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Sex and morph differences in age-dependent trait changes in a polymorphic songbird.

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ABSTRACT

There is growing evidence of important variation in how animals age, in particular in how the expression of traits changes with age among different species and populations. However, less is known about variation within populations, which may include variation in ageing patterns between different types of individuals (e.g. sexes or distinct polymorphisms) and between different types of traits (e.g. general traits versus those used in social signalling contexts). We used six years of longitudinal data to examine age-related changes in trait expression in a captive population of Gouldian finches (*Erythrura gouldiae*), a socially monogamous songbird with genetically determined colour morphs that differ in behaviour and physiology. We contrasted ageing patterns of different types of traits (social signalling versus size-related) in both sexes and in two colour morphs, using a mixed model approach to account for both within- and between-individual effects. We found pronounced sex differences in the change in social signalling traits with age, showing a quadratic pattern in males, but not changing with age in females. In contrast, we observed no sex-specific ageing patterns in size traits. We also found subtle morph differences in how size-related traits changed with age, with black morphs stable or increasing with age while red morphs showing a decline with age. Finally, we found interesting sex by morph interactions in the measures in one important social signal (headband width). These results highlight the importance of using within-individual approaches to understand ageing patterns across types of individuals (sex, morph, etc.) and the need for further research on the ageing patterns of traits that experience different selective pressures.

INTRODUCTION

There is growing evidence that animals, especially vertebrates, exhibit age-related changes in the level of trait expression (Jones et al. 2008; Monaghan et al. 2008; Nussey et al. 2013). It is also clear that there is huge variation between populations and species in those ageing patterns (Clutton-Brock and Isvaran 2007; Jones et al. 2008; Monaghan et al. 2008; Nussey et al. 2013). However, less is known about variation within populations: between different types of trait (e.g. under natural versus sexual selection) or different types of individual (e.g. the two sexes). Further, species with phenotypic morphs that exhibit different life history strategies offer a particularly interesting angle for examining the role of life history in shaping ageing patterns, and an especially powerful way of testing for the implications of investment in traits that are important for social competition versus survival.

Considerable theoretical and empirical work has sought to understand whether and how trait expression changes with age. For traits important in social competition and reproductive contexts, some hypotheses predict that the net benefits of increased investment in reproductive effort increase with age (Kirkwood and Rose 1991), thus allocation of resources to traits that increase reproductive success (sexually-selected traits, competitive traits, fecundity, etc.) should also increase with age, e.g. terminal investment (Clutton-Brock 1984). However, because such traits are expected to be costly and condition-dependent (Zahavi 1975; Hamilton and Zuk 1982; Andersson 1994; Nussey et al. 2009), they may also be especially sensitive to senescent declines in physiology (Møller and de Lope 2002; Nussey et al. 2009; Evans et al. 2011; Kervinen et al. 2015), and thus may be the first traits to exhibit declines late in life, and these constraints may drive the observed decrease in reproductive performance. Other models argue that in many taxa, a reduction of investment in reproductive traits in animals is beneficial (McNamara et al. 2009). In these models, it is condition, rather than age that limits future performance, and by reducing investment in reproduction (which lowers condition), individuals can prolong their reproductive lifespan (McNamara et al. 2009). Thus in this model, reductions in reproductive trait investment are adaptive, rather than driven by constraints. For instance, in zebra finches, age is unrelated to bill redness, but in the final year of life, males show a terminal decline just before death, but no increase or decline prior to that point (Simons et al. 2016). In contrast, general morphological traits, which often experience different selective pressures than reproductive or competitive traits, are favoured to follow a different pattern of age-related change (Galván and Møller 2009; Evans et al. 2011; Nussey et al. 2013).

Trait differences in ageing patterns have important implications for understanding the evolution of senescence. Researchers have recently begun to investigate differences in age-related in multiple traits, e.g. rutting behaviour and antler size in red deer (*Cervus elaphus*) (Nussey et al. 2009) and an array of sexually selected traits in black grouse (*Tetrao tetrix*) (Kervinen et al. 2015). However, there are few data contrasting the ageing patterns in different types of traits, i.e. ornaments or signals used in social contexts and general morphological traits (but see Galván and Møller 2009; Evans et al. 2011). Males and females often face sex-specific selective pressures (Trivers 1972; Stearns 1992). These differences could favour differences in age-related trait expression, particularly for traits that are important in reproductive contexts or experience sex-specific selection (Clutton-Brock and Isvaran 2007; Bonduriansky et al. 2008; Nussey et al. 2009; Kervinen et al. 2015). For example, males might benefit from increased allocation to traits important for sexual or social competition (signalling traits hereafter), while females that invest heavily in signalling traits may suffer due to reduced energy available for investment in offspring production, or may benefit, due to increased resource access (Cain & Rosvall, 2014). However, relatively little is known about the ubiquity of sex differences in how trait expression changes with age. If female expression of signalling traits is due to shared genetics and strong selection on males (Lande 1980a), and thus regulated by the same mechanisms, males and females would be expected to age in a similar fashion. However, if the traits are independently shaped by sex-specific selective pressures, we may see the sexes ageing differently, particularly in traits that serve sex-specific roles.

Species with distinct behavioural or morphological morphs that use contrasting life-history strategies offer a particularly powerful way of examining the effect of life history strategies on ageing patterns and senescence (Sinervo and Svensson 1998; Sinervo and Zamudio 2001). Heavy investment in competition or signalling traits often comes at a cost in terms of survival (Williams 1966), which may favour different ageing patterns or even differences in longevity. In many polymorphic species, one morph often invests more in competitive traits (ornaments, aggression, etc.) (Lank et al. 1995; Comendant et al. 2003; Tuttle 2003; Pryke and Griffith 2009b). This difference may lead to morph-specific differences in ageing patterns that are as strong, or stronger, than sex differences. Such differences may be important in understanding how different life-history strategies can coexist, and how a less competitive morph can persist in the face of a morph with a competitive advantage (Sinervo and Svensson 1998; Comendant et al. 2003; Kokko et al. 2014).

At the population level, average values of performance and trait expression generally increase with age, reach a maximum, and then decline later in life (Kirkwood and Rose 1991; Jones et al. 2008; Bouwhuis et al. 2009). There are two non-mutually exclusive processes that could explain this general pattern. First, population level changes may be due to within-individual changes in trait expression. In this scenario, individuals increase trait investment as they age, either because they have better access to resources, or optimal resource allocation favours increased investment late in life (Kirkwood and Rose 1991; Balbontin et al. 2007; Bouwhuis et al. 2009; Monaghan et al. 2008; Jones et al. 2008). The other process is selective disappearance: individuals that vary in quality may appear or disappear from the population in a non-random, selective manner (van de Pol and Verhulst 2006; Hayward et al. 2012; Salmón et al. 2017). For example, animals with low levels of trait expression may be lower quality, and die or leave the population sooner. As a result, only animals with high levels of trait expression live to old age. Selective disappearance can drive population-level associations between age and trait expression due to between-individual effects, rather than within-individual effects, and can mask within-individual changes or senescence (van de Pol and Verhulst 2006; van de Pol and Wright 2009; Bouwhuis et al. 2009; Nussey et al. 2009; Kervinen et al. 2015). Consequently, it is important to test for such between-individual changes in trait expression in order to understand the mechanisms driving population-level observations.

