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Differences in wing shape of captive, critically endangered, migratory orange-bellied parrots *Neophema chrysogaster* relative to wild conspecifics

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ABSTRACT

Living in a captive environment may compromise phenotypic traits critical to survival in the wild. Captive animals that differ from the ideal wild phenotype may have impaired fitness after release, especially if there is extreme phenotypic selection during some life history stages. Wing shape of migratory birds is crucial to migration efficiency, and changes to wing shape in captivity may severely affect survival after release. We investigate wing shape of migratory Orange-bellied Parrots *Neophema chrysogaster* in captivity and the wild. The first two flight feathers were shorter in captive birds, and the fifth and sixth feathers were longer than wild conspecifics. These differences altered wing shape, producing a more proximal tip and a more convex trailing edge than the wild phenotype, which likely alters flight performance. This wing shape contravenes expectations from general patterns of wing shape in migratory birds. Wing shape in the captive birds sampled was independent of inbreeding, generations in captivity and ancestry. Captive environments may affect feather development or impose some selective pressure on wing shape. Alternatively, release from intense phenotypic selection during migration may allow parrots with wing shapes poorly adapted to migration to survive and breed in captivity. Altered wing shape may contribute to low observed survival of parrots released to the wild.

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Introduction

Breeding and release of captive bred animals into the wild is a globally important conservation tool aimed primarily at preventing extinction in the wild (Jansson *et al.* 2015; Bacon *et al.* 2019; Heinrichs *et al.* 2019). Release from natural selective pressures in captivity may compromise traits critical for life in the wild and simultaneously select for different phenotypes in captivity (Frankham 2008; Christie *et al.* 2012a). Captive animals that differ from the ideal wild phenotype may have impaired fitness after release (Araki *et al.* 2007; McGinnity *et al.* 2009; Christie *et al.* 2012b; Willoughby and Christie 2017), making it crucial to identify phenotypic traits at risk of change in captivity. Species with demanding life stages in the wild are under strong selection for the most functional phenotypes (Davis *et al.* 2020). For example, migratory birds experience extreme selection on their ability to move long distances (Faaborg *et al.* 2010; Sanz-Aguilar *et al.* 2012), so changes in wing shape arising from captivity may impose severe survival penalties if flight efficiency is impaired. Migratory birds have more pointed wing tips than sedentary birds because pointy wings allow

faster, more aerodynamically efficient flight than rounded wings (Lockwood *et al.* 1998; Sheard *et al.* 2020). Pointed wings have more distal tips than rounded wings, which reduces drag but also manoeuvrability at lower speeds (Lockwood *et al.* 1998). Differences in life history and mobility can result in divergent wing shapes between (Minias *et al.* 2015) and within species (Carvalho Provinciano *et al.* 2018), including differences between sexes (Anderson *et al.* 2019). Given the dramatic differences between life in the wild and captivity (in terms of selection, lifestyle, individual survival and fitness), it stands to reason that the selective pressures that shape the wings of wild birds would change in captivity. Surprisingly, there have been no studies of whether bird wing shapes in captivity differ to those of wild conspecifics. This gap in knowledge may be important for conservation projects on migratory species that may face extreme selection for wing shape after release to the wild. Identifying if wing shape can change in captivity, and what that change looks like, is a first step towards understanding the factors that predict whether captive bred birds are capable of surviving in the wild after release.

We evaluate whether the wing shape of captive, critically endangered, migratory Orange-bellied Parrots *Neophema chrysogaster* is different to that of their wild conspecifics. The world's most endangered parrot (Stojanovic *et al.* 2018), the species has been bred in captivity since 1986 (Smales *et al.* 2000). The ~45 g bird migrates from their breeding area in south-western Tasmania to their winter foraging grounds on the Australian mainland (Higgins 1999). Unfortunately, the annual survival of captive-born birds released into the wild is low, and the overall survival of both captive and wild-born juvenile parrots on their first migration is only 20% (Stojanovic *et al.* 2020b). This low juvenile survival during migration/winter is likely responsible for the collapse of population size in the wild (Drechsler *et al.* 1998). Body size of captive and wild birds is comparable (Stojanovic *et al.* 2019), but it is not known whether there are phenotypic effects of captivity on wing shape in this species. If captive environments impose different selection or developmental pressures on birds, wing shape of captive-born Orange-bellied Parrots should differ from wild conspecifics. We hypothesised that life in an aviary demands better agility at low speeds than required of wild birds. If this hypothesis is true, we expect that captive birds should have a more proximal wing tip than wild birds. We test this prediction using measurements of the flight feathers of specimens of captive- and wild-born parrots. To evaluate if pedigree-based genetic management of the captive population can explain the wing shape phenotype in captivity, we use detailed individual metrics of founder genome contribution, inbreeding estimates and generations of captive breeding.

