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Body mass is not a useful measure of adaptation to captivity in the Orange-bellied Parrot *Neophema chrysogaster*.

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Running Head: Body mass and adaptation to captivity

Abstract

In captivity, novel selective pressures can lead to divergence from the wild source population, which can be a liability for animals released into the wild. Easily measured indices of change, like body mass, might be important for early detection of adaptation to captivity. We hypothesized that for species subject to long-term captive breeding body mass may be a useful proxy for detecting morphological adaptations to captivity. We test this (and alternative explanatory variables) with 22 years of pedigree data on Orange-bellied Parrots *Neophema chrysogaster* and predict that adult body mass would change over successive generations in captivity. The best model of adult body mass showed a relationship with maternal effects both directly (heavier mothers produced heavier offspring) and indirectly (different founding maternal lineages produced heavier or lighter descendants), plus circumstances in the year of birth (e.g. years with better food quality produced heavier birds). Body mass did not change with increasing generations of captive breeding. Our results suggest that either adaptation to captivity has not occurred, or if it has, that body mass is too coarse an index to detect it. Captive breeding programs should

directly measure traits of interest and ideally, compare these to traits of wild birds to identify an ideal morphological base line.

Key Words

Maternal effects; adaptation to captivity; pedigree; captive breeding; endangered species

Introduction

Captive breeding is an important tool for conservation of threatened species. But because captive environments are benign, they relieve natural selective pressures faced in the wild. In captivity, novel selective pressures can act on populations, and lead to genetic, behavioral and morphological divergence of captive and wild populations. Adaptation to captivity can be a liability for animals released into the wild. Furthermore, release of maladapted captive animals can negatively affect key demographic parameters of wild populations (Araki *et al.* 2007; Araki *et al.* 2009; Willoughby and Christie 2018). Preventing adaptation to captivity is a high priority for captive breeding programs, and careful genetic management is crucial to this outcome (Frankham 2008). However, despite genetic management, mainly based on pedigrees, some degree of adaptation to captivity may be unavoidable (Chargé *et al.* 2014).

Early detection of adaptation to captivity is critical if captive populations are intended for release to the wild. But morphological changes in captive animals may be difficult to detect if there is no *a priori* reason to suspect a given trait could be undergoing adaptation. Easily measured indices of change might be important for early detection of adaptation to captivity. If change is detected in the index, this should trigger closer evaluation to identify the underlying trait/s undergoing selection in captivity that could be driving the patterns observed in the index.

Body mass is commonly considered a reasonable index of potential changes arising from adaptation to captivity (O'Regan and Kitchener 2005). Body mass may also be informative about other aspects of life history because it has important implications for individual survival and reproductive success in the wild (Blums *et al.* 2002; Rioux Paquette *et al.* 2014). Furthermore, measurements of body mass are routinely collected in captive breeding programs and mass is relatively repeatable (Broggi *et al.* 2009), making it a potentially useful proxy if more precise data on other traits are unavailable. However, few bird captive breeding programs have evaluated the extent of adaptation to captivity. Whether body mass could serve as an index of potential adaptation to captivity has only been considered in very few species (Chargé *et al.* 2014). Adult bird body mass is highly sensitive to a range of extrinsic and intrinsic factors including age (Limmer and Becker 2007), parental investment (Gaston 2003), variation in food quality during development (Hsu *et al.* 2017), reproductive (Golet and Irons 1999) and pathological status (Møller *et al.* 1998; Newth *et al.* 2016; Norte *et al.* 2013). To disentangle the impacts of adaptation to captivity from other extrinsic and intrinsic factors, detailed data on individual traits is critical.