Here we use longitudinal data on several morphological traits from six years of a large, captive population of Gouldian finches (*Erythrura gouldiae*) to address these issues. The Gouldian finch is a small, brightly coloured, tropical, Australian estrildid finch with a socially monogamous mating system and a relatively short lifespan (Brush and Seifried 1968; Woinarski and Tidemann 1992; Tidemann et al. 1999). In the wild, individuals are rarely observed for more than one breeding season (~15 months), though this may be because they are highly nomadic, but in captivity, they can live up to six years (this study, Tidemann 2010). In Gouldian finches, both sexes have a bright yellow belly, an ultraviolet/violet breast, a blue/ultraviolet headband, and green wings and back (Figure 1) (Brush and Seifried 1968; Pryke et al. 2007). Although both sexes are colourful, males display brighter plumage and longer tail streamers, which provide benefits in mate attraction (Pryke and Griffith 2006). It is currently unclear whether females possess bright plumage and tail streamers to advertise quality, to signal to competitors, or because of strong between-sex genetic correlations. Both sexes also occur in three discrete, genetically-determined head-colour morphs (Figure 1, red, black or yellow) (Brush and Seifried 1968; Tidemann et al. 1999, Kim et al. 2019). Red or black morph is determined by the *Red* locus on the Z-chromosome, with alleles R/r: the R allele is dominant, such that red males can be either homozygous (ZR/ZR) or heterozygous (ZR/Zr), and black males are ZrZr; red females are ZR and black females Zr (Pryke 2010; Kim et al. 2019). The yellow morph is a very rare in free-living populations (<0.1%; Brush & Seifried, 1968; Franklin & Dostine, 2000) and occurs due to an interaction between the *Red* locus and an autosomal gene that regulates carotenoid deposition (Pryke 2007). The morphs exhibit different life-history patterns: red morphs of both sexes are more aggressive and dominant to the other morphs in competitive scenarios, but also show reductions in parental care and elevated androgens and glucocorticoids in these contexts (Brazill-Boast et al. 2012; Pryke and Griffith 2006; Pryke 2007; Pryke et al. 2007; Pryke and Griffith 2009b; Pryke et al. 2012; Cain and Pryke 2017a, b). Gouldian finches also show sex and morph specific responses to energetically demanding conditions (heatwaves and moult; Fragueira et al. 2019), and sex and morph specific differences in risk-taking behaviours (Fragueira and Beaulieu 2019; O'Reilly et al. 2019), although there is no difference between red and black-headed males in either resting or maximal metabolic rate (Buttemer et al 2021).

The existence of bright plumage in both sexes makes this species an excellent model for investigating sex-specific and morph-specific, age-dependent expression of secondary sexual traits, something that would not be possible in a species with sex-limited trait expression. Here, we determine whether traits change across age, and whether those changes differ according to sex or morph, and whether changes are due to within-individual variation over time, or the selective disappearance of some phenotypes over cohorts of different age (between-individual effects).

METHODS

Study species

The Gouldian finch (family *Estrildidae*) is an endangered, endemic Australian finch found in savannah woodlands of tropical Northern Australia (Pryke and Griffith 2007). The data used here were compiled from monitoring of six years (and nearly 5,000 individuals) of captive wild-type Gouldian finches housed in captivity at the Save the Gouldian Fund Research Facility in Martinsville, Australia, from 2005 to 2011. The initial population was founded in 2005 from 278 wild-type individuals acquired from aviculturists located throughout Australia (Pryke and Griffith 2007). In this analysis we included only birds born in captivity. Birds left the study due to death or rehoming with aviculturists. Birds were bred in large free-flight aviaries (15m long, 5.5m wide, 3.8m high) in small groups, or in breeding cages (1.2 m^3). A complete pedigree has been constructed for other analyses and preliminary analysis suggests inbreeding was not an issue in this population (K. Cain, unpubl. data). All birds were provided with artificial nest boxes designed to mimic the hollows used in the wild and with ad libitum access to dry seed and various fresh food supplements. All aspects of the study were approved by Animal Ethics Committees at the University of New South Wales (2005-2008) or Macquarie University (2008-2011).

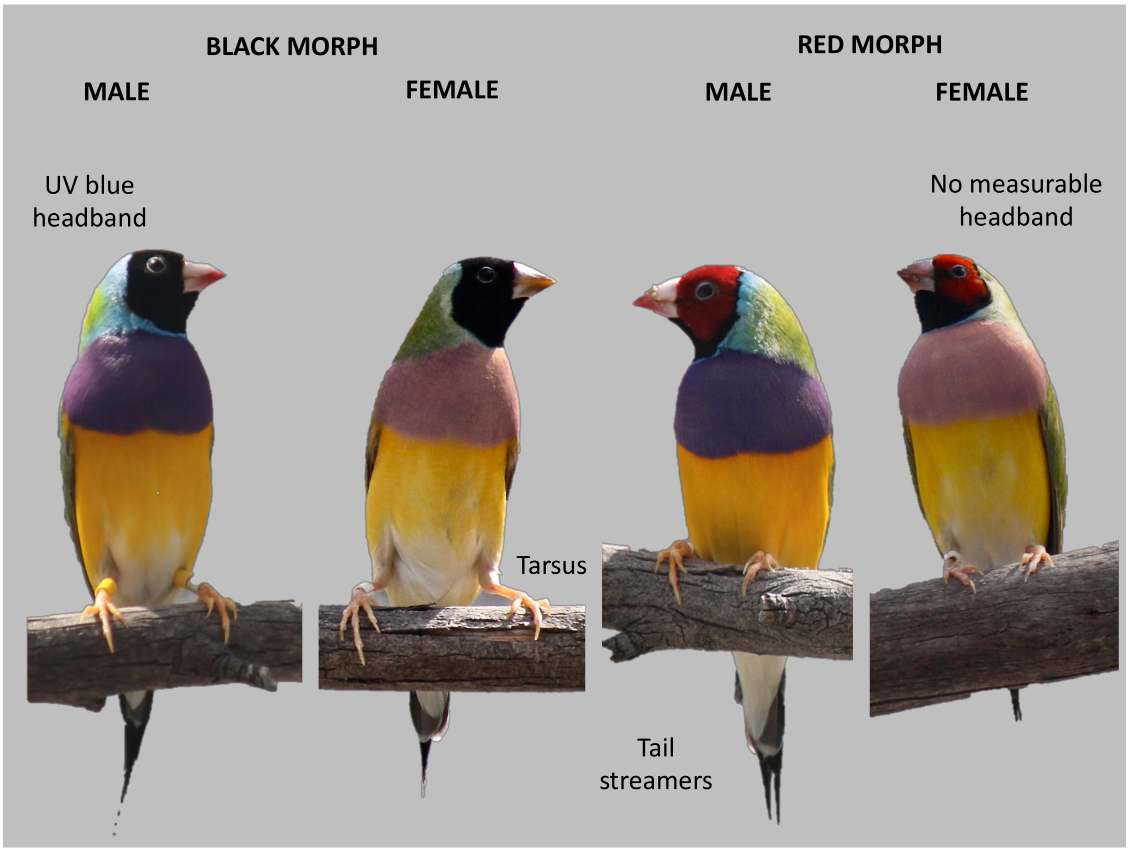


Figure 1: Male and female Gouldian finches of the black and red colour morphs illustrating limited sexual dichromatism, colour morphs, and signalling traits.

Gouldian finches occur in three colour morphs: red, yellow, and black. However, as yellow is very rare in the wild (<1%) and in our captive populations, we focus on the two common morphs. The genotypes for females and black males can be directly inferred from the phenotype (i.e., red females – ZR, black females – Zr, black males - ZrZr); red male genotypes (either ZRZR or ZRZr) were determined from pedigrees and knowledge of parental phenotype (Pryke 2010, Pryke et al. 2010). The study population was used for a number of experiments examining the role of colour in social dominance (behavioural observation studies) and mate choice contexts, and the effects of diet, hormone levels or disassortative pairing on reproductive investment, all in the context of the colour morphs. We describe these experiments and test for their effect on trait expression in the supplemental material (Appendix 1 Experimental effects).