Methods

Specimen details and data collection

We present data on the wing shape of 201 Orange-bellied Parrot specimens, comprising 147 captive-born, and 54 wild-born animals. We sourced specimens from the captive population and museum collections. The captive breeding project began in 1986/87 and has been intermittently supplemented with new (2–4 individuals per supplementation) wild founders, most recently in 2010/11 when 21 wild birds were captured for captive breeding (Martin *et al.* 2012). We sourced the captive specimens from the Tasmanian Government Tarooma Wildlife Centre ($n = 70$) and Healesville Sanctuary ($n = 77$). We sourced wild specimens from the Australian National Wildlife Collection ($n = 3$), Australian Museum ($n = 3$), American Museum of Natural History ($n = 8$), Harvard Natural History Museum ($n = 5$), Museum of Victoria ($n = 6$), South Australian Museum ($n = 20$), and the Tasmanian Museum and Art Gallery ($n = 6$). The

mean collection date was 1946 for wild-born birds (range: 1857–2016) and 2006 for captive-born birds (range: 1986–2018).

Captive specimens were frozen but wild-born specimens were study skins, so we excluded soft tissues from our study. Feather lengths measured on live birds do not change in the preservation process of making study skins and do not shrink over time (Jenni and Winkler 1989), unlike soft tissues (Harris 1980). Shrinkage of museum skins does not affect the length or position of individual feathers (and their tips) relative to one another (Jenni and Winkler 1989; Lockwood *et al.* 1998), and museum skins stop shrinking after three years (Green 1980; Harris 1980). Furthermore, distal primary feathers are attached directly to the bones of digits II and III of the avian hand (not to soft tissue) (Hieronymus 2016). Based on the resilience of feathers against shrinkage and their attachment to bone, we had no reason to suspect that the relative position of the tips of the feathers should change in frozen specimens versus skins. There is no evidence to suggest freezing changes feather length. Consequently, we only used feather lengths in our analysis, measured as the distance between the tip of each flight feather and the tip of the longest flight feather (see below). Based on these considerations, we consider the comparison of specimens of different ages and preservation histories reasonable.

We measured all specimens with folded wings (i.e. in the standard study skin posture). Specimens were measured using electronic calipers (to the nearest 0.01 mm) and a thin, soft, flexible plastic ruler (1 mm). We measured: (1) L_W – unflattened wing chord, (2) unflattened length of the longest primary flight feather (measured from the point where the calamus inserted into the skin – we followed Jenni and Winkler (1989) to measure feather length), (3) ΔQ values (following the method of Lockwood *et al.* 1998, including the feather numbering system where p1 forms the leading edge of the wing), i.e. distances between the primary flight feather tips from the longest primary feather tip, and (4) S_L – the distance between the carpal joint and the tip of the most distal secondary on the folded wing. We excluded juveniles (identified from specimen tags and metadata), specimens with broken or worn flight feathers, and specimens where the wings were not in the resting position. Orange-bellied Parrot specimens are scarce, so we included some birds that had individual missing feathers (p4 – p7), and estimated the ΔQ value as midway between the two feathers adjacent to the gap. DS measured all birds, and measurement repeatability was high. Observer error accounted for a mean of 12.6% of the variance across the traits measured (range: 5–23%) irrespective of the specimen preservation method.

