The phenotypic costs of captivity

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ABSTRACT

The breeding of threatened species in captivity for release is a central tool in conservation biology. Given gloomy predictions for biodiversity trends in the Anthropocene, captive breeding will play an increasingly important role in preventing future extinctions. Relative to the wild, captive environments drastically alter selection pressures on animals. Phenotypic change in captive animals in response to these altered selection pressures can incur fitness costs post-release, jeopardising their potential contribution to population recovery. We explore the ways in which captive environments can hinder the expression of wild phenotypes. We also stress that the phenotypes of captive-bred animals differ from their wild counterparts in multiple ways that remain poorly understood. We propose five new research questions relating to the impact of captive phenotypes on reintroduction biology. With better use of monitoring and experimental reintroductions, a more robust evidence base should help inform adaptive management and minimise the phenotypic costs of captivity, improving the success of animal reintroductions.

Key words: animal behaviour, animal husbandry, conservation, natural selection, phenotypic change, reintroduction biology, threatened species recovery, zoology.

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I. INTRODUCTION

The world is in the midst of a biodiversity crisis and extinction rates will increase over the coming century (Ceballos, Ehrlich & Dirzo, 2017; Powers & Jetz, 2019). Never before has there been a greater need to develop effective ways to conserve biodiversity (Paul *et al.*, 2020). Captive breeding and release, or reintroductions, are a common approach to facilitate threatened species recovery (Conde *et al.*, 2011). Captivity shelters a subset of individuals from the threatening processes that contribute to population decline in the wild (Caughley, 1994). Individuals bred in captivity can insure against extinction (Dobson & Lyles, 2000) and be used to supplement or re-establish wild populations (Ewen *et al.*, 2012). Captive breeding for release is a recommended conservation strategy for over 2000 threatened species globally (IUCN Conservation planning specialist group, 2020).

Despite clear potential, reintroductions do not always result in self-sustaining wild populations and are resource intensive (Fischer & Lindenmayer, 2000). Managing the California condor *Gymnogyps californianus*, for example, costs more than a million US$ per year (U.S. Fish and Wildlife Service, 2012). Investment of this magnitude requires confidence that reintroductions will result in population recovery. If not, conservation funds may arguably be better spent elsewhere (Gerber, 2016), particularly if species are likely to rely on long-term intensive management (Heinsohn *et al.*, 2022). Reintroduction of captive-bred animals can also result in unforeseen loss of fitness in wild populations (Araki, Cooper & Blouin, 2009), through the introduction of deleterious alleles and exposure to pathogens (Araki, Cooper & Blouin, 2007; Peters *et al.*, 2014). Doubts about whether reintroductions are based on effective applied science (Taylor *et al.*, 2017) call for a better understanding of how and when *ex-situ* management can be a viable conservation measure (McGowan, Traylor-Holzer & Leus, 2017). A key component of answering this question is understanding whether captive animals differ from their wild counterparts.

Captive environments impose substantially different selection pressures on animals relative to the wild environments in which they evolved. Some negative genetic fitness effects of captive breeding are unavoidable because only a subset of wild gene diversity can typically be represented in captive pedigrees (Frankham, 2008). Given that genetic adaptation to captivity can occur in only a few generations (Christie *et al.*, 2012), avoiding deleterious changes is challenging (Ford, 2002; Frankham *et al.*, 2017). Altered traits of captive animals can also arise through phenotypic plasticity; the potential for organisms to produce different phenotypes in different environments (Edelaar & Bolnick, 2019). However, the capacity of individuals to alter their phenotype according to their environment is limited and takes time (DeWitt, Sih & Wilson, 1998), meaning it is not easy to distinguish genetic change from phenotypic plasticity. Recent evidence shows that captive animals differ from wild conspecifics in ways that are not entirely attributable to genetics (Davis, Smith & Ballew, 2020; Tenger-Trolander *et al.*, 2019). Maintaining viable wild populations by reintroducing captive-bred individuals is much more than a numbers game (Fischer & Lindenmayer, 2000) and it is becoming increasingly apparent that the phenotypic quality of captive-bred animals is as important as their quantity in determining reintroduction success (Berger-Tal, Blumstein & Swaisgood, 2020; Shier, 2016). Understanding the myriad ways that animal phenotypes can change in captivity is critical for managing risk, ensuring the efficacy of captive breeding, and is also an important animal welfare consideration (Webster, 1995). This in turn can have implications for the way captive breeding for reintroduction is designed and managed to ensure animals are treated ethically in captivity and post-release.

In wild populations, natural selection acts on the variance between individuals in reproductive success and mortality (Darwin, 1859). In captivity, variance in reproductive success and mortality is reduced through food provisioning, veterinary practices aimed at maximising lifespan and reproductive output, and the absence of predation (Driscoll, Macdonald & Brien, 2009). However, the importance of selection in captivity is under-appreciated (Schulte-Hostedde & Mastromonaco, 2015). Non-random variance of traits in captive animals may also signal that new anthropogenic selective pressures have emerged. Examples of 'captive selection' include behavioural traits, for example where less-neophobic individuals have higher reproductive success or lower mortality and stress levels (Price, 1999). Because captive population sizes are typically small, altered selection pressures and genetic drift can drive phenotypic divergence of captive animals from their wild ancestors (Frankham, 2008; Kitada *et al.*, 2009).

A typical approach to mitigating phenotypic change in captive animals involves management of studbooks to maximise retention of genetic diversity (Frankham, 2008). However, genetic management alone is unlikely to detect or mitigate phenotypic change unless traits are monitored proactively; this is rarely achieved in captivity for a number of reasons. First, trait changes may be cryptic (Stojanovic *et al.*, 2021a) or hidden by the protective environment, e.g. lack of selection against maladaptive traits (Kohler, Preston & Lackey, 2006). Second, invasive handling of animals required to detect subtle morphological changes is often avoided because it can cause stress (Gouveia & Hurst, 2019). Third, there are often knowledge gaps about how captive phenotypes compare to those in the wild. Lastly, because

most species lack detailed genetic studies, mapping of genotypes and corresponding phenotypic traits is usually poor or non-existent (Brandies *et al.*, 2019; Pierson *et al.*, 2016). A detailed understanding of the role of selection in driving differentiation of captive animals from wild conspecifics may only be achieved when research methods are developed that allow collection of this cryptic information.

