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

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Abstract
Captive breeding and release to the wild is a globally important conservation tool. However, captivity can result in phenotypic changes that incur post-release fitness costs, especially if they affect strenuous or risky behaviours. Bird wing shape is critical for migration success and suboptimal phenotypes are strongly selected against. In this study, I demonstrate surprising plasticity of bird wing phenotypes in captivity for 4/16 studied species. In a model species, captive-born juveniles with wild wing phenotypes (a 1-mm longer distal primary flight feather) survived post-release at 2.7 times the rate of those with captive phenotypes (i.e. a shorter distal feather). Subtle phenotypic changes and their fitness impacts are more common than widely realised because they are easily overlooked. To improve captive breeding for conservation, practitioners must surveil phenotypic changes and find ways to mitigate them.

KEYWORDS
captive breeding, conservation of migratory species, conservation reintroduction and release, flight efficiency and aerodynamics, phenotypic plasticity, wing shape and feather length

INTRODUCTION

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

that might jeopardise survival after release (Berger-Tal et al., 2020; Shier, 2016).

Phenotypic changes to traits involved in strenuous or risky phases of life history may be disproportionately important for fitness post-release from captivity (Crates et al., 2022). For example, migration strongly selects for the most capable individuals (Dingle, 2014). Captive-born animals are often less successful migrants than wild-born conspecifics (Crates et al., 2022). This is sometimes attributable to behavioural differences. For example, some captive-born birds depart later and travel shorter distances than wild conspecifics (Burnside et al., 2017), and captive-bred butterflies sometimes 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 (Burnside et al., 2017; Davis, 2010; Hutchins et al., 2018; Stojanovic, Potts, Troy, et al., 2020; 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 and Estrildidae) to evaluate the ubiquity of captive wing phenotypes. Then, using a critically endangered migratory bird as a model, I aimed to demonstrate that a captive wing phenotype can incur 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 specimen availability was patchy in museum collections—I aimed for at least five captive and wild specimens per species and excluded those that were under-represented. Species inclusion was limited by (i) collection bias toward attractive Australian native species which are preferred in captivity (Valllosera & Cassey, 2017), (ii) for non-Australian species, absence of wild specimens for comparison, and (iii) sex biased collections of some species (Cooper et al., 2019). Only specimens in perfect feather condition were included (e.g. moulting individuals or those with broken feather tips were excluded). I selected common species in zoological and private collections because, like multigenerational conservation-focused captive breeding programmes, specimens were likely to be captive-born

(not wild-collected). Although I previously showed that wing shape change in orange-bellied parrots, *Neophema chrysogaster*, is independent of generations of captive breeding, I aimed to minimise this risk in other species 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 versus 1938 for wild specimens, reflecting the emergence of Australian avicultural trapping and trade last century (Franklin et al., 2014).