Analysis of wing shape

We undertook our analysis of wing shape in three steps, following the methods described elsewhere (Stojanovic *et al.* 2020a). We used adjusted ΔQ values (length of the longest feather minus ΔQ , scaled to account for size differences among specimens by subtracting the overall mean length from the length of each individual feather to remain on a mm scale and model the 'leftover' variation) as the response variable for steps one and two. In the first step, we used MANOVA to compare adjusted ΔQ values of each flight feather of captive and wild parrots (provenance, i.e. captive- or wild-born, was included as the fixed effect) in a multivariate framework. Second, we implemented size constrained component analysis (SCCA) using adjusted ΔQ values from the primary feathers (Lockwood *et al.* 1998). This approach is similar to principal component analysis, and collapses the ΔQ values from all feathers of the wing into three main components that can be used in downstream analysis. The first component is size, the second component is a measure of wing roundness/pointedness (hereafter C2), and the third component is the concavity/convexity of the trailing edge of the wing (hereafter C3). Size was removed from the analysis to account for differences between large and small individuals, but we use C2 and C3 to capture overall variation in wing shape (Lockwood *et al.* 1998). Third, we calculated hand-wing index (HWI), which is related to dispersal ability of birds (Sheard *et al.* 2020) because it is a simple index of wing aspect ratio that can easily be measured on skins (Claramunt and Wright 2017). We calculated HWI using the formulation presented by Claramunt *et al.* (2012):

$$HWI = 100 \times \frac{(L_W - S_L)}{L_W}$$

Finally, we used linear models to test for differences in C2, C3 and HWI among the captive and wild birds. We used C2, C3 and HWI as response variables, and fitted provenance (captive/wild) as fixed effects.

We also tested for the possibility that wing shape of wild Orange-bellied Parrots changed due to evolution over the time period when museum skins were collected by fitting linear models using C2 and C3 as response variables, and collection date (recorded from museum labels) as a categorical fixed effect. We did not consider captive animals in that analysis. Finally, we used linear discriminant analysis to obtain a linear combination of components (C2 – C5) derived from the SCCA that best discriminate between captive and wild-born Orange-bellied Parrots and we evaluate the performance of the linear discriminator.

Effects of captivity

To understand factors that may drive changing wing shape in captivity, we collected data on intrinsic genetic variation between individuals for the subset of captive-born Orange-bellied Parrots in our sample for which data were available from the species' SPARKS studbook Lacy *et al.* (2012). Captive parrots are a metapopulation across multiple institutions, so variation among different institutions is limited by interbreeding, similar husbandry and transfer of birds between institutions. We collected the following traits: (1) number of generations of captive breeding that produced the focal individual (hereafter referred to as 'generations of captive breeding' – calculated from the species studbook), (2) the inbreeding coefficient F – from the studbook, (3) the contribution (expressed as a percentage) of old (2010 or earlier) and new (2011 onward) founder bloodlines to individual genotypes (Zoo and Aquarium Association 2018). The differentiation between old and new founder bloodlines represents the period before and after the largest influx of new wild parrots into the captive population (Morrison *et al.* 2020). We also recorded sex, and year of birth. We used the linear discriminator value (calculated above for differentiating captive and wild-born Orange-bellied Parrots by wing shape) and also C3 as response variables in two sets of linear models. To each of these variables in turn, we fitted a suite of models including only the main effects of sex, cohort and the four genetic variables. We only considered main effects to reduce the likelihood of overfitting due to our small sample, and based on the results of these main effects we did not consider it necessary to fit more complex additive or interactive models. We compared competing models using $\Delta AIC < 2$ (Burnham and Anderson 2002).

All analyses were undertaken in R (R Development Core Team 2020) and SCCA was implemented using the package *factoextra* (Kassambara and Mundt 2017). Code, raw data and additional exploratory analysis are presented in Supplementary Materials.

Results

The multivariate test found significant differences in adjusted ΔQ values between captive and wild Orange-bellied Parrots (Pillai's Trace = 0.14, $F = 4.67$, d.f. = 1, $p < .1$). Differences in adjusted ΔQ values for individual feathers (i.e. pairwise contrasts of captive – wild) were significant for the first (estimate -0.81 ± 0.18 se, t. ratio = -4.56 , $p < .1$), second (estimate -0.46 ± 0.18 se, t. ratio = -2.58 , $p < 0.01$), fifth (estimate 0.44 ± 0.18 se, t. ratio = 2.46 , $p < .1$) and sixth flight feathers (estimate 0.43 ± 0.18 se, t. ratio = 2.41 , $p = .2$). The model estimates and standard errors are presented in Figure 1 for all feathers. We found no difference in wing roundness (i.e. C2) ($P = 0.26$) or HWI ($P = .54$)