We aim here to review the ways that animal phenotypes can change in captivity, and to develop a conceptual framework to highlight the role of the captive phenotype in influencing the success of captive breeding for reintroduction (Edelaar & Bolnick, 2019). We first explore how captive environments can alter animal phenotypes and the relationships between phenotypic traits. We then discuss how adaptive management – a process to enhance knowledge and improve conservation decisions through monitoring (Canessa *et al.*, 2016) – can reduce the phenotypic costs of captivity and increase reintroduction success (see Section IV). Finally, we identify five key research questions, the answers to which could improve the success of future reintroduction efforts.

II. THE CAPTIVE PHENOTYPE

We define the captive phenotype as the behaviour, morphology and health of captive individuals that may differ from those of wild conspecifics due to altered (or lack of) selection pressures in captivity and/or phenotypic plasticity. Below we outline the ways in which captive phenotypes can emerge. In most cases, there has been little evaluation of the ways in which captive phenotypes impact reintroduction outcomes, however the few cases where this information is known are discussed below.

(1) Behavioural

Captive environments are often unavoidably simplified relative to the wild, meaning that behaviours associated with life skills may also be simplified. An inability to learn or express the behaviours needed to survive in the wild may result in development of behaviours that are disadvantageous after release. Animals may fail to develop particular behaviours in captivity for a number of reasons. These include restriction of the ability to express behaviours related to survival and reproduction (Lewis *et al.*, 2022), a mismatch between the timing of developmental periods and opportunities to gain relevant experience (Crates *et al.*, 2021), or lack of stimulation (Burn, 2017). Many behaviours are also learned from associates, facilitating the maintenance of behavioural norms through conformity (Brakes *et al.*, 2019). Behaviours acquired in captivity can emerge because captive-bred animals are typically unable to associate with and learn from wild conspecifics. The erosion of and divergence from wild behaviours can occur quickly in captivity (Courtney Jones, Munn & Byrne, 2017) and the need to maintain learned animal behaviours (i.e. cultures) in conservation is increasingly being recognised (Brakes *et al.*, 2019).

(a) Vocalisation

Similar to humans, many animals including cetaceans, primates and birds learn vocalisations from conspecific tutors (Nowicki & Searcy, 2014). Vocalisations are under selection given their role in mate and territory acquisition, conspecific recognition, dispersal and antipredator behaviour (Lindström, 1999). Vocal differences between captive-bred and wild conspecifics could compromise the success of reintroductions if such differences lead to assortative mating, higher predation rates or other negative impacts on social associations (Freeberg, 1996). Captive Hawaiian crows *Corvus hawaiiensis* have lost territorial broadcast calls from their repertoire (Tanimoto *et al.*, 2017), but appear to have retained functional responses to such vocalisations (Sabol *et al.*, 2022). The songs of captive and wild conspecifics differ drastically in regent honeyeaters *Anthochaera phrygia* (Crates *et al.*, 2021) and Puerto Rican parrots *Amazona vittata* (Martínez & Logue, 2020). Experimental changes to social group composition caused dialect change in captive common marmosets *Callithrix jacchus* (Zürcher, Willems & Burkart, 2019). Shifts in vocal cultures following fragmentation of social groups have also been shown in orcas *Orcinas orca* (Foote *et al.*, 2006) and humans (Walsh, 2005).

(b) Animal movement

Whilst animal movements often have a genetic basis (Liedvogel, Akesson & Bensch, 2011), there is a substantial learned component to movements of many species. Migration routes can be learned by accompanying older conspecifics (Mueller *et al.*, 2013) or refined through individual experience (Campioni *et al.*, 2020). Changes to the movement patterns of captive-bred animals are generally a barrier to successful reintroduction of mobile species, although there have been suggestions that interrupting cultural transmission of dispersal pathways may actually benefit reintroductions in heavily modified environments (Dinets, 2015). Captive-reared Asian houbara *Chlamydotis macqueenii* departed their breeding grounds 20 days later and travelled on average 480 km less than wild conspecifics (Burnside, Collar & Dolman, 2017). Surviving captive-born houbara were also faithful to wintering locations across years, suggesting minimal phenotypic plasticity in their dispersal behaviour. Hatchery-reared Atlantic salmon *Salmo salar* had similar migratory performance to wild conspecifics in terms of migration speed, but were 13.9 times less likely to survive than naturally reared smolt (Larocque, Johnson & Fisk, 2020). Appenine chamois *Rupicapra pyrenaica* reared in an enclosure moved less frequently and shorter distances than wild founders after release (Bocci *et al.*, 2014), whilst captive-bred monarch butterflies *Danaus plexippus* (Fig. 1A) rapidly lost their migratory tendency and failed to orient south (Tenger-Trolander *et al.*, 2019).