Figure 1 illustrates the measurements taken in this study. Using electronic callipers (0.01 mm) and rulers (1 mm), 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). For the proximal and distal feathers adjacent the L_P, I measured the distance between their tips and the tip of L_P (i.e. ΔQ, per Lockwood et al., 1998). Our sample included 16 species from three families: Phasianidae, $n = 1$ sp.; Psittaculidae, $n = 9$ spp.; Estrildidae, $n = 6$ spp. This wide array of species involves variance in wing shape; for some species, the $L_P = P9$ (i.e. second proximally from P10 on the leading edge of the wing) and for others, $L_P = P8$ (see Table S1). For simplicity, I hereafter refer only to the 'proximal' and 'distal' flight feathers adjacent the L_P (i.e. in some species this corresponds to P8 and P10 respectively, and in others it is P9 and P7). Furthermore, male princess parrots *Polytelis alexandrae* develop secondary sexual ornamentation—an elongated, spatulate tip on P8—which makes this the L_P (Higgins, 1999). In contrast, P9 is the L_P in female princess parrots and other *Polytelis* species (Higgins, 1999). Consequently, I excluded male princess parrots to avoid skewing measurements due to sex. I aimed for equal sex ratios (Table S1) but due to collection biases (Cooper et al., 2019) and inclusion of monomorphic species without sex data, I did not always achieve parity. Consequently, I ignore the effect of sex in this study. For all species (bar princess parrots), there were reasonable enough sex ratios that the results are unlikely be attributable to sex (Table S1). I caution that sundown parrots *Neopsephotus bourkii* have sex differences in flight feather lengths (Stojanovic,
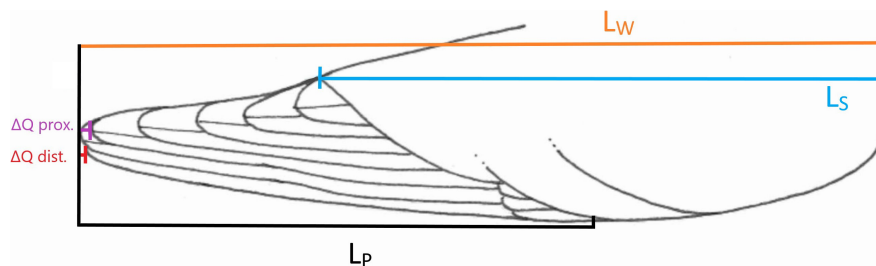
FIGURE 1 Measurements used in this study. In this example of a turquoise parrot wing, the longest primary feather (L_P – black) is P9 – measured from where the feather inserts into the skin, to its tip. Relative to L_P I measured ΔQ for the adjacent distal (red) and proximal (purple) flight feathers. I also measured the wing chord (L_W – orange) and most distal secondary feather length (L_S – blue). Artwork by Peter Marsack.

Neeman, & Heinsohn, 2020) but the sexes were well represented in this study, unlike in princess parrots, L_P is P9 for both males and females (Table S1).

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 as a model because they: (i) are bred in captivity and released in large numbers (Pritchard et al., 2022) which overcomes the common hindrance of small sample sizes; (ii) undertake a migration that results in mortality of 80% of contemporary juveniles (Stojanovic, Potts, Troy, et al., 2020); (iii) their recovery programme is among the largest, most complex, longest running and most well resourced of Australian threatened species' recovery efforts (Pritchard et al., 2022) making it a 'best case' of captive breeding for conservation; (iv) The wings of captive and wild orange-bellied parrots have different shapes (Stojanovic et al., 2021) so identifying any fitness consequences is a priority; and (v) within the captive population, there is variance in wing shape (Stojanovic et al., 2021), providing an opportunity to study the impact of different phenotypes on fitness in the wild.

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 behaviourally (e.g. sudden transition from supplemental to natural food, Stojanovic, Neeman, Crates, et al., 2020). Consequently, most juveniles die in their first year of life (Stojanovic, Potts, Troy, et al., 2020). Individual survival is monitored via daily observations of ringed birds at supplementary food tables during the summer breeding season (Stojanovic et al., 2018; Stojanovic, Potts, Troy, et al., 2020). There is only one extant population (Stojanovic et al., 2018), so non-detection at feeders is attributed to mortality (not emigration). The captive population is held across several participating institutions that use comparable husbandry approaches (Pritchard et al., 2022) and a studbook to minimise genetic adaptation to captivity (Morrison et al., 2020). Regular releases have resulted in full admixture of the captive and wild populations (Morrison et al., 2020; Stojanovic et al., 2022).