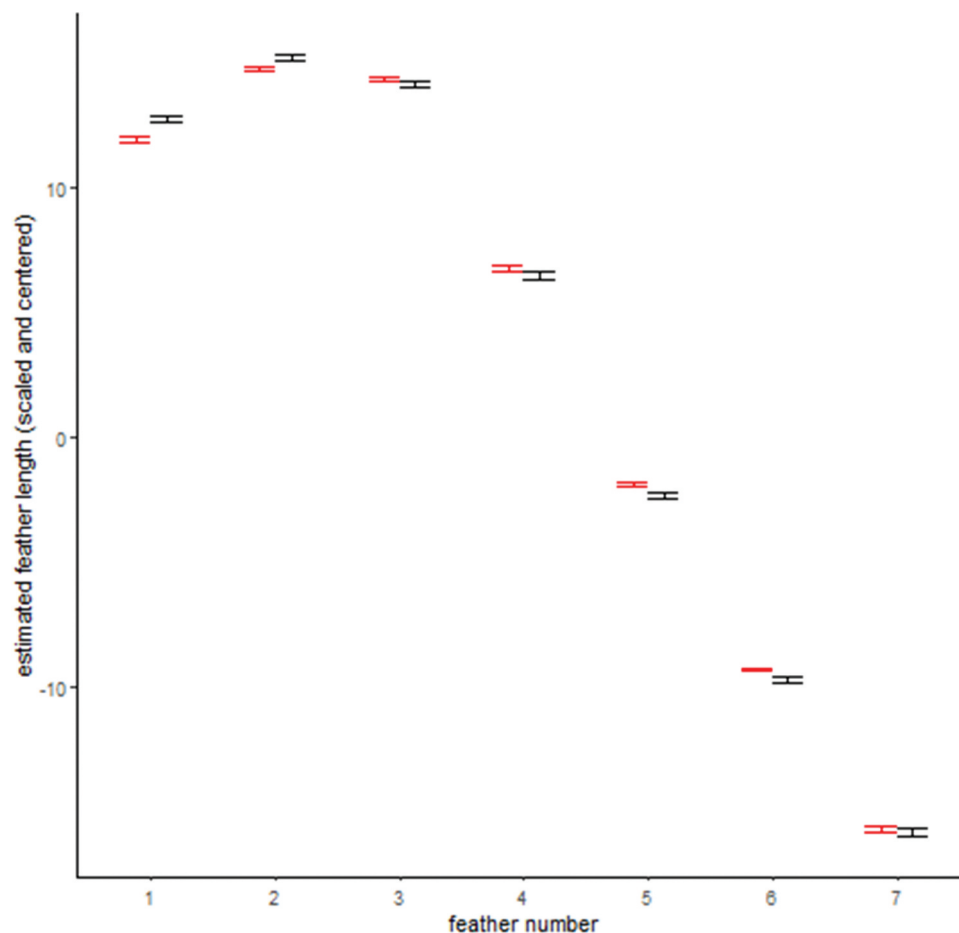


Figure 1. Modelled standard errors for the mean length (means are midway between the error bars, but not indicated on the figure for the sake of clarity) of each primary feather. Captive birds are red and wild-born are black. There were significant differences in feather length among captive and wild-born populations for feather numbers one, two, five and six. We scaled and centred feather lengths to remove size from the analysis, and these estimates reflect population means corrected for body size.

but there was a significant difference in wing concavity (i.e. C3) (d.f. = 1, $F = 19.8$, $P < .1$, Figure 2) between captive and wild-born Orange-bellied Parrots. The first three primaries were longer and the fourth to sixth primaries were shorter in individuals with high values of C3 compared to individuals with low values of C3 (raw data and an illustration of what the extremes of C3 look like are presented in Figure 2). There was no evidence of the evolution of wing shape of wild Orange-bellied Parrots because museum skin collection date was independent of variation in C2 and C3. The linear discriminant analysis (raw data presented in Figure 3) was able to successfully identify captive-born Orange-bellied Parrots with high sensitivity (96% or 141/147 cases) but had less success for wild-born individuals (26% or 14/54 cases).

