Altered wing phenotypes of captive-bred migratory birds incur post-release fitness costs

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Introduction

Captive animal phenotypes can diverge from the ideal 'wild type', and these changes can affect behavior, morphology and physiology (Crates *et al.* 2022). However, the specific nature and combination of 'captive phenotypes' can vary widely between species (Crates *et al.* 2022). Whether changes are important depends on the intended use of captive-bred animals. For display animals, phenotypic changes may be inconsequential. Conversely, conservation breeding programs – a globally popular tool to combat species extinctions (Conde *et al.*2011) – should ideally produce animals optimized for life in the wild after release, but this more easily said than done (Taylor *et al.*2017). If altered captive phenotypes incur a fitness cost in the wild, conservation breeding may be less effective than hoped (Crates *et al.* 2022). Thus, it is important that conservation breeding programs quantify optimal wild phenotypes, and be vigilant of changes arising from life in captivity that might jeopardize survival after release (Shier 2016; Berger-Tal *et al.* 2020).

Phenotypic changes to traits involved in strenuous or high-risk phases of life history may be disproportionately important for fitness post release from captivity. For example, migration is a high-risk behavior that strongly selects for the most capable individuals (Dingle 2014; Rotics *et al.* 2016). Captive-born animals are often less successful migrants than wild-born conspecifics (Crates *et al.*2022). This is sometimes attributable to behavioral differences. For example, some captive-born birds depart later and travel shorter distances than wild conspecifics (Burnside *et al.* 2017), and captive-bred butterflies fail to orient themselves or even attempt migration (Tenger-Trolander *et al.* 2019). Morphological changes also likely contribute to poor migration outcomes post release, but evidence for their effects on fitness is surprisingly limited. Davis et al. (2020) recently showed that captive-bred monarch butterflies *Danaus plexippus* have differently shaped wings and lower migration success than wild conspecifics. Wing shape strongly predicts flight efficiency (Lockwood *et al.* 1998; Sheard *et al.*2020). Given that migratory birds are commonly bred in captivity for reintroduction (Davis 2010; Burnside *et al.* 2017; Hutchins *et al.* 2018; Stojanovic *et al.* 2020b; Tripovich *et al.* 2021), quantifying the ubiquity of deleterious captive wing shape phenotypes and their post-release fitness consequences is critical information.

I aimed first to compare captive/wild wings of 16 species representing three commonly captive-bred bird families (Phasianidae, Psittacidae, Estrildidae) to evaluate the ubiquity of captive wing shape phenotypes. Then, using a critically endangered migratory bird as a model, I aimed to demonstrate that a captive wing shape phenotype incurs a fitness cost post release.

Methods

Data collection (Aim 1)

For the first aim of my study (to evaluate the ubiquity of changes to the flight apparatus of captive birds) I measured study skins at the Australian National Wildlife Collection, Australian Museum, American Museum of Natural History, Harvard Natural History Museum, Museum of Victoria, South Australian Museum and

the Tasmanian Museum and Art Gallery. I assigned individual provenance (captive/wild) based on specimen metadata. Captive specimens were rarer in museum collections – I aimed for at least five captive and wild specimens per species, so some species were excluded. I selected common species in zoological and private collections because, like multi-generational conservation-focused captive-breeding programs, specimens were likely to be captive-born (not wild-collected). Although I previously showed that wing shape change in orange-bellied parrots was independent of generations of captive breeding (Stojanovic *et al.* 2021), I aimed to minimize this risk by using older captive-bred specimens that were less likely to be multi-generational captive-bred (however, the individual histories of captive-born specimens in this study were unknown). The mean collection date of captive specimens was 1955 vs. 1938 for wild specimens, reflecting the emergence of Australian avicultural trapping and trade last century (Franklin *et al.*2014). Species inclusion was limited by (i) collection bias toward attractive Australian native species which are preferred in captivity (Vall-llosera & Cassey 2017), and (ii) for non-Australian species, absence of wild specimens for comparison.