I measured 78 juvenile captive-bred parrots that were subsequently released to the wild over 3 years (2019: 30, 2020: 31, and 2021: 17). No wild-born parrots are included because at the nestling phase when wild juveniles are typically handled their wing feathers are still developing. In contrast, my sample of captive-bred parrots were between the ages of 3–5 weeks post-fledging and their wing feathers were fully grown (Stojanovic, Alves, Webb, et al., 2020). Only juveniles with perfect wing feathers were included in this study. Juveniles are selected for release based on metapopulation management considerations (Morrison et al., 2020; Troy & Lawrence, 2021) but not for any particular phenotypic trait bar good body mass and good general feather condition. As shown in Figure 1, I measured ΔQ of the feathers proximal (P8) and distal (P10) to the L_P (P9), which are known to vary between captive and wild parrots (Stojanovic et al., 2021). I dropped L_S, but recorded L_W, tail length (L_T) and body mass (g). As an index of individual condition, I divided body mass by L_W to scale for overall size. I scored individuals as having survived (1) or died (0) in their first year of life based on whether or not they returned from their first migration. I used the same criteria as previous survival analyses for this species using sightings data from supplementary feeders in the wild (Stojanovic, Potts, Troy, et al., 2020).

Analytical approach

I conducted all analyses in R (R Development Core Team, 2021) and scaled and centred 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 (proximal and distal flight feathers) as 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 × 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, ν = 0.002). I ran the model for 100,000 iterations and set burn-in to 1000 and used 100 for thinning for a total posterior sample of 990. All chains were checked for proper mixing, and I checked for autocorrelation 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 and *ggplot2* (Wickham, 2016) for data visualisation.

Aim 2—To evaluate if wing phenotype predicts survival of the first migration, 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 (proximal and distal flight feathers), L_W, L_T and the index of body condition as additive 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 1000 and used 100 for thinning for a total posterior sample of 990. All chains were checked for proper mixing, and I checked for autocorrelation using the command 'autocorr' with 0.1 as a target threshold.

RESULTS

Evaluate the ubiquity of captive wing shape phenotypes

The interaction between feather $ID \times species \times provenance$ had significant explanatory power for the length of the feathers I measured (see R Markdown). The highest posterior density intervals did not overlap zero for contrasts between captive-wild specimens in the length of at least one flight feather for 4/16 species (Figure 2). Relative to wild conspecifics: (i) captive budgerigars *Melopsittacus undulatus* had longer proximal feathers, (ii) captive turquoise parrots *Neophema pulchella* had a longer distal feather but a shorter proximal feather, (iii) captive sundown parrots had a shorter distal feather and (iv) captive Gouldian finches *Chloebia gouldiae* had a longer distal feather. There were indicative trends (with highest posterior density intervals slightly overlapping zero) in other species as well. The distal feathers of captive princess parrots and zebra finches *Taeniopygia guttata* tended longer, whilst in star finches *Bathilda ruficauda* and red-throated parrotfinch *Erythrura psittacea* they tended shorter. Similarly, the proximal feathers of captive king quail *Synoicus chinensis* and scarlet-chested parrots *Neophema splendida* tended shorter. L_W, L_P and L_S 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

Overall, 16/62 (25.8%) orange-bellied parrot juveniles released from captivity survived their first migration. Post-release survival of captive-bred juvenile orange-bellied parrots had a negative relationship with ΔQ P10 (i.e. the distal feather on the leading edge of the wing) (Table 1). Smaller values of ΔQ P10 indicate that feather is longer, which is more like the wild phenotype (Figure 3). Based on the model, the estimated survival rate of a juvenile captive-born orange-bellied parrot with a ΔQ P10 of 1 mm was 0.0664 (highest posterior density intervals: $1.06e^4$–0.49), compared with only 0.0254 (highest posterior density intervals: $6.96e^6$–0.23) for an individual with a ΔQ P10 of 2 mm.

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). I present the first multi-species evaluation of the prevalence and fitness impact of captive bird wing phenotypes. I found captive phenotypes in 4/16 species, usually involving the proximal and distal feathers that determine wing tip shape around the L_P. However, the changes I observed were inconsistent even among related species. For example, congeneric orange-bellied and turquoise parrots had a shorter distal feather (P10) in captivity, but closely related sundown parrots had the opposite effect. Among finches, there were contradictory trends in the length of the distal feather (P9) across multiple species, and I did not find comparable changes to feather lengths in zebra finches observed in other studies (Carr & Zann, 1986). Interestingly, even king quails (which fly infrequently) had an indicative trend of a shorter proximal feather (P10), but the sample size for this species was small. In this study, why related species experienced such inconsistent morphological changes is not clear.