We had studbook data for 86 of the captive-born Orange-bellied Parrots in our sample (20 from the Tasmanian Government and 66 from Healesville Sanctuary) comprising 31 females, 40 males and 15 of unknown sex born between 1993 and 2008. For the following variables we present means \pm standard deviation, with a range in parentheses: linear discriminant score = -0.18 ± 1.05 (-3.60 to 2.48);

C3 = -0.21 ± 1.46 (-5.31 to 2.59); generations of captive breeding = 3.58 ± 1.77 (0 to 7.21), $F = 0.05 \pm 0.05$ (0 to 0.29), percent old blood-line = 0.41 ± 0.28 (0 to 1), percent new blood-line = 0.22 ± 0.34 (0 to 1). Most of the genetic and intrinsic variables we compared in our analysis for both the linear discriminant score and C3 were $< 2 \Delta AIC$ from the null model (Table 1). Because these variables had equivalent support to the null model, we conclude that the pedigree-based genetic variables we tested do not explain either the linear discriminant score or C3 of captive-born Orange-bellied Parrots.

Discussion

We found evidence that wing shape of captive Orange-bellied Parrots was different to the wild phenotype, which supports the hypothesis that life in captivity can result in changes to wing shape. We demonstrate that captive-born adult Orange-bellied Parrots have shorter distal flight feathers, and longer proximal flights than wild adult conspecifics. These changes result in a more convex trailing edge to the wing and a more proximal wing tip in captive birds. We found no difference in C2 or HWI, but