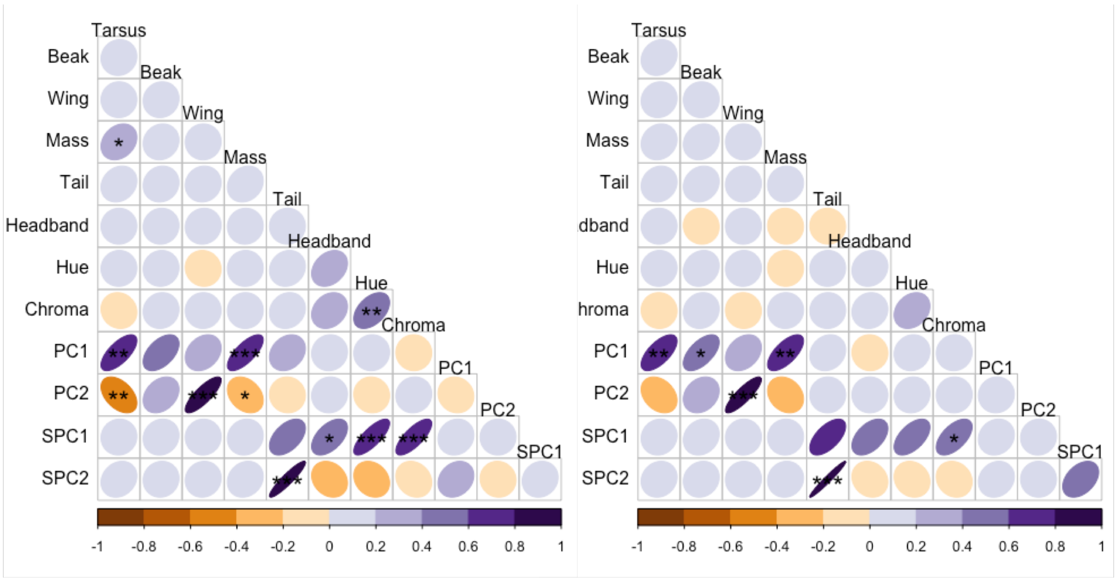
Trait measures

For each individual in the dataset, we measured a range of morphological traits. At least once each year, we measured four size-related traits ('size traits', Fig 1): *tarsus length* and culmen *(beak) length*, to the nearest 0.1mm, *wing length*, to the nearest 0.5mm, and *body mass* to the nearest 0.1g. We did not expect large changes in tarsus length with age, although in some songbirds tarsus length does show age related changes (Smith et al. 1986). We also measured four plumage (or 'signalling') traits related to social signalling (Fig 1, (Pryke and Griffith 2006; Pryke 2007; Pryke and Griffith 2009b). Total *tail length* was estimated from the average of the two tail pinfeathers. The width of the blue/UV headband (to the nearest 0.1mm) was measured using callipers (*headband width*). Spectral reflectance of the ultraviolet (UV)/blue headband was determined using a spectrometer, and from this we calculated *headband hue* (spectral location) and *headband chroma* (spectral purity) (see Pryke 2001, Pryke and Griffith 2006; Pryke 2007). Generally, the morphological and plumage measures were taken just prior to the breeding season each year (~ October/November) and before any natural or experimental pairing. Offspring were typically banded in Jan/Feb of each year. Traits were generally highly repeatable: Table S2 provides estimates of the proportion of variance that was explained by ID after accounting for the fixed effects.

A large portion of females (~900 of 1444) had headbands that were not too small to measure accurately. Whether or not a female had a measurable headband in a given year did not change across her lifetime: of 2144 records of headband presence or absence, females switched from present (>1mm wide) to absent (<1mm in width) only 9 times (0.4%), and there were no cases of switching from absent to present. Black morph females were more likely to have a measurable headband (41% vs 35%; Chi-sq test, $X^2 = 7.5$, df=1, p =0.006).

Statistical analysis

To reduce the number of traits examined, we used principal components analysis (PCA) using the correlation matrix. Because theory predicts that traits used in signalling contexts should vary with age and sex more than those that are not known to be important in social contexts, we examine the two types of traits ('signalling' and 'size' respectively) independently. We performed two PCAs: one for the size traits, and one for the signalling traits, and extracted the two main principal components (PC1 & PC2) for each. Loadings and eigenvalues for both PCAs are reported in Table S1. Briefly, tarsus length and mass loaded on Size PC1 (eigenvalue 1.1, 32% of variance explained), whereas wing and beak length after tarsus and mass were accounted for, loaded on Size PC2 (eigenvalue 1.0, 25% of variance explained). Signalling PC1 was largely determined by the three measures of the blue headband (width, hue, chroma) (eigenvalue 1.65, 63% of variance explained), whereas Signalling PC2 reflected the length of tail streamers, after the colour effects, (eigenvalue 0.84, 18% of variance explained). We then tested for correlations between Signalling and Size PCs, to investigate associations between the two types of traits (Figure 1). We used individuals' PC values to address our questions. Because only a portion of females had measurable headbands, only that portion of females received Signalling PC scores.



A) Male correlation Matrix B) Female correlation Matrix

Fig* 2 – Correlation matrices** of male (Panel A) and female (Panel B) traits used in principal component analyses illustrating relationships between traits and PC scores (PC 1 and 2 for size traits; SPC 1 and 2 for signalling traits); asterisks indicate p-value (for P<0.001, ** for P< 0.01, * for P< 0.05). Neither Size P2 was related to either Signalling PC in either sex. The presence/absence of a headband was unrelated to either Size PC score in females (*t*-tests, $p > 0.05$ in both cases).

To determine how different types of traits age, and whether there are sex or morph differences in those ageing patterns, we built a series of linear mixed models with Gaussian error distributions. The 4 PC scores were set as response variables, fitted models that included sex, morph (red or black), age, age squared (quadratic), and age they left the population (disappearance), as well as interactions between sex and age measures, and morph and age measures.

To account for the repeated measures, year (2006-2011) and individual ID were included as random factors. We also ran similar models using each original trait that was used in the PCA analysis (Table S2). Because we wanted to determine whether the observed age-related changes in trait expression were due to within-individual differences, we controlled for selective disappearance by including an estimate of each individual's total number of years present in the population as a covariate in these models (van de Pol and Verhulst, 2006). The last year that a bird was measured was used to estimate its age when it left the population. Including disappearance tests for between-individual effects, excluding disappearance from the model could lead to false conclusions about how individuals age if individuals leave the populations in a non-random manner. In our study, birds left the population either due to death, or to being transferred to other breeding populations. 'Disappearance' may therefore not be biologically meaningful, so we do not assign any biological relevance to effects of this variable. However, including it allows us to distinguish between within-individual levels of change in trait expression and between individual effects caused by animals leaving the population. Ideally, we would have also included a random slopes term in the model to account for individuals having different relationships between trait expression and age (van de Pol and Verhulst, 2006; Schielzeth & Forstmeir 2009), but doing so resulted in models that repeatedly failed to converge. Red males may be homo- or heterozygous at the *Red* locus, thus we repeated the PC score analysis using genotype instead of morph for males only (Table S3).

Throughout, we report results from full models with all variables; there was no model selection or variable removal. All analyses and figure generation (except Figure 1) were completed in R (3.6.3) using the following packages: AICcmodavg (Mazerolle 2020), lme4 (Bates et al. 2014), effects (Fox 2018), ggdist (Kay 2021), corrplot (Wei, 2021), and ggplot2 (Wickham 2016).

RESULTS

Ageing patterns differ according to sex

There was no evidence of sex differences in age-related changes in either of the two Size PCs (Figure 3A and B, Table 1a). In contrast, both Signalling PC1 and PC2 showed significant interactions between sex and age measures (Table 1b), reflecting differences in the degree of change with age, i.e. there were greater age-related increases in males than in females (Figure 3C and D). Signalling PC1 also showed sex differences in the quadratic relationship with age: decreasing with the quadratic term for age in males but not in females. These effects were significant after controlling for sex-specific selective disappearance. Females with higher Signalling PC scores and higher Size PC1 scores left the population earlier than lower scoring females.

These patterns were generally supported when looking at specific traits (Table S2). Tarsus, beak, mass and wing showed no sex differences in aging patterns. Headband width also showed no sex differences in aging patterns and no age related changes in general. However, chroma, hue and tail length all showed some sex differences in aging, increasing overall in males, and showing a decrease with quadratic age in male chroma and tail length.