Wing tip shape affects flight performance (Lockwood et al., 1998; Swaddle & Lockwood, 2003), but whether the changes I report result in aerodynamic impairment remains unclear. However, this possibility is supported by evidence that a 1 mm shorter P10 in released juvenile captive orange-bellied parrots was associated with lower survival rates. This is the first demonstration that altered wing phenotypes may incur fitness costs. Overall, survival of captive-born juveniles released to the wild in this study (25.8%) was comparable to wild-born conspecifics (20%; Stojanovic, Potts, Troy, et al., 2020). Understanding the prevalence of different wing phenotypes within the contemporary captive population may help inform how to improve survival rates. Orange-bellied parrots are the beneficiary of careful genetic management and professional husbandry techniques in a large-scale captive breeding for reintroduction programme (Pritchard et al., 2022). Despite this care, subtle changes to wing phenotypes emerged in captivity (Stojanovic et al., 2021), while other components of phenotype, e.g. body size, remained unchanged (Stojanovic et al., 2019). Juvenile orange-bellied parrots face a gauntlet of obstacles to survival of their first year of life (Stojanovic et al., 2022; Stojanovic, Potts, Troy, et al., 2020)—perhaps greater drag of a rounder wing tip (Minias et al., 2015; Tucker, 1995) is enough to further disadvantage captive phenotypes during long flights. At the breeding ground where supplementary food and predator control is available, post-release survival of captive-bred parrots is very high (Troy & Lawrence, 2021). Stronger selection occurs later during the migration/winter phases of life history (Stojanovic, Potts, Troy, et al., 2020) when juveniles develop survival skills and physical endurance. During this more challenging life history phase, small changes to flight efficiency may become an impediment to survival, but this theory remains untested.

My results raise important new questions both for orange-bellied parrots and conservation breeding programmes more generally.