We evaluate evidence for adaptation to captivity against other factors that could affect adult body mass of Orange-bellied Parrots *Neophema chrysogaster*. The species may be the rarest parrot in the world, and its migratory wild population declined to only two breeding females in 2016 (Stojanovic *et al.* 2018). Bred in captivity since 1986 (Smales *et al.* 2000), parrots have been released annually since 2013 to augment the surviving wild population (Troy and Kuechler 2018). Given the species has been captive-bred for several generations, it is possible that adaptations to captivity have occurred, which might disadvantage released animals. We use 22 years of data from the largest breeding facility of Orange-bellied Parrots to test the hypothesis that the species has morphologically adapted to captivity, using body mass as an index of change. We had no *a priori* reason to expect either an increase or decrease in mass, since both directions of change have been recorded in other captive animals (O'Regan and Kitchener 2005), so we instead simply look for evidence of change. We compare alternative explanations of mass variation by testing eight intrinsic and extrinsic factors (including generations of captive breeding) to identify determinants of adult body mass. Based on evidence from other species, if our hypothesis is true, we predict that adaptation to captivity will result in a changing body mass with increasing number of generations of captive breeding.

Methods

We collated data on all individual Orange-bellied Parrots, both alive and dead, born at or held within the Taroona wildlife center, Tasmania. This is the largest captive breeding facility for the species and is managed by the Tasmanian Government (Department of Environment, Land, Water and Planning 2016). At this facility, changes to animal husbandry practices are confounded with time because they are typically implemented simultaneously for the entire population, so we did not explicitly include aspects of management (e.g. diet) in our analysis.

We used body mass as an index because this data was: (i) available for most individuals born in captivity, and (ii) we assumed this measure is more likely to be repeatable between observers. Other morphometric data (e.g. wing length or other measures of body size) were not recorded for most captive-born parrots, or were collected by multiple staff without quantifying observer error. Data were collated from records collected by keepers over the lifetimes of all individual birds, and we extracted: (1) all records of individual body mass; (2) the mean mass of each individual’s mother (dam) over her lifetime; (3) the maternal lineage (the identity of the founding wild-born dam in the maternal line); (4) the year of birth; (5) the number of offspring produced; (6) the number of generations in captivity; (7) number of maternal generations in captivity; and (8) sex. For variables six and seven we used the species studbook software PMx (Lacy *et al.* 2012) to calculate values for each individual. We selected these variables because they were available for most individuals in the population, and we excluded individuals from analysis if any of these data were missing. We included the dam's lifetime mean mass to account for different investment in offspring by mothers of varying quality (i.e. non-heritable maternal effects). We included maternal lineage to account for heritable components of body mass and excluded individuals whose parentage was uncertain and those descended from founding mothers that produced fewer than five descendants. Year of birth was included as a proxy for factors that could influence environmental conditions experienced in early life that could result in carry-over effects (Burton and Metcalfe 2014). For example disease outbreaks in captivity occurred in 2016 (Raidal and Peters 2017; Stojanovic *et al.* 2018) and in 2017 the diet of the captive population was switched from seed to more nutritious pellets. These and other events experienced during the nestling period of captive Orange-bellied Parrots are confounded with year of birth, and thus we consider this variable a coarse proxy for unmeasured impacts of stochastic events on the population. We excluded the wild-born founders of the captive population from our analysis because it is unclear whether the morphological impacts of being born in the wild are equivalent to those of individuals that are born in captivity.

We used mass as the response variable in a linear mixed model with a normal error distribution, and individual ID was included as a random term to account for repeated measurements from the same birds over their lives. We used stepwise backward selection from a saturated model to derive the most parsimonious model based on ΔAIC >2. Analyses were undertaken in R version 3.6 (R Development Core Team 2019).