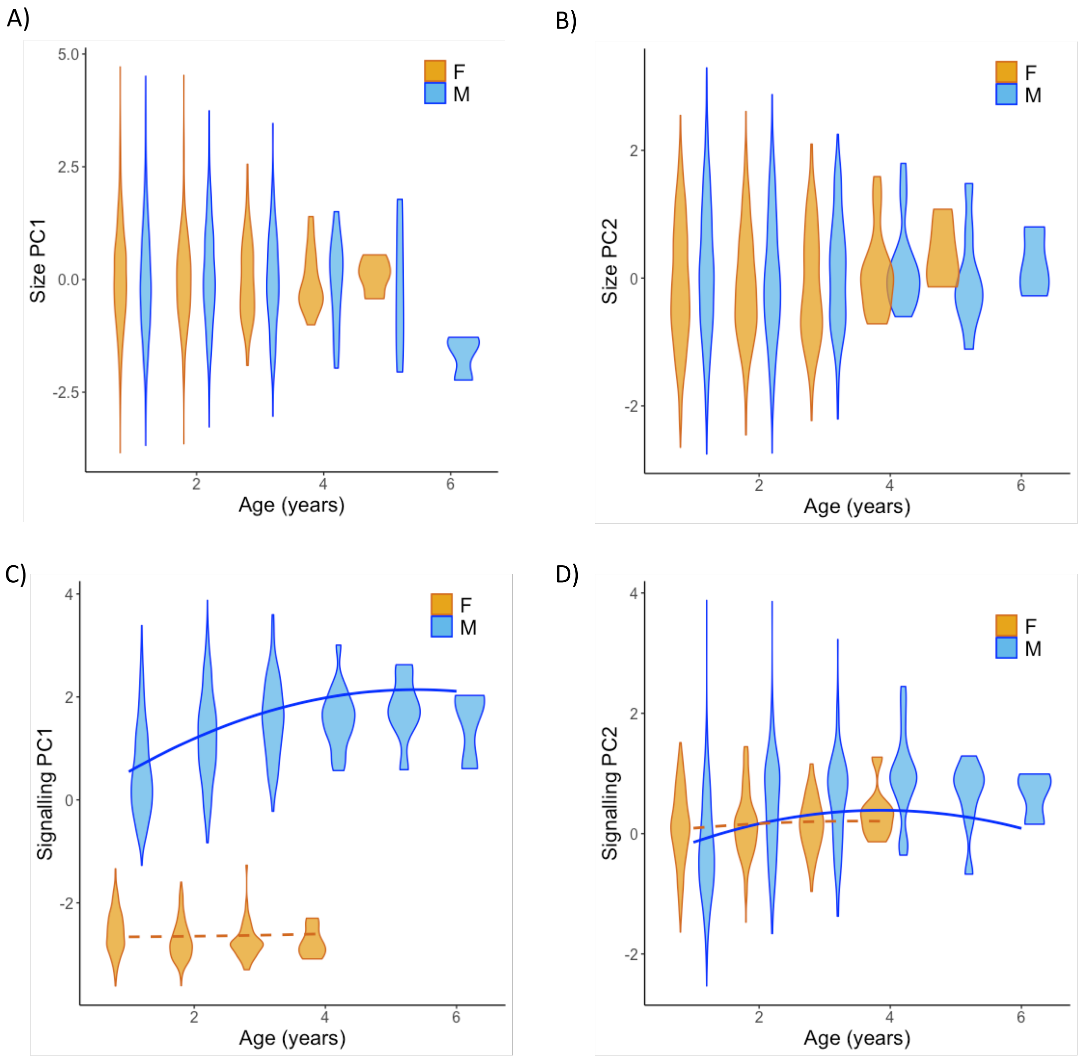


Figure 3: Changes in the expression of size and signalling traits across age, according to sex (F, Female: orange, dashed line; M, male: blue, solid line). Raw data is shown using violin plots (similar to a boxplot, but includes the full distribution of the data) for each age group. Lines are generated using predicted values from models (Table 1) and include age, quadratic age, last age measured (disappearance) and random effects. These lines indicate within-individual change as individuals age, while the violin plots show population level changes in trait levels with age (between-individual effects). Panels A and B illustrate size traits; panels C and D illustrate signalling traits.

Some ageing patterns differ according to morph

We observed morph differences in age-related changes in both of the Size PCs, increasing early in life in red morphs, followed by a steep decline, while black morphs increased later in life (Figure 4A and B, Table 1a). In contrast, neither Signalling PC1 or PC2 showed significant interactions between morph and age measures (Table 1b). These effects were significant after controlling for non-random selective disappearance.

The morph specific ageing patterns in Size PCs were driven by wing length changes with age. In black morphs, there was a slight decrease followed by an increase with age. In contrast, red morphs showed an initial increase followed by a decrease (Figure 3, Table S2). Morph genotype is sex-linked; all females are homozygous while males can be homozygous black, homozygous red or heterozygous red. When we examined genotype differences in males, we found a similar pattern – black males increasing across age, homozygous red male decreasing across age and heterozygous red males showing little change – though the effects were subtle (Figure S1, Table S3).

Though headband width showed no age-related change, we did observe a significant interaction between morph and sex. In males, black morphs had large headbands, while in females, red morphs had larger headbands (Figure 4C, Table S2).

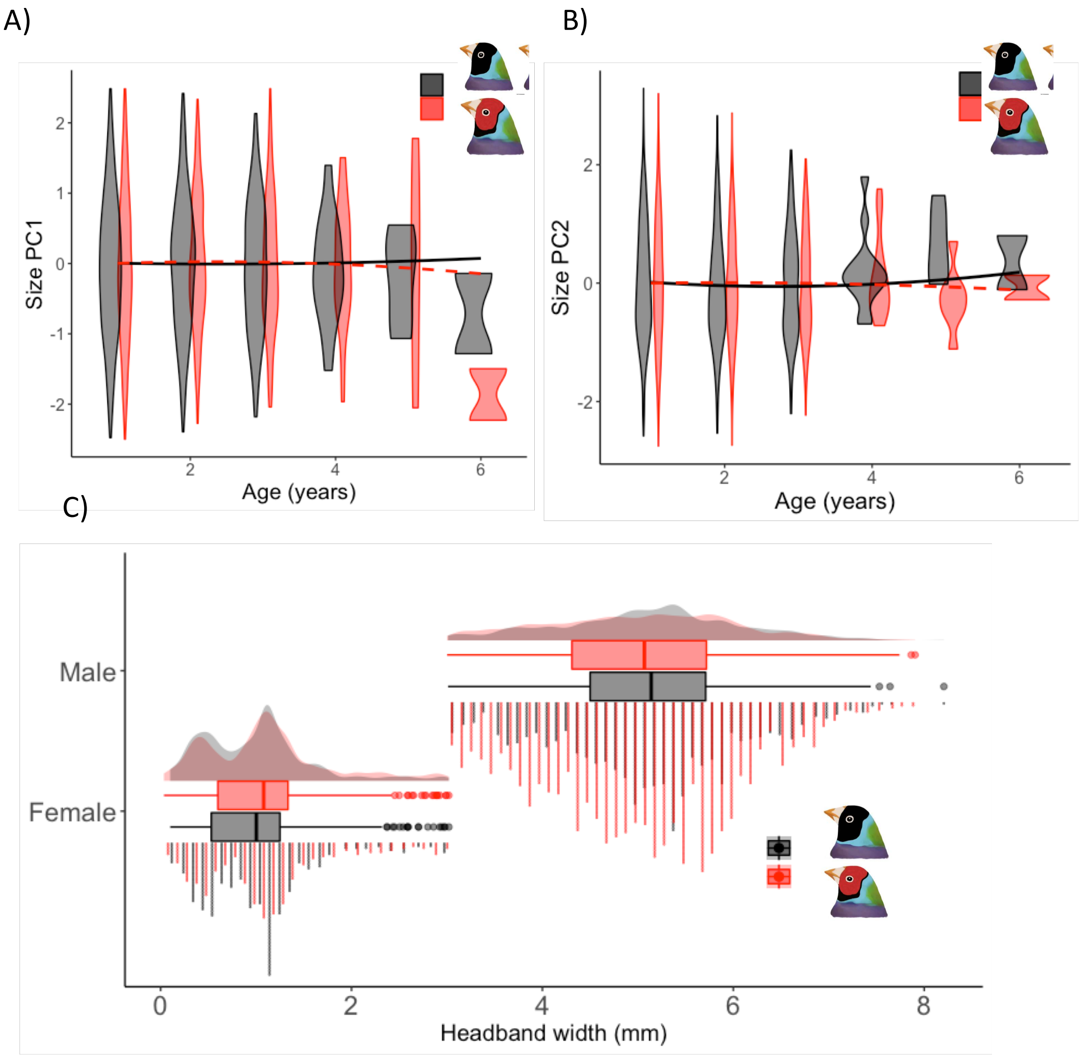


Figure 4 – Panels A and B: Morph differences in age-related changes in trait expression; sexes plotted together (2071 observations of black morphs, 2897 observations of red morphs). Lines are generated using predicted values from models (Table 1) and include age, quadratic age and last age measured (disappearance), and ID as a random effect; for visual clarity the y-axis is constrained (-2.5 to 2.5). These lines indicate how traits change as individuals age, after accounting for selective disappearance: black solid lines are black morphs, red, dashed lines are red morphs. Note the scale of the y-axis is different from Figure 2, and differs across panels. Panel C illustrates sex by morph interaction in headband width (see Table 1) using boxplots and raincloud plots (half-density distribution

plot – similar to histogram or violin plot), points are individual data points. Females without measurable headbands were excluded (796 observations of females, 2769 observations of males). Illustration of morphs by IG Moran.