First, why is the length of flight feathers of birds plastic? Whether wing shape is under genetic control or
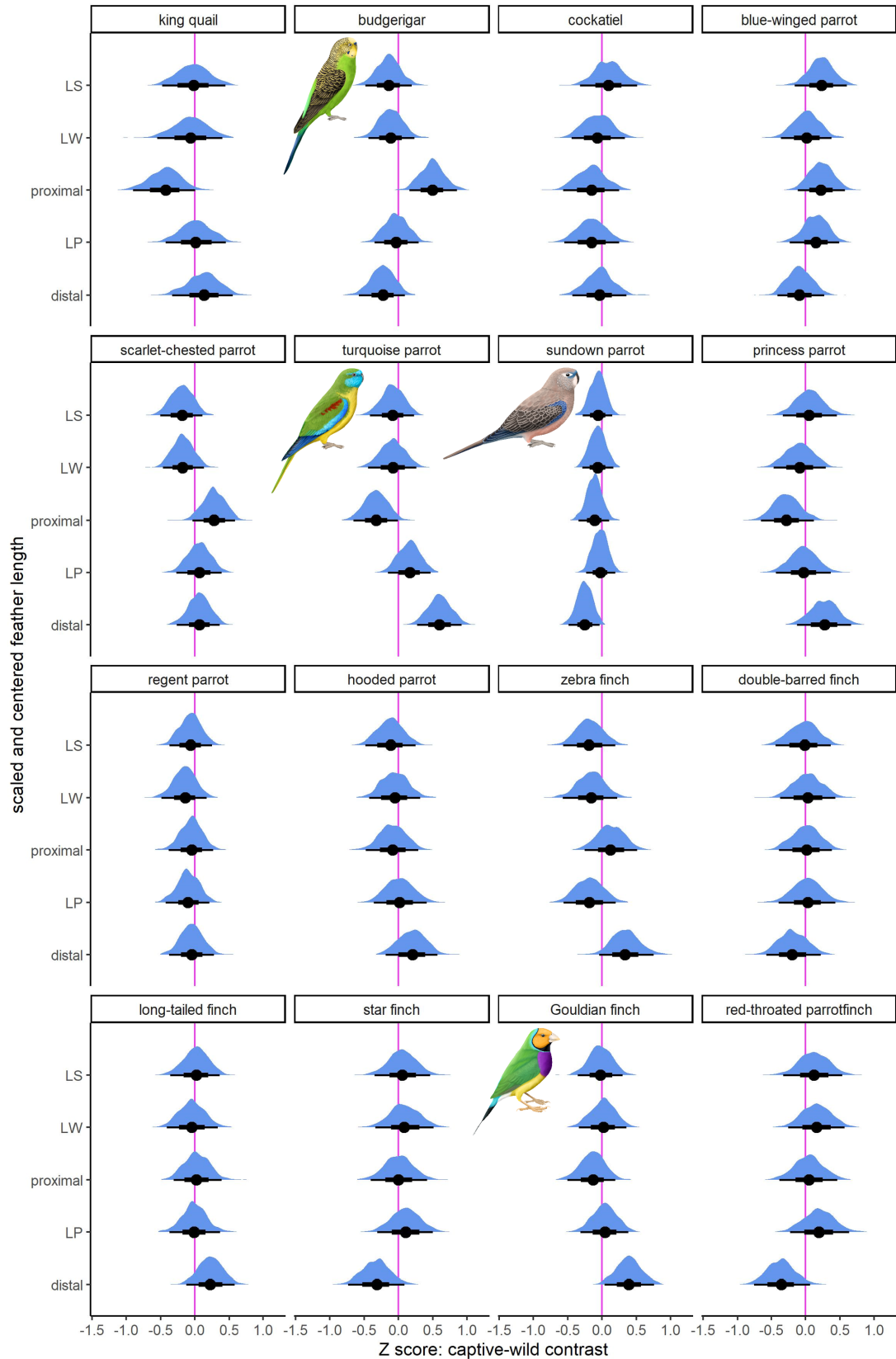
FIGURE 2 Captive vs. wild pairwise contrasts of feather lengths showing Z scores and 66% and 95% credible intervals (black bars) computed with Bayesian mixed models. For each species I present data on the flight feathers proximal and distal to the longest flight feather in the wing (LP). Together, these three feathers form the wing tip. LW, unflattened wing chord, 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.

Fixed effect	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample	p
(Intercept)	−1.77	−4.06	1.23	990	0.12
P10	−0.99	−1.94	−0.19	730	0.02*
P8	0.07	−0.64	0.91	1180	0.84
L_W	0.40	−0.44	1.32	839	0.38
L_T	−0.74	−1.71	0.16	870	0.12
Body mass	0.45	−0.47	1.56	686	0.37

TABLE 1 Summary of fixed effects from Bayesian linear regression of juvenile survival of orange-bellied parrots reared in captivity.

Note: CI, credible interval.