(c) Sociality

Most captive-breeding programs house individuals together based on necessary priorities including logistics and
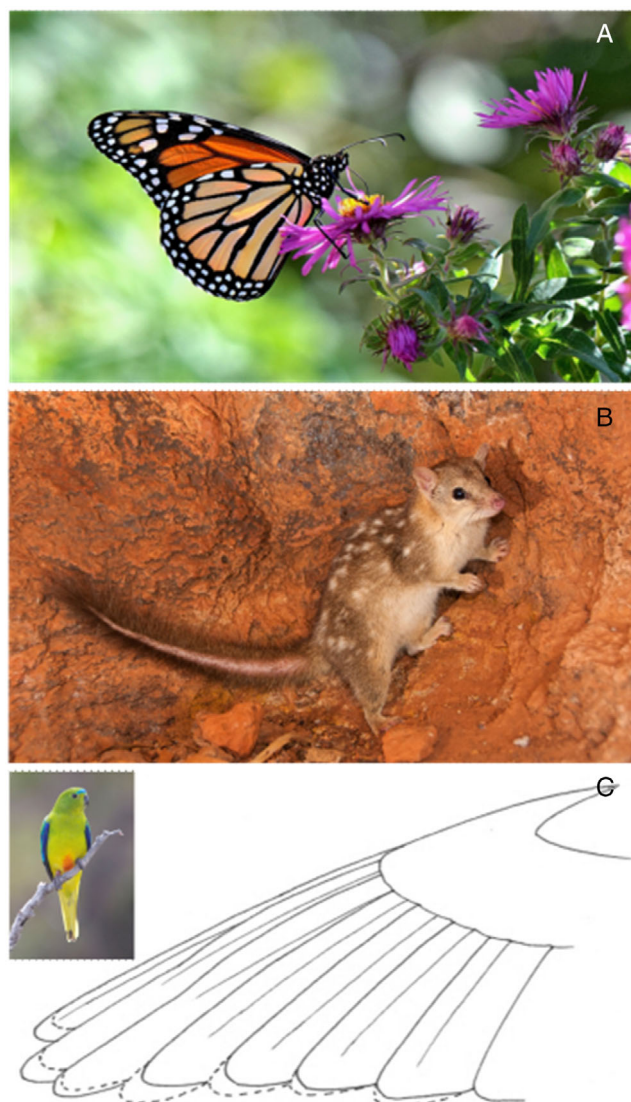
Fig. 1. (A) Monarch butterflies *Danaus plexippus* are migratory, but captive-bred individuals lose key behavioural traits associated with migration, including the ability to orient south. They also suffer developmental and physiological impacts including different wing shape and weaker grip. Image: Yi-Kai Tea. (B) Northern quolls *Dasyurus hallucatus* translocated to predator-free islands lose predator aversion within 13 generations. Image: Henry Cook. (C) The wing shape of orange-bellied parrots *Neophema chrysogaster* bred in captivity (dotted lines) differs significantly from that of wild conspecifics (solid line). Captive-bred parrots have a more convex trailing edge of the wing, which is less suited to long-distance migratory flights. Illustration: Peter Marsack, image: Dejan Stojanovic.

resourcing capacity. Consequently, captivity may create an artificial social environment because individuals have little autonomy over whom they associate with (Koene & Ipema, 2014; Rose & Croft, 2015). Social relationships, roles and cohesion acquired in captivity are important

considerations in reintroductions (Goldenberg *et al.*, 2019). Quantifying how social aspects of the captive phenotype affect reintroduction success is complex (Rose & Croft, 2015) because by definition the social components of an individual's phenotype are dependent upon the nature of its social network. Factors like pre-existing relationships, genetic relatedness and the potential impact of both negative and positive social relationships can affect the behaviour and fitness of both captive and wild animals (Letty, Marchandeau & Aubineau, 2007).

Reintroduced hihi *Notiomystis cincta* that gained more associates post-release tended to show higher survival, suggesting that social individuals are more likely to found reintroduced populations (Franks *et al.*, 2020). Post-release dispersal distance of captive river otters *Lontra canadensis* was predicted by prior history of positive social interactions in captivity (Hansen *et al.*, 2009). In reintroduced western lowland gorillas *Gorilla g. gorilla*, group cohesion declined markedly after the death of a single, highly social wild-born individual (Le Flohic *et al.*, 2015). Demographic composition of captive groups can also determine post-release group cohesion. Social group maintenance in released Asian elephants *Elephas maximus* hinged on the presence of juveniles (Thitaram *et al.*, 2015). After release, house mice *Mus musculus* engaged in assortative mating where captive-reared and wild-provenance individuals did not interbreed (Slade *et al.*, 2014). Increasingly sophisticated ways to track animals and analyse their social structure (Papageorgiou & Farine, 2021) offer exciting opportunities to assess better how the social functionality of captive-bred animals differs from that of wild conspecifics, and the role that social factors could play in determining the success of reintroduction efforts.

(d) Cognition

Cognitive ability is a central component of survival in the wild because it impacts spatial awareness, foraging ability and antipredator behaviour (Shettleworth, 2001). Captive environments are often less complex than wild environments, jeopardising cognitive development (Reading, Miller & Shepherdson, 2013). For example, captive Mexican jays *Aphelocoma wollweberi* exhibit reduced problem-solving performance relative to wild conspecifics (McCune *et al.*, 2019). Captive Atlantic salmon that were denied 8 weeks of environmental enrichment showed less neural plasticity and inferior spatial learning ability than enriched conspecifics (Salvanes *et al.*, 2013). Black-footed ferrets *Mustela nigripes* exhibit both learned and innate components of their predatory behaviour, and captive animals that practise hunting in large enclosures built on top of colonies of their preferred prey are most successful after release (Dobson & Lyles, 2000). An important element of cognition critical to reintroduction success is the ability to recognise and respond appropriately to predators. Northern quolls *Dasyurus hallucatus* translocated to predator-free islands lost aversion to predators after only 13 generations (Fig. 1B; Jolly, Webb & Phillips, 2018), and

such effects have been shown in multiple captive-bred species (McCleery *et al.*, 2013; McPhee, 2004; Watkins *et al.*, 2018). Inadequate anti-predator behaviour was identified as the main cause of failure for parrot reintroductions globally (White *et al.*, 2012).

(2) Morphological

The morphology of animals is the outcome of developmental plasticity (Shettleworth, 2001), natural selection and artificial selection (Brandenburger *et al.*, 2019). There is abundant evidence of morphological change in captivity relative to wild conspecifics with respect to body and organ size, shape and skeletomuscular structure.

(a) Body and limb form

Captive animals may increase (Connolly & Cree, 2008; Turner *et al.*, 2016) or decrease in size (Faleiro & Narciso, 2013; Hard *et al.*, 2000) relative to wild conspecifics. Captive Atlantic salmon (Blanchet *et al.*, 2008) and rainbow trout *Oncorhynchus mykiss* (Pulcini *et al.*, 2013) develop deeper body profiles than wild fish, and changes to fin length can reduce swimming performance. Shortening of total limb length of the legs and wings of captive birds has been observed in zebra finches *Taeniopygia guttata* (Carr & Zann, 1986) and European goldfinches *Carduelis carduelis* (Domínguez, Vidal & Tapia, 2010). Flight feathers of captive-bred orange-bellied parrots *Neophema chrysogaster* differ subtly in length to those of wild, migratory conspecifics, resulting in wings with a more rounded tip and convex trailing edge (Fig. 1C; Stojanovic *et al.*, 2021*a*). These small changes may make wings less suited for migratory flights but are easy to overlook as there is no overall difference in body size between captive and wild individuals (Stojanovic *et al.*, 2019). Similar changes to wing shape of captive butterflies make them less suited to long-distance migration, reducing post-release survival (Davis *et al.*, 2020).

