have the resources to do so without stronger evidence to support the link between behavioural structure and increased translocation success. This is particularly true for the many conservation translocations that involve endangered species population reestablishment because it simply might not be feasible to conduct experimental studies that explore the causal mechanisms of behavioural structures on translocation. Experimental approaches using common species in the laboratory (e.g., some widely used insects, fishes, or birds) should be utilized to help identify cause-and-effect relationships (Cooke et al., 2017), helping us understand not only why some past programmes have failed, but to also improve the cost-efficiency of future translocations.

It is important to note that even if behavioural studies provide details on the relationships between behavioural structures and surrounding environments, accurately determining what structures are appropriate in a specific translocation project is still essential. Given that there is no "one size fits all" criteria about what kinds of individuals are most likely to achieve translocation success (Crates et al., 2023), practitioners thus should consider incorporating common theories about the relationships between structural characteristics and captivity into behavioural training and measuring responses from the onset. Subsequently, training initiatives should be strengthened based on subsequent iterative releases and monitoring to identify better criteria and further corrective actions (Crates et al., 2023) to improve the likelihood of translocation success.

CRediT authorship contribution statement

Lyu Nan: Conceptualization, Funding acquisition, Resources, Supervision, Writing – original draft, Writing – review & editing, Visualization. **Dong Lu:** Writing – review & editing. **Zhang Yan-Yun:** Conceptualization, Writing – review & editing. **Wu Xiao-Yuan:** Resources, Visualization, Writing – original draft, Writing – review & editing, Conceptualization. **Lloyd Huw:** Writing – review & editing.

Declaration of Competing Interest

The authors have no conflict of interests to declare.

Data Availability

No data was used for the research described in the article.

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