Results

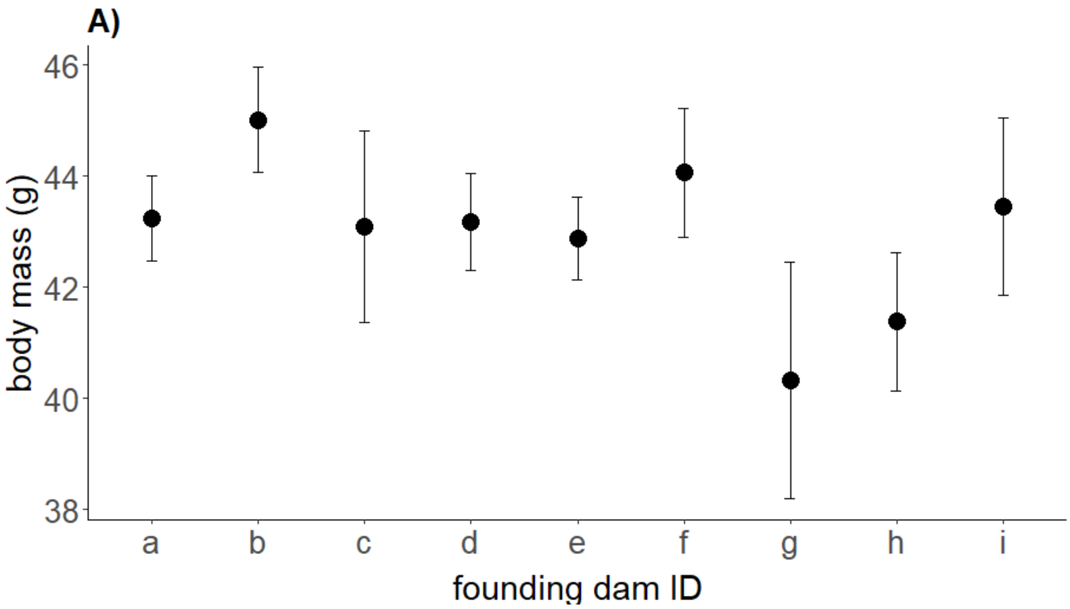
We present data on 374 orange bellied parrots (183 male, 178 female, 13 unknown) born between 1994 and 2018. The birds in our sample were the descendants of nine founding mothers, and were born to 94 individual dams. Only 156 birds in our sample bred, producing on average 6.5 fledglings each. There were 4753 records of body mass, and individuals were weighed on average 14 times (range: 1 – 109) over their lives.

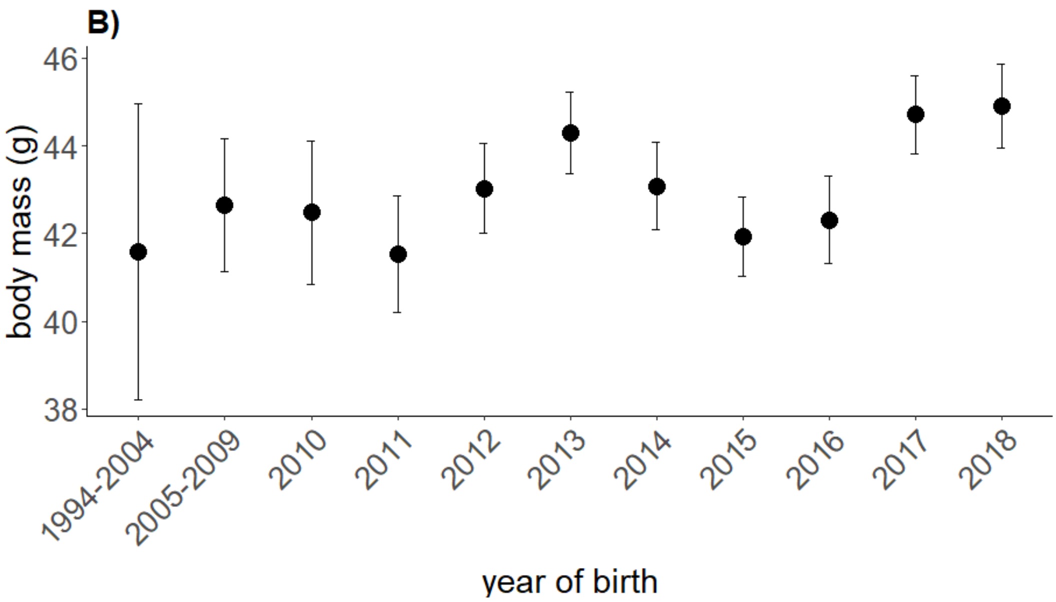
We found no support for the hypothesis that body mass changed with increasing generations in captivity based on model selection using AIC. We report the AIC values of all single-term models and the preferred model in Table 1 for comparison. The most parsimonious model of adult body mass in captive Orange-bellied Parrots included additive effects of mean dam body mass, maternal lineage and year of birth (model estimates and confidence intervals are presented in Figure 1).