DISCUSSION

We tested for morph and sex differences in how expression of size and signalling traits changed across life in a polymorphic songbird. We found no evidence of sex-difference in how size-related traits change across age, but found substantial sex differences in how signalling traits changed with age, indicating increases in males and no change in females. We also observed morph differences in how size traits changed with age, while in females there was some evidence of morph differences in signalling traits and how they age. Finally, there were sex difference in how morphs express headband width – larger in red females and black males. By using longitudinal data, we were able to determine which population-level age differences were due to within-individual changes in trait expression rather than simply selective disappearance of high/low quality individuals.

Age-related changes in trait expression

Classic theory on ageing generally argues that changes with age are due to coordinated changes in physiological function across the phenotype (Williams 1957; Hamilton 1966). More recent data suggest that different physiological systems might follow different patterns (Herndon et al. 2002; Amdam and Page 2005; Grotewiel et al. 2005; Burger and Promislow 2006). Our findings add to this pattern and suggest that not all traits change in a coordinated fashion. We observed only limited age-related changes in size traits, and no sex differences in the way those traits change across age. However, signalling traits showed marked sex-dependent changes with age – increasing with age in males, but not changing in females. Female expression of ornaments may be partially driven by cross-sex genetic correlations in trait expression, however, the observed sex difference in ageing patterns suggests that male and female trait expression are sufficiently independent to follow different ageing trajectories. Together, these two findings provide rare evidence that the physiological systems that underlie senescence of different traits may be uncoupled (Nussey et al. 2013).

Age-related changes in signalling traits in males

In males, the expression of sexually selected traits is often higher in older individuals (Andersson 1994), and theoretical models suggest that an increase in the expression of sexually selected traits is favoured in a wide range of contexts (Kokko 1997). Empirical studies have reported the predicted increases in signalling traits across age, including in structural colouration (blue, metallic, or UV reflective feathers) (Keyser and Hill 2000; Komdeur et al. 2005; Siefferman and Hill 2005; Delhey and Kempenaers 2006; Bitton and Dawson 2008). However, these population-level patterns may be due to age-related changes in trait expression, i.e. males becoming more elaborate as they age (Doucet et al. 2007), or to between-individual differences in survival, i.e. high-quality males surviving longer (Jennions et al. 2001; van de Pol and Wright 2009), or both. In our longitudinal study, we found evidence that male signalling trait expression showed significant within-individual increases with age as well as non-random disappearance of less ornamented males and more ornamented females (Fig 4).

Though we observed increases in signalling trait expression with age, in very old males trait expression stabilised or decreased (Table 1, S2), suggesting that senescence plays a role (Møller and de Lope 2002; Jones et al. 2008; Nussey et al. 2008; Galván and Møller 2009). Many studies have reported declines in male reproductive function late in life, but in most cases, sexually selected traits such as ornaments and armaments appear to plateau rather than decline: e.g. in male red deer (*Cervus elaphus)*, antler size is relatively unaffected by age in late life (Nussey et al. 2009), male barn swallows increase plumage melanisation consistently across age (Galván and Møller 2009), in collared flycatchers (*Ficedula albicollis*), an ornamental trait (white wing patch) increased across age in both sexes (Evans et al. 2011), and in houbara bustards (*Chlamydotis undulata*), male display effort appears to remain stable throughout life (Preston et al. 2011). In contrast, senescent declines in signalling traits following a peak in middle age have been reported in two studies: in male black grouse (*Tetrao tetrix*), both morphological and behavioural traits associated with sexual competition declined late in life (Kervinen et al. 2015) and in barn swallows, tail length decreased at old age (Balbontin et al. 2011). Further research is clearly needed, in a variety of taxa and mating systems, to determine when and why we observe senescent declines in some traits and species, but not others.

Age-related changes in signalling traits in females

There has been considerable work done on female reproductive investment, and how that might change with age (e.g., Bérubé et al. 1999; Bowen et al. 2006; Nussey et al. 2006; Cooper et al. 2020). However, relatively little empirical data is available on how female morphological traits might change with age, and even less has focused on female expression of signalling or competitive traits with age; e.g. song, armaments, and ornaments (West-Eberhard 1979; Riebel et al. 2005; Cain and Ketterson 2012; Cain and Ketterson 2013; Tobias et al. 2012; Cain and Rosvall 2014; Doutrelant et al. 2019). The few studies that have examined female colouration across age report conflicting results. Some studies report a lack of change in blue plumage, e.g. in bluebirds (Siefferman et al. 2005), blue tits (Henderson et al. 2013), and blue-throats (*Luscinia s. svecic*) (Amundsen et al. 1997). In contrast, in pied flycatchers (*Ficedula hypoleuca*), ornamentation in the form of white plumage patches and mantle colour increased with age in both sexes (Evans et al. 2011; Potti et al. 2014). Similar data exists in other signalling traits. For instance, female song is an important social signal related to reproductive success in female superb fairywrens (*Malurus cyaneus*; Cain et al 2016) and New Zealand bellbirds (*Anthornis melanura;* Brunton et al. 2016), and song diversity has been shown to increase with age in both sexes in superb starlings (*Lamprotornis superbus;* Keen et al 2016), but repertoire size declined with age in European starlings (*Sturnus vulgaris;* Pavlova et al. 2010). Further investigation into ageing patterns in female signalling traits is clearly needed.

Morph differences

Unexpectedly, we observed morph differences in how some size-related traits changed with age. The effects were subtle, but black morphs showed initially lower measures, followed by a steady increase through life. In contrast, red morphs measures increased initially but then declined. These patterns were mirrored in the homozygous red and black males, but not the heterozygous red males. These differences may reflect different life-history strategies. Red morphs are generally dominant to black, and can outcompete black morphs for breeding cavities (Brazill-Boast et al 2013), and pigment based traits, especially carotenoid based colours, are signals in contests (Young et al. 2016). However, red morphs (males) suffer in terms of more intense physiological responses to challenges, including hormone and immune function, and reductions in parental care (Pryke et al. 2012), although there are no differences in either basal or maximal metabolic rate in the two morphs (Buttemer et al 2021). The differences observed between the two morphs may counter some of the adaptive benefits of competitive trait expression observed in previous studies of this species (Brazill-Boast et al. 2013; Kokko et al. 2015; Pryke and Griffith 2006, 2009b; Pryke 2007; Pryke et al. 2012), and so may be important in contributing to the maintenance of polymorphism and variation in this species.

Interestingly, though we generally did not find strong morph differences in signalling trait expression, we did observe a significant sex-specific difference between morphs in headband width. Red females had significantly larger headband measures than black females; black males had larger headbands than red males. The role of the headband in Gouldian finches, and thus the relevance of morph differences in headband width, is currently unclear. Generally blue colours are structurally produced and considered a potential indicator of quality (Keyser & Hill, 1999). Understanding whether and how blue plumage plays a role in social signalling in this species is necessary before we can speculate as to the importance of this finding.