(b) Skeletomuscular structure and organs

Altered cranial morphology in captivity is common across taxa, with reports from captive reptiles (Connolly & Cree, 2008; Drumheller, Wilberg & Sadleir, 2016), birds (Carr & Zann, 1986) and mammals (Geiser & Ferguson, 2001; Hartstone-Rose *et al.*, 2014). These differences can include changes to the mandibles (Zuccarelli, 2004) and teeth (Crossley & del Mar Miguélez, 2001; Taylor *et al.*, 2014). Wild Mexican wolves *Canis lupus baileyi* have larger and differently shaped skulls to captive conspecifics, with reintroduced individuals exhibiting intermediate features (Siciliano-Martina *et al.*, 2021). Some of these changes arise due to consumption of soft and processed diets in captivity. Captive lions *Panthera leo* fed soft foods exhibit smaller mandibular and maxillary regions of the skull and weaker bite force than wild conspecifics (Zuccarelli, 2004). Diets in captivity also change

gastrointestinal organ morphology, including the rumen (Mason *et al.*, 2019), length of the intestines and other digestive organs (Moore & Battley, 2006), kidney and spleen mass (Courtney Jones, Munn & Byrne, 2018). There is also evidence that the brains of fish (Kihslinger, Lema & Nevitt, 2006; Marchetti & Nevitt, 2003; Mayer *et al.*, 2011), birds (Guay & Iwaniuk, 2008; Smulders *et al.*, 2000) and mammals (Kruska, 1996) decrease in size in captivity relative to wild conspecifics, but how these changes affect cognition and behaviour is unclear. The mechanisms underlying these changes warrant further study – although gastrointestinal and oral changes are often linked to the types of diets fed to captive animals, why other organ systems change remains poorly understood. Furthermore, the extent to which these changes are detrimental after release may vary among species and phenotypic traits, and evidence of the impacts of these changes on post-release fitness is lacking.

(3) Health

We define animal health as 'a state of complete physical, mental and social well-being and not merely the absence of disease or infirmity' (WHO, 2006, p. 1). Captivity has been likened to both a prison and a haven, depending on the behavioural and ecological traits of individual species and the associated captivity environment (Clubb & Mason, 2003). These differences can affect the health of animals as well as underlying aspects of their physiology.

(a) Stress

Several studies report elevated stress in captive birds (Dickens, Earle & Romero, 2009; Love, Lovern & DuRant, 2017) and mammals (Franz-Odendaal, 2004; Marino *et al.*, 2020; Rangel-Negrín *et al.*, 2009; Terio, Marker & Munson, 2004). Orcas become stressed from confinement and sensory deprivation in captivity, which results in chronic morbidity, shorter lifespan and high reproductive failure (Marino *et al.*, 2020). Social stressors can negatively affect Indo-Pacific bottlenose dolphin *Tursiops aduncus* health (Waples & Gales, 2002) and African grey parrot *Psittacus erithacus erithacus* telomere length, which may reduce their lifespan (Aydinonat *et al.*, 2014). These stressors can manifest in a wide range of abnormal behaviours of captive animals (Mellor, Brilot & Collins, 2018). Surprisingly, there are few examples of how stress in captivity or during release affects reintroduction outcomes (but see Teixeira *et al.*, 2007).

(b) Disease and parasites

Disease is a major stressor in captive environments, where pathogens can be highly prevalent. The types of diseases/parasites present in captivity often differ from wild populations. Captivity is associated with higher disease prevalence in reptiles (Jacobson, 1993; Scheelings, Lightfoot & Holz, 2011), birds (Jones & Shellam, 1999; Raidal &

Peters, 2017), and mammals (Kołodziej-Sobocińska *et al.*, 2018; Munson *et al.*, 2005). Although too much disease is harmful, there are also negative impacts of its absence. Diseases may become overly rare in captive populations that are too small to maintain density-dependent endemic infections. This 'fade-out' of endemic diseases can diminish herd immunity (Raidal & Peters, 2017). For example, disease fade-out heightened susceptibility to novel strains of psittacine beak and feather disease in immune-deficient captive orange-bellied parrots (Das *et al.*, 2020; Raidal & Peters, 2017). Similar problems can occur if parasites are eliminated in captivity *via* use of anti-parasitic drugs, compromising host immuno-competence and increasing susceptibility to infection post-release (Northover *et al.*, 2018). Reintroduced, parasite-free wolves *Canis lupus* experienced parasite spill-over from sympatric reservoir hosts, which limited population growth (Almberg *et al.*, 2012).

(c) Gastrointestinal system

The quality of food in captivity has important implications for gastrointestinal and overall health. Oral health of captive animals appears to be especially vulnerable to changes in diet. Predominantly soft diets fed to captive carnivores can result in tartar build up on teeth and periodontal disease due to the altered mechanical properties of food arising from the lack of bone and connective tissue (Kapoor *et al.*, 2016). Highly abrasive diets result in premature tooth wear of captive black rhinoceros *Diceros bicornis* (Taylor *et al.*, 2014), whereas soft diets result in less wear of captive Tasmanian devil *Sarcophilus harrisii* teeth (Pollock *et al.*, 2021) and tooth elongation and dental disease in captive chinchillas *Chinchilla lanigera* (Crossley & del Mar Miguélez, 2001).

Gut microbiomes have important impacts on the health and behaviour of animals (Mueller & Sachs, 2015). Gut microbiomes of captive reptiles (Kohl, Skopec & Dearing, 2014), birds (Xenoulis *et al.*, 2010), mammalian herbivores (Frankel *et al.*, 2019; Tang *et al.*, 2020) and carnivores (Cheng *et al.*, 2015; Nelson *et al.*, 2013) can differ significantly from wild conspecifics. This trait may be plastic in response to dietary shifts (Cheng *et al.*, 2015), but animals with more natural diets before release are better prepared for life in the wild (Yang *et al.*, 2020). Captive-bred animals that are unfamiliar with novel wild food items ca shift from atypical to typical foods over time (Põdra *et al.*, 2013) and the temporal composition of their microbiomes relative to wild-born conspecifics changes in a similar way (Chong *et al.*, 2019).