Using electronic calipers (0.01mm) and rulers (1mm) I measured: wing chord (L_W), the length of the most distal secondary feather (L_S), the length of the longest primary feather (L_P) (per Jenni & Winkler 1989), the distance between the tips of the outermost eight primary flight feathers (P10-P3) to the tip of the longest primary feather (i.e. ΔQ, per Lockwood *et al.*1998). P10 is the most distal flight feather that forms the leading edge of the wing, and P3 is the most proximal flight feather I measured. In passerines p10 is vestigial (Hall 2005) and I did not measure this feather. However, to improve visualization and interpretation of the results, I relabel P9 of passerines as P10 because this is the most distal functional flight feather in non-passerines. Our sample included 16 species from three families (Table S1): Phasianidae, n=1 sp.; Estrildidae, n=6 spp.; Psittaculidae, n=9 spp. I aimed for equal sex ratios (final sex ratio: 127 males, 123 females, 116 unknown) and the total sample comprised 146 captive-born specimens and 220 wild-born specimens.

Background and Data collection (Aim 2)

For the second aim of the study (evaluate the fitness consequences of the captive wing phenotype) I used orange-bellied parrots (Department of Environment Land Water and Planning 2016) as a model because they: (i) are bred in captivity and released in large numbers (Smales *et al.* 2000) which overcomes the common hindrance of small sample sizes, (ii) undertake a migration that results in strong selection and survival of only a fraction of individuals (Stojanovic *et al.* 2020b), (iii) their recovery program is among the largest, longest running and most well-resourced of threatened species' recovery efforts (Department of Environment Land Water and Planning 2016; Pritchard *et al.*2022) making it a 'best case' of captive-breeding for conservation, and (iv) I have previously demonstrated that the wings of captive and wild parrots have different shapes (Stojanovic *et al.* 2021), so identifying fitness consequences of this difference a priority. Captive-bred juveniles are released at the end of the breeding season so that they can integrate with wild fledglings and migrate northward together. This migration is demanding both physically (e.g. a sea crossing) and behaviorally (e.g. sudden transition from supplemental to natural food (Stojanovic *et al.* 2020a)). Most captive-born juveniles do not survive their first year of life (Stojanovic *et al.* 2020b). Their survival is monitored via daily observations of ringed birds at supplementary food tables during the summer breeding season (Stojanovic *et al.* 2018; Stojanovic *et al.* 2020b). The captive population is held across several participating institutions that use comparable husbandry approaches (Pritchard *et al.* In Prep) and a studbook to minimize genetic adaptation to captivity (Morrison *et al.* 2020a). Regular releases have resulted in full admixture of the captive and wild populations (Stojanovic *et al.*2022). I measured 78 juvenile captive-bred parrots released to the wild over three years (2019: 30, 2020: 31, and 2021: 17). Juveniles are selected for release based on metapopulation management considerations (Morrison*et al.* 2020b; Troy & Lawrence 2021), but not for any particular phenotypic trait other than good body mass and general feather condition. To reduce the welfare impact of measuring live birds, I only measured ΔQ for P10-P5 because these are the most likely feathers to vary in their length (Stojanovic *et al.* 2021). I also dropped L_S to further reduce handling time, but I did record L_W, tail length (L_T) and body mass (g). P9 was excluded from analysis as it was the longest feather in the wing of each parrot (and thus there was no variation to model). As an index of individual condition, I divided body mass by L_W to scale for body size. I scored individuals as having survived (1) or died (0) their first year of life based on whether or not they returned from their first

migration (Troy & Lawrence 2021).

Analytical approach

I conducted all analyses in R (R Development Core Team 2021) and scaled and centered all variables. Code, data summaries and full results are supplied in a supplementary R Markdown script.

Aim 1 (evaluate the ubiquity of captive wing shape phenotypes) – I used the lengths of L_W, L_S, L_P, and ΔQ (P10-P3) the response variable in Bayesian logistic regression (family: 'gaussian') implemented in the package *MCMCglmm* (Hadfield 2010). I included a three-way interaction between the measured feather ID, species ID and provenance (captive/wild) as the fixed effect, and the specimen ID as the random effect. I used inverse-Wishart priors for the random effect and residual variance ($V = 1$, $\nu = 0.002$). I ran the model for 100,000 iterations and set burn-in to 1,000 and used 100 for thinning for a total posterior sample of 990. All chains were checked for proper mixing, and I checked for auto correlation using the command 'autocorr' with 0.1 as a target threshold. I used *emmeans* (Lenth 2018) to estimate Z values of pairwise captive-wild contrasts for visualization with *ggplot2* (Wickham 2016).