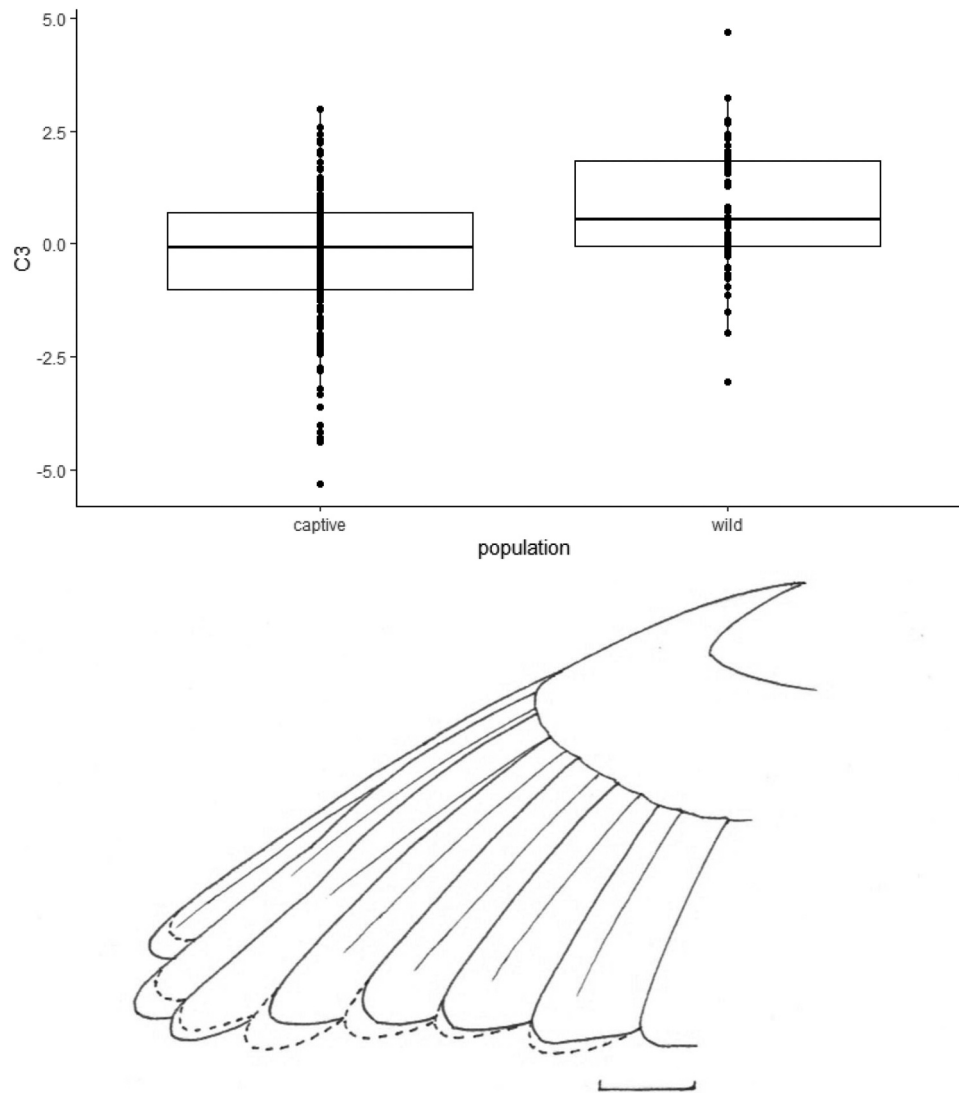


Figure 2. Box plot showing the means, quantiles and raw values of wing concavity (C3) for wild- and captive-born Orange-bellied Parrots. The illustration shows the extremes of very high (solid lines) and very low (dotted lines) values of C3 on an outspread wing. The illustration is based on the mean feather lengths of the ten birds with the highest and lowest values of C3 in the sample. Captive birds had 9/10 of the lowest values for C3, but only 4/10 of the highest values. Wings with high C3 had longer distal primaries, but shorter proximal primaries than wings with low C3. These differences result in a more convex trailing edge of the wing for captive-born Orange-bellied Parrots. The scale bar represents 1 cm.

the latter result is not surprising because HWI is too coarse to detect fine changes in the lengths of individual feathers if these changes do not affect wing length or width. Wings with more proximal tips and convex trailing edges are less suited to fast, long distance flight (Lockwood *et al.* 1998), and similar changes to the wings of captive butterflies reduce migration survival (Davis *et al.* 2020). Artificial length reduction of flight feathers in Harris' hawk *Parabuteo unicinctus* increases drag (Tucker 1995) and lowers take-off speed in starlings *Sturnus vulgaris* (Swaddle *et al.* 1996). Furthermore, wing tip shape in starlings is related to the angle of escape take-off (Swaddle and Lockwood 2003), and barn swallows *Hirundo rustica* with damaged feathers have low migration survival (Pap *et al.* 2005). Evidence from these and other studies suggests that the combination of poor feather condition in some captive parrots (Stojanovic

et al. 2018) and the differences in wing tip shape we discovered, may be an impediment during the physically challenging migration flights necessary for life in the wild. The wing shape of captive-born Orange-bellied Parrots contravenes general patterns of wing shape among migrating birds (Mönkkönen 1995).

Why the wings of the captive population differed in wing shape is not clear. The intrinsic genetic variables we tested did not predict wing shape of captive parrots, suggesting that wing shape may be more complex than simple genetic inheritance alone. Although we have no reason to suspect that the founders of the captive population had biased wing shapes, we cannot rule this possibility out as a potential explanation for our results. Furthermore, the captive population has undergone variation in heterozygosity over time depending on the collection of new founders

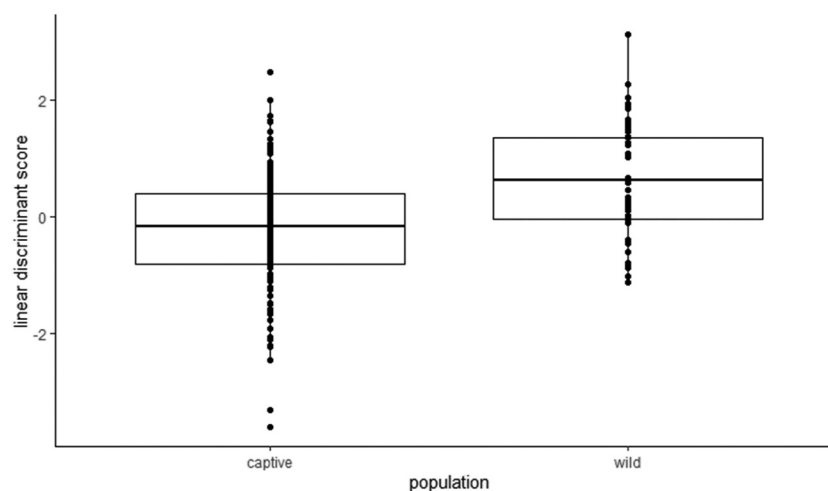


Figure 3. Linear discriminant scores (raw data presented as points, with a boxplot overlay) for captive and wild Orange-bellied Parrots. Linear discriminant analysis was used to obtain a linear combination of feather measurements that best discriminate wild and captive populations.

Table 1. Models ranked by AIC testing the relationship between the (i) linear discriminant score (derived from the components two to five from the SCCA) and (ii) the wing concavity value (C3) of captive-born Orange-bellied Parrots, and the six genetic variables derived from the species stud-book. The preferred model is indicated by *.