(d) Physical ability

Captive animals may have less physically demanding lifestyles than wild conspecifics. Compared to wild individuals, captive-bred monarch butterflies were 56% weaker in grip strength, which is an important trait for surviving migration (Fig. 1A; Davis *et al.*, 2020). Captive eastern hellbenders *Cryptobranchus a. alleganiensis* reared in still water were weaker swimmers than those reared with flow (Kenison &

Williams, 2018) and captive mouse lemurs *Microcebus murinus* experienced earlier decline in grip strength than wild conspecifics (Hämäläinen *et al.*, 2014). Captive-bred golden lion tamarins *Leontopithecus rosalia* had worse locomotor and foraging skills than their wild-born offspring (Stoinski & Beck, 2004).

III. LINKS BETWEEN PHENOTYPIC TRAITS

A small but growing number of studies are demonstrating associations between behavioural, morphological and health-related aspects of the captive phenotype. For example, increased levels of stress hormones resulted in reduced organ mass and reduced immune responses in captive house sparrows *Passer domesticus* (Love *et al.*, 2017). Captivity disrupted the endocrine and immune responses of sparrows and also intraspecific interactions. Body size also differed between wild and captive-bred house mice, and this morphological difference may have contributed to pronounced assortative mating post-release (Slade *et al.*, 2014). Multiple behavioural, morphological and physiological traits in two weaver species were found to be exposed to selective pressure before release to the wild (Baños-Villalba *et al.*, 2021). In wild river otters subjected to temporary captivity, the position of individual males within social networks was related to testosterone levels, and higher testosterone was correlated with a reduction of positive social interactions and withdrawal from the social network (Hansen *et al.*, 2009). Such studies hint at complex interactions between different elements of animal phenotypes, which could substantially affect reintroduction success (Table 1).

IV. ADAPTIVE MANAGEMENT OF THE PHENOTYPIC COSTS OF CAPTIVITY

Adaptive management is widely considered to be best practice for managing biological systems where uncertainty is inherent (Westgate, Likens & Lindenmayer, 2013). Adaptive management is 'learning by doing' (Walters & Holling, 1990), balancing the need for immediate action with a plan for learning and refinement (Van Wilgen & Biggs, 2011; Westgate *et al.*, 2013). There are surprisingly few examples where adaptive management addresses practical conservation problems (Westgate *et al.*, 2013), because adaptive management relies on robust monitoring programs that are expensive to deliver (Nichols & Williams, 2006; Likens & Lindenmayer, 2018).

Practitioners could use adaptive management to detect deleterious phenotypic changes in captive animals by developing monitoring protocols for each component of a recovery project, including connections between components. Monitoring requires significant resourcing to develop and implement approaches that yield sufficient data (Stojanovic

Table 1. Aspects of phenotypic change in captive animals, links between phenotypic traits, and adaptive management mechanisms for minimising phenotypic divergence between captive and wild phenotypes.

Category of phenotypic change	Individual traits	Examples	Potential links between traits	Monitoring indicators relative to wild conspecifics	Related aspects of animal husbandry	Related aspects of release protocols
Behaviour	1. Vocalisation	Regent honeyeater (Crates *et al.*, 2021); Hawaiian crow (Tanimoto *et al.*, 2017)	2, 3	Vocal complexity and repertoire size; context-specific vocalisations, e.g. alarm calls	Presence of tutors, presence of stimuli; opportunities to learn and refine vocalisations	Selection of suitable animals for release that produce / recognise appropriate vocalisations; releases when/where wild tutors present; age of release cohort
	2. Animal movement	Monarch butterfly (Tenger-Trolander *et al.*, 2019); Appenine chamois (Bocci *et al.*, 2014)	1, 3, 5, 8, 9	Timing, direction, duration, stop-over and settlement locations	Ability to experience migration cues, enclosure size, ability to exercise	Social integration with experienced conspecifics; selection of suitable individuals (e.g. animals exhibiting migratory restlessness); timing and location of release.
	3. Sociality	Hihi (Franks *et al.*, 2020); house mouse (Slade *et al.*, 2014)	1, 2, 4, 7, 8	Number and strength of social connections among individuals; size, structure and cohesion of social groups; indices of boldness and neophobia	Opportunity to engage in social interactions; some autonomy over choice of social associations	Consideration of social structure in planning releases; soft releases; post-release provisioning, e.g. supplementary feeding
	4. Cognition	Mexican jay (McCune *et al.*, 2019); northern quoll (Jolly *et al.*, 2018)	1, 2, 3, 7, 9	Behavioural flexibility in response to novelty; appropriate response to predation risk, food recognition, handling and processing; problem-solving capacity	Enrichment, stimulation, social learning opportunities, exposure to novelty; opportunity to learn foraging and antipredator behaviours; exposure to natural and novel foods	Age of release cohort; post-release reinforcement of antipredator behaviour; complexity of environment at release location
Morphology	5. Body and limb form	Atlantic salmon (Blanchet *et al.*, 2008); orange-bellied parrot (Stojanovic *et al.*, 2021a)	2, 5, 8, 9, 10	Body size and shape; limb functionality; growth rate and asymptote; contrast development and growth of captive and wild populations	Diet and environment; opportunities for complex movement, endurance and agility	Selection of suitable individuals for release based on similarity to wild phenotype; pre-release conditioning/exercise; soft releases
	6. Skeleto-muscular	Mexican wolf (Siciliano-Martina *et al.*, 2021); red deer (Mason *et al.*, 2019)	2, 3, 5, 10	Size, shape and strength of bones and muscles; movement ability	Enclosures facilitating movement including high-intensity exercise, complex motor skills; diet modifications	Selection of suitable individuals; pre-release exercise training; soft releases