Experimental effects on ageing and selective disappearance

We found some effects of experiments on trait expression, especially hormonal implants, though the direction and strength of the effect was dependent on sex and the type of implant. Corticosterone is often referred to as the stress hormone, but it is also closely tied to metabolism and involved in trade-offs in the investment of resources to reproductive versus self-maintenance (Hau et al. 2010, Almasi et al. 2013). Further, previous correlative and experimental studies have shown that there are links between corticosterone levels and ornament expression (Dupont et al. 2011, Lendvai et al. 2013, Fairhurst et al. 2014). Thus, it is perhaps not surprising that the effects we observed were in the expression of signalling traits, which are often regarded as condition dependent, and influence reproductive outcomes. However, as these experiments were not designed to test for these effects, we advise caution and suggest further research before any conclusions are drawn.

In many of our analyses, we found evidence that selective disappearance played an important role. This finding underscores the importance of testing for within-individual ageing patterns, instead of using population-level associations between age and trait expression. If selective disappearance is indicative of early death, such a result would suggest the more ornamented females had lower longevity, while more ornamented males had greater longevity. Both would have important consequences for understanding life-history trade-offs, and the costs and benefits or signalling trait expression in the two sexes. However, an important caveat here is that individuals left the study population either because they had died, or because they were removed from the study population and were rehomed with aviculturists, and we were unable to determine individual fate for all of the individuals in the dataset

Conclusions

Understanding the degree and timing of investment in different types of traits is a critical goal for biologists interested in ageing. This study provides insight into how males *vs* females, and black *vs* red morphs, differ in trait expression investment across the lifespan of a polymorphic songbird. We found important sex differences in how signalling traits age, but not more general size traits. Together, these data illustrate that traits age differently, and that the sexes can age differently, two important findings for researchers interested in ageing. We also report surprising morph differences in how some traits change with age, suggesting that differences in how individuals manage trade-offs between competition and survival might have consequences for how traits change with age. Although previous studies have reported similar cross-sectional age patterns in other species, few have simultaneously examined within and between individual variation. Finally, these results point to the critical lack of comparable analyses of ageing patterns in traits that experience different selective pressures, particularly sex comparisons.

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Table 1: Results from linear mixed models examining **sex and morph differences in age related** changes in trait expression. Shown are parameter estimates with standard errors and significance (*P* <0.05 in bold). All models were fitted using Maximum Likelihood, and Gaussian error distributions with identity links. Loaded traits indicates the traits which loaded most strongly for the relevant principal component (PC).

	(a) General traits N observations: 4,281 N individuals: 2,941		***(b) Signalling traits*** N observations: 3,094 N individuals: 2,193	
PC score Loaded traits (PCA)	**Size PC1** Tarsus, mass	**Size PC2** Wing, beak	**Signalling PC 1** Colour	**Signalling PC 2** Tail
Intercept	0.174 (0.102) p = 0.088	-0.042 (0.099) p = 0.671	-2.261 (0.133) p <0.0001	-0.016 (0.125) p = 0.899
Sex (female)	**-0.307 (0.119)** **p = 0.010**	**0.407 (0.115)** **p = 0.0005**	**2.057 (0.145)** **p <0.0001**	**-1.145 (0.142)** **p <0.0001**
Morph (black)	-0.149 (0.120) p = 0.215	-0.186 (0.116) p = 0.108	0.022 (0.137) p = 0.872	0.051 (0.134) p = 0.705
Age (years)	-0.013 (0.038) p = 0.726	-0.057 (0.066) p = 0.386	-0.134 (0.113) p = 0.238	0.104 (0.110) p = 0.348
Age (quadratic)	0.0005 (0.009) p = 0.959	0.003 (0.016) p = 0.826	0.018 (0.025) p = 0.481	-0.014 (0.025) p = 0.579
Disappearance	-0.054 (0.051) p = 0.290	0.017 (0.044) p = 0.701	**-0.123 (0.051)** **p = 0.016**	0.011 (0.049) p = 0.830
Sex x Morph	0.119 (0.089) p = 0.184	-0.029 (0.076) p = 0.700	-0.061 (0.086) p = 0.476	0.047 (0.083) p = 0.569
Morph x Age	**0.110 (0.048)** **p = 0.021**	**0.191 (0.080)** **p = 0.017**	-0.025 (0.117) p = 0.835	-0.014 (0.115) p = 0.903
Morph x Quadratic age	**-0.024 (0.011)** **p = 0.028**	**-0.041 (0.019)** **p = 0.027**	0.025 (0.027) p = 0.358	0.007 (0.027) p = 0.787
Morph x Disp.	0.003 (0.056) p = 0.956	0.0003 (0.049) p = 0.995	-0.021 (0.047) p = 0.661	-0.039 (0.045) p = 0.389

Sex x Age	-0.037 (0.048) p = 0.440	-0.136 (0.081) p = 0.094	**1.049 (0.137)** **p <0.0001**	**0.428 (0.134)** **p = 0.002**
Sex x Quadratic age	0.013 (0.011) p = 0.252	0.034 (0.019) p = 0.069	**-0.122 (0.032)** **p = 0.0002**	-0.058 (0.031) p = 0.064
Sex x Disp.	**0.113 (0.055)** **p = 0.041**	-0.060 (0.049) p = 0.217	**0.122 (0.055)** **p = 0.026**	**0.291 (0.053)** **p <0.0001**
	Variance components			
Individual var.	1.33	0.86	0.41	0.38
Year var.	0.0	0.001	0.009	0.002
Residual variance	0.05	0.15	0.24	0.23