Table 1. Models of adult body mass of captive-bred Orange-bellied Parrot ranked by AIC for comparison of each fixed effect against the preferred model (indicated by bold).

Fixed Effects	**df**	**AIC**	**ΔAIC**
founding dam id + year of birth + mean mass of dam	22	22766.58	0
year of birth	13	22803.67	37.09
founding dam id	11	22819.95	53.37
mean mass of dam	4	22837.7	71.12
null	3	22854.4	87.82

sex	5	22855.83	89.25
generations in captivity	4	22856.3	89.72
maternal generations in captivity	4	22859.23	92.65
Number of offspring	4	22860.51	93.93





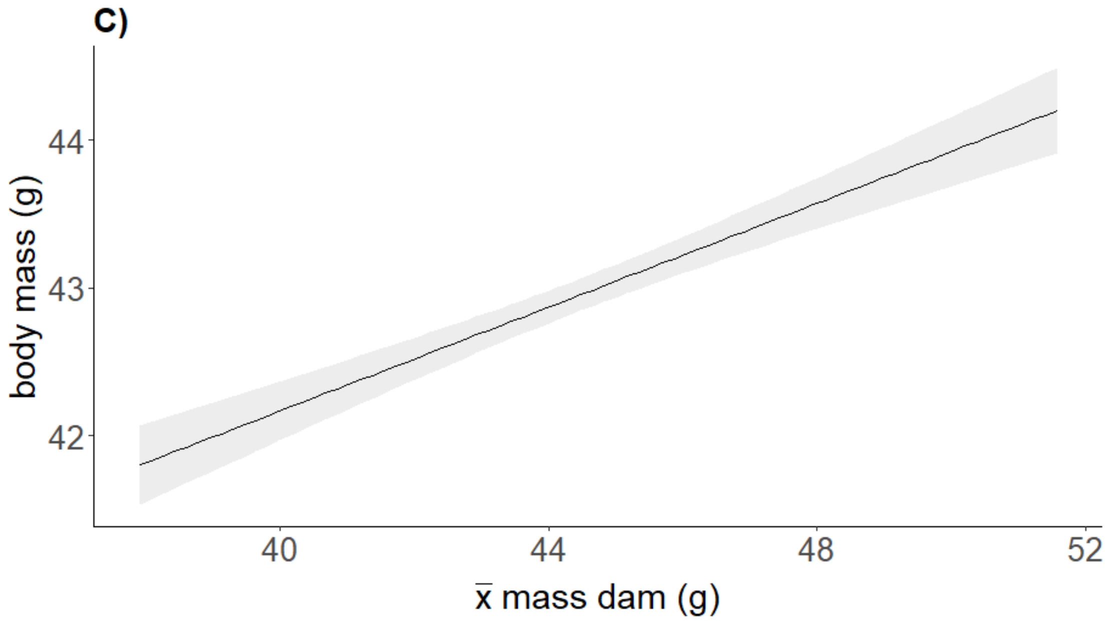


Figure 1. Estimates from the most parsimonious model of adult body mass of captive-bred Orange-bellied Parrots. The figures show relationships between lifetime mean body mass estimates (± 95 % confidence intervals) of individual birds and their: A) founding dam ID, (B) year of birth, and (C) lifetime mean body mass of their dam.