Response variable	Model fixed effect	df	AIC	ΔAIC
Linear discriminant score	Generations of captive breeding	3	254.73	0.00
	Null*	2	255.02	0.30
	% old founder	3	255.07	0.34
	Inbreeding coefficient	3	255.66	0.94
	Year of birth	3	256.36	1.63
	% new founder	3	257.01	2.29
	Sex	4	258.23	3.50
C3	Null*	2	312.32	0.00
	Inbreeding coefficient	3	312.52	0.19
	Year of birth	3	313.15	0.83
	% old founder	3	314.03	1.70
	% new founder	3	314.08	1.76
	Generations of captive breeding	3	314.28	1.96
	Sex	4	316.17	3.84

from the wild (Morrison *et al.* 2020), but whether these (or other undetected) genetic changes have any bearing on morphology is not known. There may be other potential explanations for why the genetic variables we tested did not explain wing shape – for example, C3 and the linear discriminant score may be too coarse to detect very small changes to individual feather lengths in captivity. Furthermore, the morphology of birds can be plastic in response to conditions during developme

nt and even over a lifetime (Brennan *et al.* 2017; Domínguez *et al.* 2010) so it is likely that multiple factors contributed to our findings. Indeed, recent evidence suggests that (at least) the body mass of captive Orange-bellied Parrots is related to maternal effects, not generations of captive breeding (Stojanovic *et al.* 2019). If wing shape in captivity depends on some combination of heritable and environmental factors, identifying

the underlying mechanisms driving change is critical to correcting wing shape.

Ideally, captive-born parrots should be as phenotypically similar to their wild conspecifics as possible in order to maximise their chances of survival during migration. Survival is chronically low in the contemporary population (both for wild and captive provenance birds), and only 20% of juveniles survive after leaving their breeding grounds (Stojanovic *et al.* 2020b). Given that migration is by its nature very physically demanding, we suggest that wing shape should be considered a factor that may influence survival after release. Furthermore, a future research priority should be to evaluate whether aspects of wing shape are heritable. If it were, then this would provide managers with new information to assist when selecting birds for breeding. This would open a new avenue of research into what aspects of the captive environment influence feather development, and whether extreme low values of C3 can be corrected and prevented from recurring. It is possible that some aspect of the captive environment (e.g. limited space for flight, the need for agility in small aviaries, inability to undertake sustained flight, artificial diet) results in altered feather development in aviaries. Indeed, although captive institutions involved in the breeding program have similar husbandry approaches and exchange birds for breeding, minor differences between the environments provided by each institution may subtly alter the feather development. Feather quality of some released captive-born Orange-bellied Parrots can sometimes be lower than wild conspecifics (Stojanovic *et al.* 2018). It is also possible that captive environments select for birds better suited to flight in aviaries. Mortality from collisions with aviary walls and furnishings may be a possible selection mechanism for slower, controlled flight in confined enclosures, and this is known as a cause of death for this species in captivity. However, this problem has become less prevalent

recently due to modifications to aviary design intended to eliminate this risk (i.e. padded walls). Another possible explanation is that relaxed selection pressure in captivity allows birds with maladaptive wing shapes to survive and breed. Most Orange-bellied Parrots (both wild- and captive-born) die during their first migration (Stojanovic *et al.* 2020b) and the elimination of this strong selection pressure in captivity may explain the phenotypic divergence we report. Each of these hypotheses warrant further investigation because the success of reintroduction efforts hinges on producing animals with the necessary phenotype for survival in the wild.

This study is a timely reminder to remain vigilant against morphological changes in captivity (O'Regan and Kitchener 2005). Captive breeding is highly resource intensive, so failure to detect changes in critical morphological traits that may impair wild survival will diminish some of the potential benefits of these investments (Davis *et al.* 2020). Altered wing shape may not be the only explanation for why captive-born Orange-bellied Parrots have low annual survival rates (particularly in context of low survival of their wild-born conspecifics), but this may be an important but hitherto overlooked component of fitness. We hope our study encourages other practitioners to reconsider fundamental aspects of the wild ecology of species targeted for captive breeding and release programs. Understanding how conditions in captivity differ to those in the wild, and early identification and correction of subtle morphological change, may translate to substantial improvement in the outcomes of conservation release programs.

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Disclosure statement

The authors declare no competing interests.

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