Aim 2 – To evaluate the relationship between survival of the first migration and individual phenotype, I used the binomial juvenile survival outcome as the response variable in Bayesian logistic regression (family: 'categorical'), implemented in the package *MCMCglmm* (Hadfield 2010). I fitted ΔQ (P10-P5), L_T, and the index of body condition as fixed effects and release year as a random effect. I specified priors for the fixed effects using the 'gelman.prior' command (v=1, nu=0.02) and fixed residual variance at 1. I ran the model for 100,000 iterations and set burn-in to 1,000 and used 100 for thinning for a total posterior sample of 990. All chains were checked for proper mixing, and I checked for auto correlation using the command 'autocorr' with 0.1 as a target threshold.

Results

Evaluate the ubiquity of captive wing shape phenotypes

The interaction between feather ID × species × provenance had significant explanatory power for the length of the feathers I measured (see R Markdown). Significant differences between captive/wild specimens in the length of at least one flight feather occurred in one quarter of sampled species (Figure 1). Relative to wild conspecifics: (i) captive budgerigars *Melopsittacus undulatus* had longer secondary feathers, (ii) captive turquoise parrots *Neophema pulchella* had a longer P10, (iii) captive princess parrots *Polytelis alexandrae*had a longer P10, P9 and P3, and a shorter P8, (iv) captive star finches*Bathilda ruficauda* had shorter secondary feathers. Although non-significant, the length of P10 in captive-born individuals tended toward being either longer (e.g. zebra finches *Taeniopygia guttata* , Gouldian finches *Chloebia gouldiae*) or shorter (e.g. sunset parrot *Neopsephotus bourkii* , red-throated parrotfinch*Erythrura psittacea*). L_W and $L_P$never differed between captive and wild specimens, regardless of whether or not there were differences in the lengths of other feathers in the wing.

Fitness cost of captive phenotypes

Survival of captive-bred juvenile orange-bellied parrots had a significant negative relationship with ΔQ P10, and to a lesser extent L_T (Table 1). Smaller values of ΔQ P10 indicate that feather is longer, and thus more like the wild phenotype (Figure 2). Based on the model, the probability of survival for a juvenile captive-born orange-bellied parrot with a ΔQ P10 of 1mm was 4.84% (highest posterior density intervals: $8.75e^5$ – 0.35), compared with only 1.8% (highest posterior density intervals: $1.34e^5$ – 1.77) for an individual with a ΔQ P10 of 2mm.

Discussion

Phenotypic traits involved in arduous or risky components of life history can exert strong selective pressure. Animals bred in captivity for release to the wild as a conservation intervention should ideally conform to optimal phenotypes for surviving these challenges (Crates*et al.* 2022). In this study, I present the first multi-species evaluation of the prevalence and fitness impact of captive wing phenotypes among birds. I

found the wing shapes of captive birds differed to wild conspecifics in a quarter of species examined. These changes usually involved the most distal primary feathers forming the wing tip or the secondary feather length. Wing tip shape determines flight performance (Lockwood *et al.* 1998; Swaddle & Lockwood 2003), but whether the changes I report result in impaired flight ability remains unclear. However, this possibility is supported by evidence that a shorter P10 in released juvenile captive orange-bellied parrots incurred a fitness cost. Juveniles with wild wing phenotypes were more than twice as likely to survive the first year of life than individuals with only a 1mm shorter P10. This is the first demonstration that altered wing phenotypes are widespread among captive-bred birds and that these changes incur a fitness cost post release.

Orange-bellied parrots are the beneficiary of careful genetic management and professional husbandry techniques in the large-scale, professional captive-breeding for reintroduction program (Pritchard *et al.*2022). Despite this care, subtle changes to wing phenotypes emerged in captivity (Stojanovic *et al.* 2021), despite similarities in other components of phenotype like overall body size (Stojanovic *et al.*2019). Juvenile orange-bellied parrots face a gauntlet of obstacles to survival of their first year of life (Stojanovic *et al.* 2020b; Stojanovic *et al.* 2022) – perhaps the likely increase in drag of a rounder wing tip (Tucker 1995; Minias *et al.* 2015) is enough to further disadvantage captive phenotypes during long flights. At the breeding ground, post-release survival of captive-bred parrots is very high (Smales *et al.* 2000), indicating stronger selection occurs during migration when juveniles are developing their survival skills and physical endurance.