Discussion

We found no support for our hypothesis that body mass of Orange-bellied Parrots changed with increasing generations of captive breeding. If morphological adaptation to captivity has occurred in Orange-bellied Parrots, our results suggest that body mass performs poorly as an index for detecting potential changes. However, we did find relationships between body mass and the other variables we measured. Maternal effects and year of birth were the best predictors of adult body mass of captive-bred Orange-bellied Parrots in our sample. Maternal effects were both direct (heavier mothers produced heavier offspring) and indirect (different founding mothers produced heavier or lighter descendants), but were also influenced by circumstances in the year of birth. For example, Orange-bellied Parrots born in 2017 and 2018 were the heaviest individuals recorded in the study, and this corresponds to a change in diet to a higher quality extruded pellet diet in those years. Interestingly in 2016 when a disease outbreak affected the captive population (Stojanovic *et al.* 2018), mean adult body mass of birds born in that year (42.4 g) was not lower than the population mean for other years, but why this is so is unclear. These results are important because they suggest that despite the benign conditions in which the captive population is maintained (*ad libitum* food, protection from predators, prevention of migration), there are still intrinsic and extrinsic factors that affect body mass of adult parrots. Given the importance of adult body mass in fitness and reproductive success of wild birds (Cornioley *et al.* 2017), understanding the factors that influence this trait in captivity may be particularly important if individuals are released to the wild. For example, if lower body mass predicts survival in the wild (Ronget *et al.* 2018), individuals from lightweight maternal lineages or cohorts may be disadvantaged.

Maladaptive morphological changes may result in failure to achieve conservation objectives (e.g. genetic rescue, sex ratio correction) if survival of captive-bred animals is impaired. Minimising adaptation to captivity is critical if release is the intended purpose of the captive breeding program. Since the commencement of the Orange-bellied Parrot captive breeding program, a mean kinship minimization strategy has been implemented to maintain wild-sourced genetic diversity (Ballou *et al.* 2010) complemented with molecular techniques in more recent years (Hogg, C., unpublished data). These pedigree-based techniques minimize adaptation to captivity (Frankham 2008) so it is perhaps unsurprising that morphological changes would be difficult to detect using a coarse index like body mass. Although body mass has been used to detect adaptation to captivity in other species (O'Regan and Kitchener 2005), this application is less useful in Orange-bellied Parrots. Based on our results, either adaptation to captivity has not occurred, or if it has, body mass is too coarse an index to detect it. Future studies looking for evidence of adaptation to captivity should directly measure traits of interest. For example, (i) dietary differences could drive adaptation of bill shape and gut morphology, (ii) flight in aviaries may affect wing shape, (iii) social isolation may affect song learning, or (iv) floor design (e.g. suspended aviaries) may affect foot/leg morphology. However, these traits may poorly correlate with body mass and thus go undetected. We suggest that the ecology and behavior of wild species be considered in context of the captive environment, so that traits that are potentially vulnerable to adaptation in captivity can be identified and monitored. Detailed morphological and behavioral data were unavailable for most parrots in our study and substantial new effort to collect morphological data may be necessary to identify potential adaptations to captivity. Captive breeding programs aimed at producing animals for release to the wild should aim to monitor adaptation to captivity. This could be achieved by establishing a database of repeated measures of multiple traits of interest, for both captive and wild individuals, to identify an ideal morphological base line. Most captive breeding programs involve different staff that handle and measure animals over the lifetime of the project. We stress the need to quantify observer error. By keeping a reference set of specimens to estimate measurement error among staff, recovery programs could ensure that enough data suitable for analysis might be available for future studies of morphological adaptation to captivity.

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Data Availability Statement

Data are held by the Tasmanian Government Orange-bellied Parrot recovery project.

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