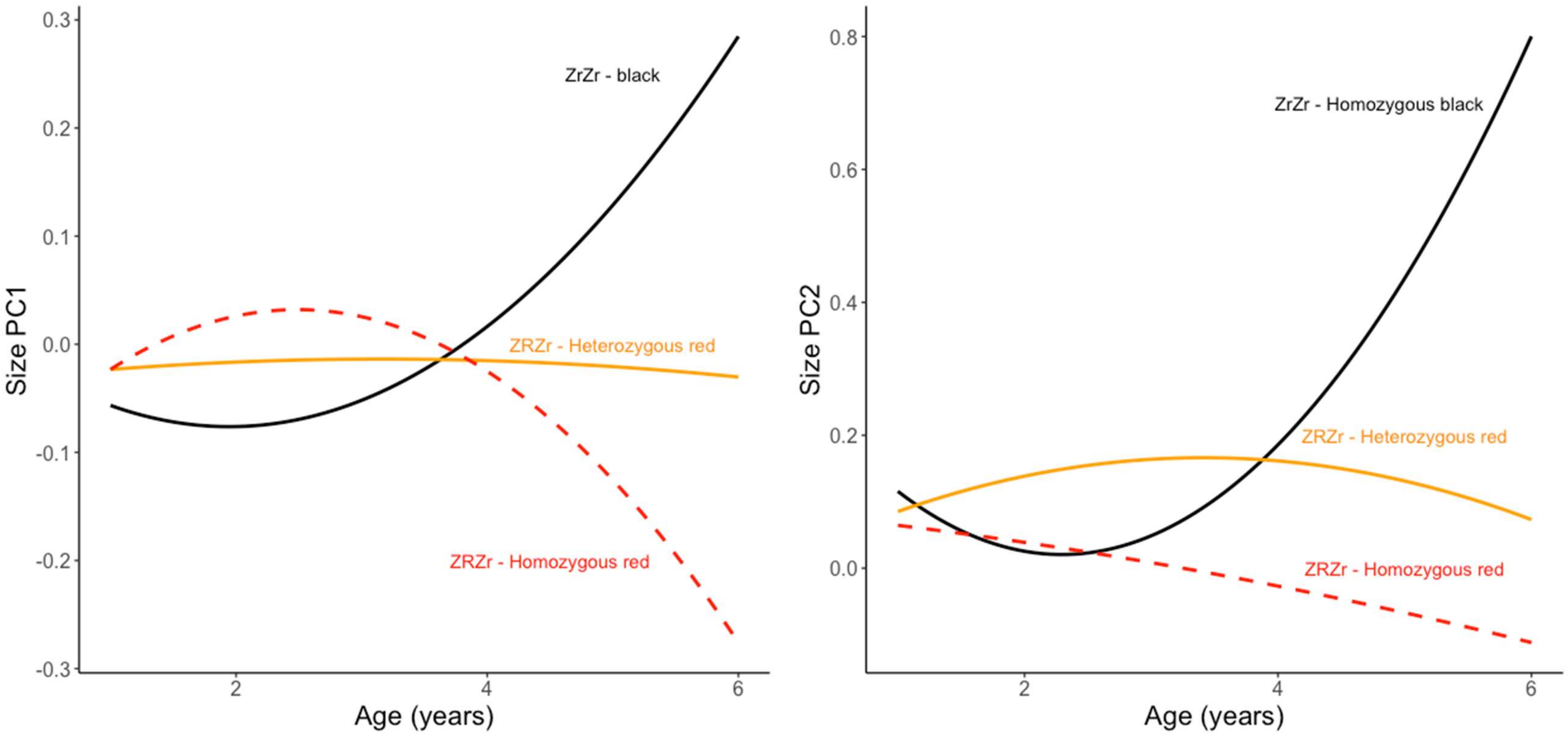

Figure S1 – Genotype differences in age-related changes in trait expression in male Gouldian finches. Lines are generated using predicted values from models (Table S3) and include age, quadratic age and last age measured (disappearance), and ID as a random effect. These lines indicate how traits change as individuals age, after accounting for selective disappearance: black solid lines are black morphs, Orange solid lines are heterozygous red males, red, dashed lines are homozygous red morphs. Note the scale of the y-axis is different from Figure 2, and differs across panels.

Table S1: Loadings for principal components analysis using correlations of traits, including both sexes. The first analysis is of size-related traits, and the second is of signalling traits.

	Trait	PC1	PC2
Size traits PCA	Tarsus length (mm)	0.568	-0.396
	Wing length (mm)	0.272	0.835
	Beak length (mm)	0.467	0.303
	Mass (g)	0.620	-0.232
	Eigenvalue	1.139	1.00
	Proportion of variance	32.5%	24.9%
	Cumulative proportion		57.4%
Signalling traits PCA	Tail length (mm)	0.383	0.923
	Hue (spectral location)	0.532	-0.218
	Chroma (spectral purity)	0.536	-0.241
	Headband width (mm)	0.532	-0.203
	Eigenvalue	1.65	0.840
	Proportion of variance	68.3%	17.6%
	Cumulative proportion		85.8%

Table S2: Sex and morph differences in individual traits aging patterns

	General					*Signalling*		
	Wing	**Beak**	**Tarsus**	**Mass**	**Headband**	**Hue**	**Chroma**	**Tail**
N obs	4591	4353	4590	4519	3230	3178	3178	4460
N indv	3121	2974	3121	3092	2267	2230	2230	3081
Intercept	66.59 (0.132) p = 0.000	11.78 (0.060) p = 0.000	14.97 (0.078) p = 0.000	14.525 (0.153) p = 0.000	1.273 (0.112) p = 0.000	0.211 (0.021) p = 0.000	0.174 (0.022) p = 0.000	46.649 (0.720) p = 0.000
Sex (female)	**0.473 (0.155)** **p = 0.003**	-0.131 (0.070) p = 0.062	-0.047 (0.088) p = 0.593	**-0.379 (0.177)** **p = 0.032**	**3.861 (0.125)** **p <0.0001**	**0.215 (0.024)** **p <0.0001**	**0.202 (0.025)** **p <0.0001**	**-1.867 (0.858)** **p = 0.030**
Morph (black)	-0.082 (0.155) p = 0.599	**-0.174 (0.070** **p = 0.014**	0.065 (0.089) p = 0.469	-0.177 (0.178) p = 0.322	0.001 (0.126) p = 0.992	-0.010 (0.023) p = 0.663	0.001 (0.024) p = 0.971	0.228 (0.853) p = 0.789
Age (years)	-0.073 (0.095) p = 0.446	-0.025 (0.022) p = 0.263	-0.002 (0.019) p = 0.927	0.047 (0.062) p = 0.450	0.006 (0.042) p = 0.881	-0.017 (0.020) p = 0.408	-0.011 (0.019) p = 0.567	1.131 (0.664) p = 0.089
Age (quadratic)	0.007 (0.023) p = 0.761	0.004 (0.005) p = 0.491	0.001 (0.005) p = 0.833	-0.009 (0.015) p = 0.535	0.001 (0.009) p = 0.899	0.002 (0.005) p = 0.622	0.002 (0.004) p = 0.685	-0.255 (0.158) p = 0.106
Disapp.	**0.150 (0.057)** **p = 0.009**	**-0.138 (0.030** **p = 0.00001**	**0.093 (0.040)** **p = 0.019**	-0.134 (0.075) p = 0.076	**-0.160 (0.059)** **p = 0.008**	-0.015 (0.008) p = 0.061	-0.013 (0.009) p = 0.146	-0.401 (0.265) p = 0.131
Sex x Morph	0.042 (0.098) p = 0.668	-0.005 (0.053) p = 0.920	0.061 (0.069) p = 0.379	0.246 (0.131) p = 0.060	**-0.230 (0.101)** **p = 0.023**	0.0001 (0.013) p = 0.995	-0.010 (0.015) p = 0.492	-0.237 (0.448) p = 0.598
Morph x Age	**0.268 (0.118)** **p = 0.023**	0.015 (0.028) p = 0.587	-0.021 (0.024) p = 0.376	0.113 (0.077) p = 0.141	0.055 (0.044) p = 0.210	0.018 (0.021) p = 0.401	-0.013 (0.020) p = 0.531	0.378 (0.816) p = 0.643

Morph x Quad age	**-0.058 (0.028)**	-0.002 (0.006)	0.003 (0.006)	-0.025 (0.018)	-0.016 (0.010)	-0.002 (0.005)	0.006 (0.005)	-0.024 (0.190)
	p = 0.037	p = 0.727	p = 0.627	p = 0.169	p = 0.128	p = 0.761	p = 0.207	p = 0.899
Morph x Disapp.	-0.099 (0.064)	**0.083 (0.033)**	-0.039 (0.043)	0.012 (0.083)	0.048 (0.052)	-0.003 (0.007)	-0.0003 (0.008	-0.303 (0.299)
	p = 0.123	**p = 0.012**	p = 0.357	p = 0.887	p = 0.351	p = 0.664	p = 0.972	p = 0.312
Sex x Age	-0.164 (0.119)	0.023 (0.028)	-0.001 (0.024)	-0.048 (0.078)	-0.011 (0.051)	**0.098 (0.025)**	**0.134 (0.024)**	**5.672 (0.826)**
	p = 0.167	p = 0.416	p = 0.963	p = 0.538	p = 0.822	**p = 0.0001**	**p <0.0001**	**p <0.0001**
Sex x Quad age	0.042 (0.028)	-0.002 (0.006)	-0.0002 (0.006)	0.013 (0.018)	0.001 (0.012)	-0.007 (0.006)	**-0.016 (0.006)**	**-0.542 (0.193)**
	p = 0.130	p = 0.714	p = 0.976	p = 0.464	p = 0.918	p = 0.204	**p = 0.005**	**p = 0.006**
Sex x Disapp.	-0.051 (0.064)	0.033 (0.033)	-0.014 (0.042)	**0.179 (0.082)**	**0.147 (0.063)**	-0.005 (0.008)	-0.001 (0.009)	**2.737 (0.298)**
	p = 0.426	p = 0.310	p = 0.743	**p = 0.030**	**p = 0.020**	p = 0.519	p = 0.944	**p <0.0001**
				Variance components				
Individual	1.41	0.46	0.85	2.9	0.83	0.008	0.12	21.89
Residual	0.36	0.018	0.014	0.15	0.03	0.008	0.007	17.49

Note: Sex is relative to female, morph is relative to black,

Table S3: Results from linear mixed models examining in **age-related** changes in **male** trait expression using genotype instead of morph. Shown are parameter estimates with standard errors and significance (*P* <0.05 in bold). All models were fitted using Maximum Likelihood, and Gaussian error distributions with identity links. Loaded traits refers to the measures which loaded strongly in the PCA (Table 1).