My results raise important new questions both for orange-bellied parrots and other conservation breeding programs more generally. Firstly, why is the length of flight feathers of birds so plastic among so many species? Whether wing shape is under genetic control or shaped by the environment is not clear, and clarifying the importance of these potential forces on feather development may provide insight into how to correct captive wing phenotypes. Second, why are the distal feathers so prone to change? The forces exerted by flight are greatest at the wing tip (Lockwood *et al.*1998) and many species in this study had altered P10 lengths (both significant and indicative effects). Investigating the relationship between feather development and curtailed flight in captive environments may help explain why distal flight feather length is plastic. Third, can individuals with captive wing phenotypes revert to a wild phenotype? If feather growth is at least partly affected by environment, it is conceivable that individuals with captive wing phenotypes could be experimentally manipulated before release to optimize wing shape (e.g. with flight training). Fourth, why do captive wing phenotypes incur a fitness cost, and is this universal? Rounded wing tips produce more drag than pointed ones (Lockwood *et al.* 1998), but the direct consequences of captive wing phenotypes on migration success is unknown, especially because the changes I report here vary in their magnitude among species. Understanding the aerodynamic cost of captive wing phenotypes is important for optimizing survival of captive-bred migratory birds.

Captive phenotypes vary from obvious to subtle deviations from the optimal wild type. I show a mere 1mm reduction in the length of a single feather significantly elevates juvenile mortality. This surprising consequence of a seemingly trivial phenotypic change is an important reminder that captive breeding for conservation is not straightforward. Importantly, the changes to wing shape I report would go unnoticed using indices of wing shape such as the hand wing index (Sheard *et al.*2020) because L_W and L_P (which are important for calculating this index) were unaffected by captivity. This result reaffirms that detailed surveillance is crucial for detecting subtle deviations from the wild phenotype. Ensuring that captive animals are in optimal condition for life in the wild is especially crucial for species that experience strong phenotypic selection from some component of life history (Davis *et al.* 2020; Crates *et al.* 2022). However, surveillance for altered captive phenotypes is negligible despite the risks that these changes pose to the success of release programs (Crates *et al.* 2022). I argue captive breeding programs should (i) clearly identify components of phenotype that could impose strong selection (e.g. migration, traits associated with foraging such as the ability to capture/subdue prey, exaggerated sexual signals), (ii) establish baseline information about variation in wild phenotypes for identified traits, (iii) surveil captive populations for extreme variance in these traits, (iv) where changes are detected, identify the mechanisms driving them, and (v) quantify the impacts of captive phenotypes on release success. Rapid post-release mortality of phenotypically maladapted animals is a waste of conservation resources, may not benefit wild populations and is ethically problematic.

This may be overcome by focusing on the phenotypic quality (not quantity) of animals produced so that the likelihood of post-release survival is increased (Crates *et al.* 2022). Given the wide diversity of taxa held in zoological collections globally (Conde *et al.* 2011), this study is likely only the tip of an iceberg of subtle phenotypic changes are overlooked among captive-bred animals. Implementing the five steps above is a good start for identifying the scale and magnitude of this conservation challenge, which is likely to become increasingly important as the global extinction crisis forces more species into captive breeding programs (IUCN Conservation planning specialist group 2020).