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Table 1. *(Cont.)*

Category of phenotypic change	Individual traits	Examples	Potential links between traits	Monitoring indicators relative to wild conspecifics	Related aspects of animal husbandry	Related aspects of release protocols
Health	7. Stress	Orca (Marino *et al.*, 2020); African grey parrot (Aydinonat *et al.*, 2014)	1, 2, 3, 4, 8, 9, 10	Physiological and behavioural responses to stress; blood hormone levels; sociality	Handling frequency; social environment; diet; enclosure conditions; perceived predation risk	Soft release and pre-release conditioning to familiarity with local foods, social groups, predator assemblages
	8. Disease and parasites	Wolf (Almberg *et al.*, 2012); Tasmanian devil (Cheng *et al.*, 2015)	1, 2, 3, 4, 5, 7, 9, 10	Type, prevalence and severity of pathogens; gut and skin microbiome	Controlled exposure to endemic pathogens; prevention of novel pathogen spill-over	Pre-release evaluation of immunocompetence, vaccination status, and parasite load both for released animals and wild conspecifics
	9. Gastrointestinal system	Black rhino (Taylor *et al.*, 2014); woodrat (Kohl *et al.*, 2014)	2, 3, 4, 5, 6, 7, 8, 10	Tooth wear rate; gut microbiome diversity and composition; food recognition, handling and processing ability	Minimisation of processed foods; exposure to natural foods from intended release area	Dietary training with natural food to improve food recognition, hunting, processing and to shift microbiome
	10. Physical ability	Eastern hellbender (Kenison & Williams, 2018); American alligator (Erickson *et al.*, 2003)	1, 2, 3, 5, 6, 8, 9	Size, shape and strength of musculoskeletal system and limbs; ability to perform actions necessary for life in the wild	Enclosures that facilitate movement including high-intensity exercise, complex motor skills	Enclosures that enable sufficient physical activity; targeted pre-release exercise training; opportunities to practice high-risk activities like hunting, climbing, jumping and flight

et al., 2021*b*), and may be challenging to sustain long term (Lindenmayer *et al.*, 2012). Experimental approaches to recovery efforts should ideally be applied to maximise confidence in analysis of outcomes (Seddon, Armstrong & Maloney, 2007).

Individual project actions such as releases to the wild should be implemented in ways designed to answer clear questions, within explicitly defined limitations. Figure 2 outlines the general form of this process. For example, practitioners might identify a component of a captive phenotype that appears harmful to fitness in the wild – this could initially be detected by observing that captive-bred animals are under-performing after release. Once identified, practitioners might investigate earlier steps in the action sequence to identify when differences emerge, and which aspects of captivity drive the changes. Experiments altering aspects of animal husbandry or release strategies could evaluate whether phenotypic divergence can be corrected, and iterative experimental releases could aim to identify possible corrective actions (red pathway, Fig. 2).

V. REDUCING THE PHENOTYPIC COSTS OF CAPTIVITY

With suitable evidence, reintroduction success can be improved through adaptive management of husbandry and release protocols to close the gap between captive and wild phenotypes (Fig. 2) (Sutherland *et al.*, 2020). To achieve this, it is necessary to identify deleterious captive phenotypes and their causes, evaluate their effect on post-release fitness and identify management approaches that return traits to the wild phenotype (Table 1).

(1) Environment

Whereas some species are intolerant of confinement and show adverse effects of captivity, others can thrive. Species with very large home ranges do worse than those that naturally live in smaller areas (Clubb & Mason, 2003). Increasing the size of Arctic fox *Vulpes lagopus* enclosures increased captive breeding success, probably by reducing stress levels in wild-caught founders (Landa *et al.*, 2017). Reduced densities of smolts during rearing increases post-release migration success of Atlantic salmon (Larsen *et al.*, 2016). For birds, extra flight space in larger aviaries can reduce behaviours associated with frustration and stress (Phillips *et al.*, 2018). Maximising the size and complexity of enclosures may be an important aspect of reducing the negative effects of captivity and may pre-empt other management needs. For example, fitness training before release of birds to the wild may be hindered if the area available for flight exercise is too small (Holz, Naisbitt & Mansell, 2006). Animals that naturally have large home ranges, or undertake long-distance movements, should be monitored for signs that confinement may be affecting one or more phenotypic traits.

Environmental enrichment has long been recognised as fundamental for welfare of captive animals (Newberry, 1995). However, providing opportunities for the expression of natural behaviours such as foraging on natural foods and predator aversion can also increase the likelihood of reintroduction success (White *et al.*, 2012). Wherever possible, the natural habitats of captive animals should be the basis for enriching captive environments. More complex captive
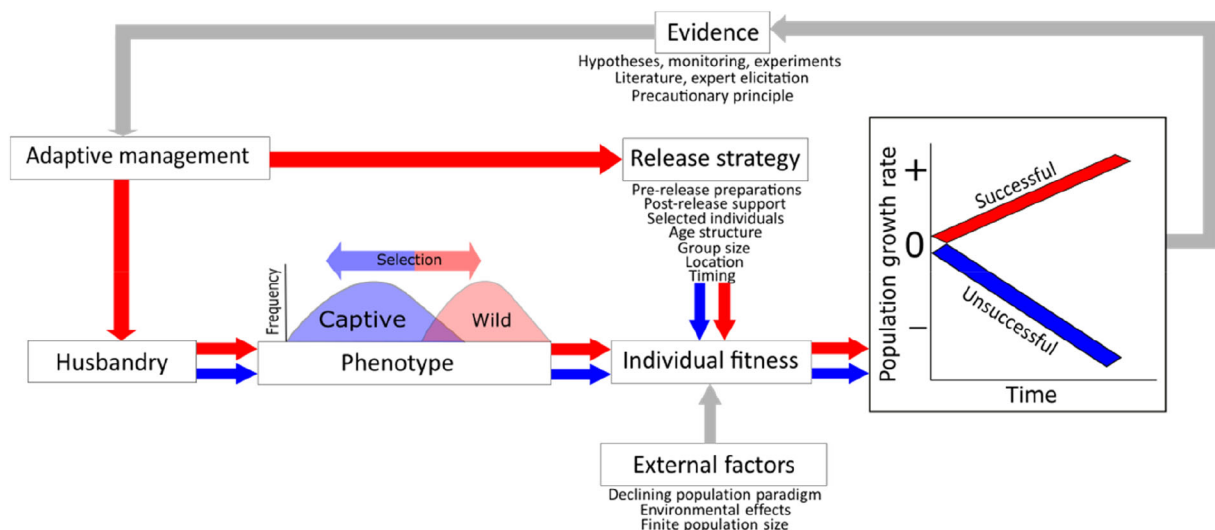

Fig. 2. Conceptual pathway for reducing the impact of captive phenotypes on the success of animal reintroductions. Captive husbandry can affect phenotypes of animals intended for release to the wild negatively (blue pathway, away from wild phenotype) or positively (red pathway, towards wild phenotype). Captive phenotype, release strategy and external factors can all affect post-release fitness, which in turn affects the wild population growth rate. Evidence from earlier steps should inform adaptive management of husbandry and release strategy to avoid captive phenotypes, promoting positive population growth rates.

environments that allow animals to develop life skills for survival after release yield better results. Raising eastern hellbenders in running water improves swim performance relative to those raised in still water (Kenison & Williams, 2018). Likewise, gobies raised in more complex environments developed better spatial learning abilities (Carbia & Brown, 2019). Environmental complexity may be especially important for species with high cognitive abilities because simplified captive environments may impair the development of problem solving (McCune *et al.*, 2019). Ensuring that enclosure design and environmental enrichment activities reflect natural behaviours and habitats can better prepare individuals for release, and can reduce the required duration of post-release support (Reading *et al.*, 2013).