	a) Size traits N observations (4,281) N individuals (2,941)		***a) Signalling traits*** N observations (4,281) N individuals (2,941)	
PC score Loaded traits (PCA)	**Size PC1** Tarsus, mass	**Size PC2** Wing, beak	**Signalling PC 1** Colour	**Signalling PC 2** Tail
Intercept	-0.112 (0.122) p = 0.358	0.446 (0.126) p = 0.0005	-0.162 (0.131) p = 0.215	-1.171 (0.113) p = 0.000
Genotype ZRZr	0.110 (0.172) p = 0.523	**-0.335 (0.169)** **p = 0.047**	0.124 (0.173) p = 0.475	**0.329 (0.161)** **p = 0.041**
Genotype ZRZR	-0.163 (0.156) p = 0.298	-0.202 (0.165) p = 0.222	-0.236 (0.170) p = 0.165	-0.056 (0.157) p = 0.724
Age (years)	-0.084 (0.046) p = 0.069	**-0.297 (0.084)** **p = 0.0005**	**0.885 (0.117)** **p < 0.0001**	**0.534 (0.107)** **p < 0.0001**
Age (quadratic)	**0.022 (0.011)** **p = 0.045**	**0.054 (0.019)** **p = 0.005**	**-0.100 (0.027)** **p = 0.0003**	**-0.073 (0.025)** **p = 0.004**
Disappearance	0.067 (0.066) p = 0.306	-0.025 (0.056) p = 0.655	-0.008 (0.046) p = 0.859	**0.311 (0.043)** **p < 0.0001**
ZRZr x Age	0.099 (0.073) p = 0.175	**0.353 (0.126)** **p = 0.005**	-0.013 (0.179) p = 0.940	-0.279 (0.166) p = 0.093
ZRZR x Age	**0.205 (0.066)** **p = 0.003**	**0.240 (0.115)** **p = 0.037**	0.043 (0.162) p = 0.789	0.169 (0.150) p = 0.259
ZRZr x Quadratic age	-0.024 (0.016) p = 0.138	**-0.070 (0.028)** **p = 0.012**	0.033 (0.040) p = 0.413	0.067 (0.037) p = 0.074
ZRZR x Quadratic age	**-0.046 (0.015)**	**-0.059 (0.026)**	0.010 (0.036)	-0.032 (0.034)

	p = 0.003	**p = 0.021**	p = 0.780	p = 0.338
ZRZr x Disp.	-0.087 (0.103)	0.030 (0.089)	**-0.151 (0.073)**	-0.047 (0.068)
	p = 0.400	p = 0.733	**p = 0.038**	p = 0.488
ZRZR x Disp.	0.020 (0.080)	-0.047 (0.077)	0.068 (0.066)	-0.048 (0.062)
	p = 0.801	p = 0.543	p = 0.300	p = 0.436
	Variance components			
Individual var.	1.43	0.96	0.47	0.42
Year var.	0.0	0.0	0.12	0.002
Residual variance	0.045	0.13	0.30	0.26

Appendix 1 – Experimental Effects –

As one of the goals of this study was to examine age-related changes in trait expression, we first determined whether any of these experiments affected sex differences in ageing patterns. Experiments include the following: low versus average quality diet (Diet, 343 birds); hormone manipulations in which birds were implanted with either corticosterone, which is important in stress response and metabolism (hereafter Cort 244 birds), or metyrapone, which blocks corticosterone production (hereafter Mety, n=224 birds); and breeding experiments in which pairs were assigned by researchers to be a compatible colour match (same morph, Compatible, n=3467), an incompatible colour match, which is stress-inducing (black and red morph pairs, Incompatible, n=1373), or a perceived mismatch that was actually a genetic match (red females were matched to compatible red males with blackened heads to appear incompatible, Blackened, n=128).

Individuals were generally only used for one experimental manipulation, in their first breeding season, though in one study birds were matched to compatible/incompatible partners and implanted with Cort/Mety (Pryke et al. 2015), and thus experienced two treatments at the same time. Measurements were conducted in adult birds after breeding and the post-breeding moult or for young birds, after they had moulted into their first adult plumage, and before their first breeding attempt (further details below). Experiments usually began after the birds were measured, so the experiments could not have affected the measures for that year, but may affect future measures. The Compatible/Incompatible/Blackened experiment may be relevant to the offspring of those manipulations, rather than the birds that experienced the manipulation themselves. For more information on experiments see references from Pryke and Griffith 2007-2011.

Because some birds had been used in experiments that might influence trait expression we also tested for sex specific experimental effects (Diet, Compatibility (offspring from compatibility experiments), and Implant). These effects were applied to individuals for measures across all ages, though the effect only occurred in one year (usually the first breeding season), to determine if the experiment has consequences for how those individuals aged. These models include each PC score, sex, experimental effects and sex by experimental effect interactions. Results from these models are reported in Table S4. We found minimal evidence that experiments had effects on ageing patterns and these experiments were not designed to test for these effect.

Table S4: Experimental effects on traits. Results from linear mixed models examining **sex and experimental effects on in age related** changes in trait expression. Shown are parameter estimates with standard errors and significance (*P* <0.05 in bold). All models were fitted using Maximum Likelihood, and Gaussian error distributions with identity links. Loaded traits refers to the measures which loaded strongly in the PCA (Table 1).

	a) Size traits N observations (4,281) N individuals (2,941)		***b) Signalling traits*** N observations (3,094) N individuals (2,193)	
	Size PC1 Tarsus, mass	**Size PC2** Wing, beak	**Signalling PC 1** Colour	**Signalling PC 2** Tail
Intercept	0.201 (0.191)	0.078 (0.163)	-3.097 (0.511)	-0.032 (0.500)
	p = 0.293	p = 0.631	p = 0.000	p = 0.950
Sex (female)	-0.240 (0.269)	-0.218 (0.230)	**3.999 (0.529)**	-0.109 (0.517)
	p = 0.372	p = 0.342	**p = 0.000**	p = 0.833
Compatible parents				
Compatible	-0.201 (0.186)	-0.128 (0.159)	0.445 (0.509)	0.148 (0.498)
	p = 0.280	p = 0.421	p = 0.382	p = 0.767
Incompatible	-0.213 (0.208)	-0.216 (0.177)	0.503 (0.518)	0.110 (0.508)
	p = 0.306	p = 0.223	p = 0.332	p = 0.830
Hormone implants				
Cort Implant	0.178 (0.179)	0.094 (0.153)	0.472 (0.360)	0.110 (0.352)
	p = 0.320	p = 0.539	p = 0.190	p = 0.754
Mety Implant	0.177 (0.109)	**-0.201 (0.093)**	0.440 (0.244)	-0.013 (0.239)
	p = 0.107	**p = 0.032**	p = 0.072	p = 0.958
Low Quality Diet	0.061 (0.107)	-0.142 (0.090)	-0.031 (0.111)	0.056 (0.116)

	p = 0.568	p = 0.113	p = 0.783	p = 0.631
Sex x Compatible	0.200 (0.261)	0.267 (0.223)	-0.551 (0.526)	-0.048 (0.514)
	p = 0.445	p = 0.232	p = 0.295	p = 0.926
Sex x Incompatible	0.209 (0.285)	0.469 (0.243)	-0.796 (0.536)	-0.132 (0.525)
	p = 0.464	p = 0.054	p = 0.138	p = 0.803
Sex x Cort Implant	-0.283 (0.212)	0.238 (0.181)	**-0.750 (0.368)**	-0.435 (0.360)
	p = 0.182	p = 0.189	**p = 0.042**	p = 0.228
Sex x Mety Implant	-0.045 (0.219)	**0.458 (0.187)**	-0.311 (0.278)	-0.303 (0.273)
	p = 0.837	**p = 0.015**	p = 0.265	p = 0.268
Sex x Low Quality Diet	0.020 (0.144)	0.201 (0.121)	0.192 (0.128)	-0.024 (0.133)
	p = 0.891	p = 0.098	p = 0.134	p = 0.854
		Variance components		
Individual var.	1.33	0.86	0.26	0.42
Residual variance	0.05	0.15	0.47	0.27