*Indicates a significant effect at 0.05.
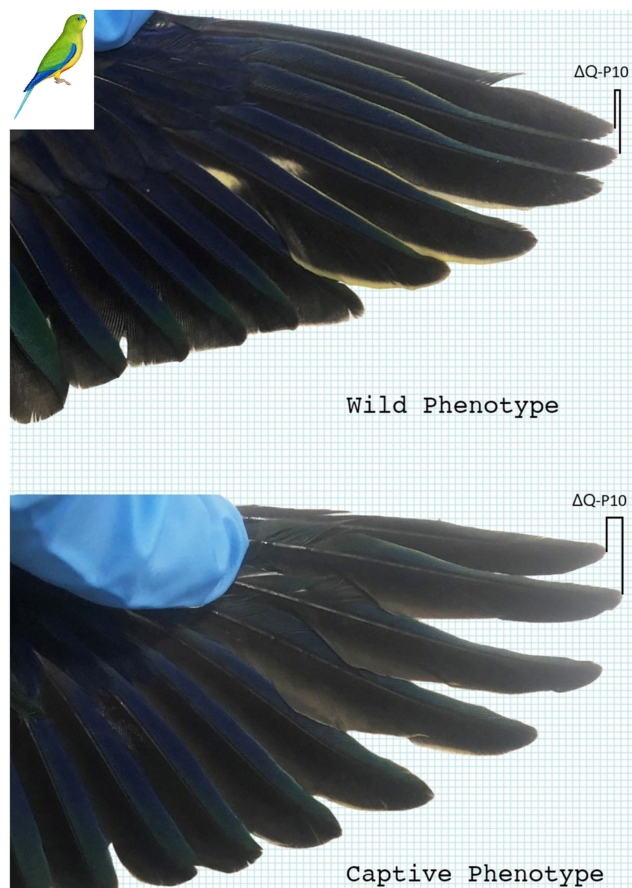
FIGURE 3 Captive vs. wild wing phenotypes orange-bellied parrots. The captive phenotype involves a shorter outermost flight feather (1 mm^2 grid), and results in worse rates of juvenile survival of the first year of life relative to the wild phenotype. Artwork by Julian Teh.

shaped by the environment is not clear. Clarifying the importance of these potential forces on feather development may provide insight into how to correct captive wing phenotypes.

Second, why are distal flight feathers prone to change? Several captive species in this study had distal feather lengths that were significantly different or tended different to wild conspecifics. Investigating the relationship between feather development and curtailed flight in captive environments may help explain why distal flight feather length seems 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 optimise wing shape (e.g. with flight training).

Fourth, why do captive wing phenotypes incur a fitness cost, and is this cost universal among species? Rounded wings generate more drag than pointed ones (Lockwood et al., 1998), but the direct consequences of captive wing phenotypes on migration success post-release is unknown. Wing tip shape also affects take-off ability, which in turn may affect predation risk (Swaddle & Lockwood, 2003). Predation is an important cause of reintroduction failure among parrots (White et al., 2012) and many other taxa (Berger-Tal et al., 2020; Shier, 2016). Given that the changes I report are small and variable between individuals and species, it is interesting that they should have a noticeable effect on mortality. Further work, for example quantifying the aerodynamic penalties of captive wing phenotypes, may provide new insights into synergies between wing shape and other factors (e.g. body condition) that cause mortality.

Captive phenotypes vary from obvious to subtle deviations from the optimal wild type. I show a mere 1 mm reduction in the length of a single feather was associated with worse 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 popular hand wing index (Sheard et al., 2020) because L_W and L_S (which are important for calculating this index) were unaffected by captivity. Detailed surveillance is crucial for detecting subtle deviations from the wild phenotype (Crates et al., 2022). Ensuring that captive animals are in optimal condition for life in the wild is especially important for species that experience strong phenotypic selection from some component of life history (Crates et al., 2022; Davis et al., 2020). However, surveillance for altered captive phenotypes is negligible despite the risks that

they pose to the success of release programmes (Crates et al., 2022). I argue captive breeding programmes 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, 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 in breeding programmes 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 to be 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 programmes (IUCN Conservation planning specialist group 2020).

AUTHOR CONTRIBUTIONS
DS conceived the idea, collected and analysed the data and wrote the manuscript.

ETHICS STATEMENT
Orange-bellied parrots were measured with approval from the Australian National University Animal Ethics Committee (protocols: A2017/38, A2020/35) and the Tasmanian Government (scientific permits: 17144, 18255, 19168).

PEER REVIEW
The peer review history for this article is available at https://publons.com/publon/10.1111/ele.14200.

OPEN RESEARCH BADGES

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DATA AVAILABILITY STATEMENT
Data and code are available at Dryad https://doi.org/10.5061/dryad.m905qfv4t

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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