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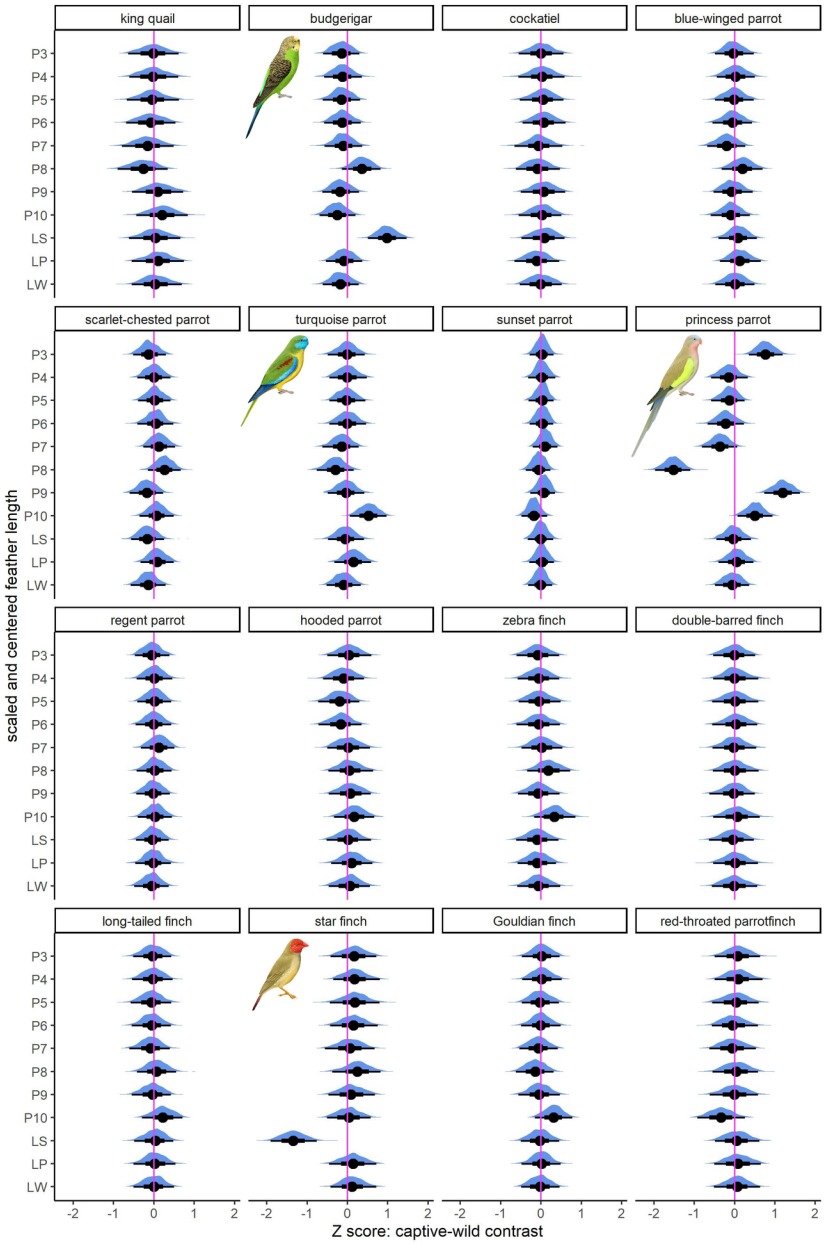

Figure 1

Figure 2

Figure Captions

Figure 1. Z scores with 66% and 95% credible intervals (black bars) computed with Bayesian mixed models showing captive-wild pairwise contrasts of wing feather lengths of birds of 16 species. Primary flight feathers are numbered in decreasing order counting inward from P10 on the leading edge of the wing. LW = unflattened wing chord, LP = length of the longest primary feather, LS = length of the most distal secondary flight feather. High Z scores indicate that feathers of captive-born individuals are longer, low Z scores indicate that feathers of wild-born individuals are longer. Species with significant effects are highlighted with illustrations (artwork by Julian Teh).

Figure 2. Wing phenotypes of captive- vs. wild-born orange-bellied parrots. The captive phenotype

involves a shorter outermost flight feather (1mm^2 grid), and results in halving of juvenile survival of the first year of life relative to the wild phenotype. Artwork by Julian Teh.

Tables

Table 1. Summary of fixed effects from Bayesian linear regression of juvenile survival of orange-bellied parrots reared in captivity. CI = credible interval, * indicates a significant effect at 0.01, ** indicates a significant effect at 0.1.

Fixed effect	**Posterior mean**	**Lower 95% CI**	**Upper 95% CI**	**Effective sample**	**P**
(Intercept)	-1.95	-4.43	0.65	1047.90	0.09
P10	-1.08	-1.97	-0.20	690.30	0.01*
P8	0.25	-0.62	1.26	990.00	0.62
P7	-0.42	-1.45	0.69	836.70	0.40
P6	0.03	-1.46	1.39	990.00	0.95
P5	0.22	-1.32	1.50	839.90	0.77
L_W	0.32	-0.54	1.30	990.00	0.52
L_T	-0.86	-1.81	0.08	734.80	0.07**
Body mass	0.39	-0.62	1.45	787.20	0.45