As well as the physical environment, behavioural traits must be factored into husbandry practices. Wild animal behaviours such as vocalisations, foraging strategies and migratory routes can drift or disappear when 'tutors' are not available for social observation in captivity (Zürcher *et al.*, 2019). Given that species acquire socially mediated behaviours in different contexts, bespoke solutions should be developed. For example, birds that learn songs from conspecifics during sensitive 'learning phases' of development might be housed near a tutor or speakers broadcasting wild-type songs (Mennill *et al.*, 2018). Not all behaviours can be facilitated in captivity, but there is evidence that some may be regained after release if captive animals encounter suitable wild tutors and environmental stimuli (Jesmer *et al.*, 2018). Whether or not naïve animals relearn behaviours may vary widely among species, and sometimes new behaviours can arise in animals descended from captivity (Mueller *et al.*, 2013; Teitelbaum, Converse & Mueller, 2019). However, learning/establishing behaviours after release depends on whether individuals survive long enough post-release to have learning opportunities. Ongoing intervention and management after release may allow naïve animals to integrate socially with wild conspecifics and/or learn appropriate wild behaviours, instead of quickly succumbing to mortality.

(2) Training

Training techniques for animals have developed rapidly in recent decades, and these approaches are important in several conservation programs (Indigo *et al.*, 2018; Loepelt, Shaw & Burns, 2016; Rowell, Magrath & Magrath, 2020; Teitelbaum *et al.*, 2019). Training can improve survival rates of captive animals released to the wild, and may help naïve released animals survive long enough to learn survival skills (Fajardo, Babiloni & Miranda, 2000). For example, training animals to return repeatedly to feeders or nesting resources may improve reintroduction success (Panfylova *et al.*, 2016). However, it is important to evaluate whether training is achieving its intended purpose (Armstrong & Perrott, 2000) and if intensive interventions can eventually be simplified or discontinued for long-running projects (Ferrière *et al.*, 2021). More complex training can be provided for some

specialised aspects of life history. Light aircraft were used to train naïve whooping cranes *Grus americana* about migration routes and safe wintering grounds (Mueller *et al.*, 2013). Predator aversion can be the difference between survival and rapid mortality after release, so anti-predator training is often essential (Shier & Owings, 2007). Failure to pre-empt predation is the main cause of failure in reintroductions of parrots, because released animals either did not recognise or responded inappropriately to predators (White Jr *et al.*, 2012). Anti-predator training has been applied successfully to a wide range of taxa (Griffin, Blumstein & Evans, 2000), but better survival is not necessarily guaranteed. Greater bilbies *Mactrotis lagotis* that received anti-predator training survived at the same rate as a control group when released to the wild (Moseby, Cameron & Crisp, 2012), and collared peccaries *Pecari tajacu* forgot unreinforced training within 30 days (de Faria *et al.*, 2020). Early-life predator exposure has also been demonstrated to improve cognitive plasticity once adulthood is reached (Vila Pouca *et al.*, 2021), and this unexpected benefit may be advantageous for captive-breeding programs seeking to maximise post-release fitness.

(3) Veterinary support

Advances in veterinary practice make it feasible to overcome or manage health problems in captive and wild populations. However, overly precautionary veterinary treatment may diminish immunocompetence of captive animals and disadvantage them post-release (Smith, Acevedo-Whitehouse & Pedersen, 2009). Loss of circulating endemic pathogens in captive populations may make them vulnerable to disease spill-over. Conserving parasites in captive populations boosts the immunity of Tasmanian devils (Wait *et al.*, 2017), and worming pre-release European bison *Bison bonasus* resulted in worse parasitism by blood-feeding nematodes than their wild conspecifics (Kołodziej-Sobocińska *et al.*, 2018). Emerging evidence supports a need for controlled exposure to pathogens in captive environments to build immune competence before release (Faria, van Oosterhout & Cable, 2010). Furthermore, loss of endemic pathogens may facilitate infection with less-coevolved pathogen strains, potentially causing significant disease (Das *et al.*, 2020; Peters *et al.*, 2014). It is important to recognise that endemic pathogens and parasites also have their own intrinsic conservation value (Gompper & Williams, 1998).

(4) Release protocols

Developing suitable release protocols may involve anything from preparation of animals in a captive environment through enrichment and training, to the provision of ongoing support post-release. The range of tools and techniques applicable may vary dramatically between species and ecosystems, and it is likely that iterative and adaptive releases may be necessary to identify the set of procedures that are most effective (Fig. 2). There exists a range of modelling approaches that might be useful for balancing competing

demands of different release strategies with overall recovery goals for wildlife populations (Heinsohn *et al.*, 2022; Oppel *et al.*, 2021) and where possible these techniques should be applied to identify the optimal approach to reintroductions.

There has been extensive investigation into the benefits of soft releases (where animals are allowed to acclimatise *in situ* before release and are supported after release) *versus* hard releases (where no post-release support is provided) (Resende *et al.*, 2021). Soft releases tend to result in less dispersal and better reintroduction outcomes (Knox *et al.*, 2017; Wanless *et al.*, 2002). For example, skin microbiomes could be restored in a soft release of variable harlequin frogs *Atelopus varius*, which may increase disease resistance (Kueneman *et al.*, 2022). Despite some exceptions (Clarke, Boulton & Clarke, 2002; Richardson *et al.*, 2013), on balance, soft releases incorporating anti-predator training and environmental enrichment are best practice for releasing captive-bred animals into the wild, because they tend to reduce movement, increase social cohesion and offer more opportunities for post-release care such as supplementary feeding (Resende *et al.*, 2021; Tetzlaff, Sperry & DeGregorio, 2019). This is important because release locations are usually selected because they are safe, contain important resources and are the environments most likely to support released animals in the longer term.

Another important factor when planning releases is to select suitable individuals. Some age cohorts can be preferred for release – either reintroduced adults (Sarrazin & Legendre, 2000) or juveniles (Troy & Lawrence, 2021) may perform better among different species. Analytical approaches are available to contrast the potential outcomes of releasing different age classes (Robert *et al.*, 2004) and such approaches should be implemented alongside experimental releases that can inform underlying model assumptions. Other reasons that individuals may be unsuitable for release include biosecurity risks, inappropriate behaviours for life in the wild, or because some other phenotypic trait makes them less likely to thrive after release (Tripovich *et al.*, 2021). There is unlikely to be a 'one size fits all' rule for which individuals are most likely to achieve reintroduction aims. Furthermore, external factors such as release date and environmental conditions can affect outcomes (Jackson, Schuster & Arcese, 2016). Conservation practitioners should be prepared to attempt multiple, small-scale 'experimental' releases to test *a-priori* hypotheses with rigorous post-release monitoring and refine bespoke strategies though adaptive management. Such attempts can reveal useful insights about how to improve reintroduction success (Tripovich *et al.*, 2021; Troy & Lawrence, 2021).

VI. FUTURE DIRECTIONS

Conservation resources are already limited in most countries, which means that the global 'ark' of captive-breeding facilities is unlikely to be sufficient given the predicted scale of biodiversity loss in coming decades (Ceballos *et al.*, 2017).

Wherever possible, captive breeding should aim to re-establish self-sustaining wild populations that no longer need intervention. If altered phenotypes unfit for the wild are unavoidable in captivity, then it may be worth reconsidering conservation aims, especially if the initial causes of wild population decline, such as habitat loss, have not been addressed (Caughley, 1994). For example, if captivity leads to loss of migratory capacity (Tenger-Trolander *et al.*, 2019), or if there is no achievable way to protect a mobile species from threats during migration (Stojanovic *et al.*, 2020), a sedentary version of a previously migratory wild population could represent the best possible outcome. As wild places become more fragmented and scarce, conservation scientists and the general public alike may increasingly face the need to adjust expectations so that even 'imperfect' phenotypes can persist in the wild. This is ethically complicated; if wide-ranging species can only survive in small areas hemmed in by inhospitable habitats, then is intentionally altering the phenotype of animals, e.g. by limiting their scale of movement to avoid negative welfare outcomes from unmitigated threats, actually the most ethical solution? Exploring whether intentional alteration of evolved phenotypes is ethical is likely to emerge as a major issue in conservation biology in coming decades. Not every species can be saved, and not all species that are saved can live in the way they evolved prior to the Anthropocene. However, this review points to untapped potential for improving the phenotypes of captive-bred species so that their fitness upon release into the wild is maximised.

(1) Outstanding questions

Our review identifies several knowledge gaps that can be distilled into the following questions:

(1) *To what extent, and how rapidly can captive animals re-acquire wild phenotypes post-release?* Understanding the extent and nature of the capacity of captive-bred animals to re-acquire components of wild phenotypes will provide important insights into the types of phenotypic changes that can be corrected through adaptive management. Multi-generational captive populations are becoming more common as insurance against extinction, so understanding the risk of irreversible changes to phenotypes is important for evaluating the suitability of these animals for future release.

(2) *What is the relationship between captive phenotypes, fitness outcomes and demographic responses of wild populations post-release?* We expect that these relationships may vary, but that the prevailing relationship between divergent captive phenotypes and post-release outcomes will be negative. Identifying these relationships will require detailed monitoring of phenotypes and fitness both in captivity and post-release.

(3) *How does the ratio of captive-bred to wild conspecifics affect the maintenance or re-establishment of wild animal behaviours?* Since many behaviours are acquired through cultural conformity, we predict that the lower the ratio of captive-bred to wild conspecifics, the greater the capacity for captive-bred

individuals to acquire wild behavioural phenotypes. This will in turn affect the timing and location of reintroductions, as well as cohort size.

(4) *How important is age at release in determining the phenotypic costs of captivity?* Many phenotypic traits such as vocalisations and predator aversion are acquired in early life. We therefore predict that releasing younger animals will reduce the phenotypic costs of captivity because they have (*i*) greater capacity to acquire behaviours important for survival in the wild, and (*ii*) fewer opportunities to acquire negative phenotypic traits associated with prolonged periods in captivity.

(5) *How pervasive are links between phenotypic traits and how do they interact with each other?* Changes to any one phenotypic component are likely to impact on other phenotypic components both in captivity and post-release (Table 1). The nature and extent of these links remain poorly resolved, so experimental approaches will be key to understanding better the links between components of the captive phenotype and how they can be addressed through husbandry and release protocols.

Answering these questions will require a closer look at the phenotypes of captive animals, and better integration of the outcomes of captive breeding with the fate of wild populations (Fig. 2). Importantly, we suggest that much theoretical knowledge to aid the refinement of reintroduction programmes could be gained from studies on species still common in the wild, thus overcoming sampling constraints inherent in experimental studies of endangered populations. Addressing these knowledge gaps will provide important insights into the ways that reintroduction efforts can be improved to address the conservation and ethical challenges that loom on the horizon for biodiversity in a changing world.

VII. CONCLUSIONS

(1) There is evidence across a range of taxa that animal phenotypes can change as a result of captivity.

(2) These effects vary from obvious deviations from (often poorly defined) wild phenotypes, to subtle changes that may go undetected.

(3) Captive-breeding programs should attempt to identify the multiple ways that captivity can affect animal phenotypes, because the phenotypic quality of animals bred for release is as important to conservation success as their quantity.

(4) Failure to detect, prevent or correct phenotypic changes arising from captive life can result in mortality of individuals and failure of expensive conservation programs.

(5) Adaptive management approaches that explicitly consider the links between different elements of captive-breeding programs and fitness in the wild post-release are essential to mitigating the phenotypic costs of captivity.

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