Inconsistent findings of ageing across different feather-quality indices in a wild passerine

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Abstract

In most animals, individuals tend to decline in performance in later life, known as ageing. In birds, studies of ageing have traditionally concentrated on metrics of survival and reproductive success, whereas morphological traits have received comparatively little attention. Feather quality is a key morphological trait for passerines as it contributes to flight performance, camouflage and thermoregulation, and is, therefore, important for survival. However, there are, as of yet, very few studies on how feather quality changes with age. In this study, we use a closely monitored natural population of long-lived Seychelles warblers to investigate whether and how three different indices of feather quality change with age within individuals. We found that feather mass-to-length ratio increased with age (indicating improving quality with age), while rachis width declined with age (indicating declining quality), and barbule density showed no ageing pattern. All feather quality indices showed no sex differences in ageing rates. The inconsistent findings of ageing across the three feather quality indices may suggest that life history trade-offs between feather quality and survival or reproduction are not as strong, and feather quality may not be a costly trait to maintain. Age-related improvements of mass-to-length ratio but not the other indices may also suggest that certain aspects of feather quality are more important than others to maintain. Opposite patterns of ageing in rachis width and mass-to-length ratio may also suggest possible trade-offs between different feather quality metrics. Our study highlights the need for further investigation on energetic trade-offs between maintenance of different phenotypic traits and fitness.

Keywords: Ageing, Feather quality, Somatic maintenance, Fitness, Disposable soma theory, Energy trade-offs, Selective disappearance.

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Introduction

Ageing, i.e. age related changes in traits have increasingly been documented across a range of taxa in natural populations (e.g. Froy et al., 2013; Nussey et al., 2011). Many ageing studies in various taxa focus on measuring changes in life-history traits (Jones et al., 2014; Lemaître & Gaillard, 2017), yet it is clear declines in function begin before survival and reproductive senescence in many organisms (e.g. Bansal et al., 2015; Yashin et al., 2007). To better understand these functional declines and mechanisms underlying actuarial senescence, we have to study ageing patterns in a wider range of traits outside of fitness traits. Morphological traits historically have received less attention despite playing an important role in survival and fitness (Nussey et al., 2011). For instance, body mass – often used as measure of condition - is a predictor of survival in many species (Haramis et al., 1986; Ronget et al., 2018). Accordingly, declines in body mass were associated with increased mortality risk in older ages (Nussey et al., 2011), highlighting the potential contribution of morphological trait ageing towards actuarial senescence. Understanding the ageing patterns of morphological traits that are key to survival and reproduction, will provide insight to functional declines that cause the uncoupling of healthspan and lifespan and subsequent demographic declines (Nussey et al., 2011).

Feathers are a defining feature of all birds, and are key to their health and survival, influencing flight ability, foraging, camouflage, sexual selection and insulation (Terrill & Shultz, 2023). Wing and tail feather condition can affect flight performance and maneuverability (Swaddle et al., 1996) (Matyjasiak et al., 2018), and may thus impair escape from predators (Møller & Nielsen, 2018), increase foraging energetic costs (Echeverry-Galvis & Hau, 2013; Swaddle & Witter, 1997), or impact offspring provisioning rate (Frankish, Manica & Phillips, 2020). Additionally, feather quality may influence fitness and selection as feathers often serve as secondary sexual characteristics (Aparicio, Bonal & Cordero, 2003; Adámková, Tomášek & Albrecht, 2022). Lower quality feathers may cause lower attractiveness (Daunt et al., 2007; Kose & Møller, 1999; Adámková, Tomášek & Albrecht, 2022). Further, birds with feathers of poor quality may have inferior plumage patterns, leading to increased predation risk through poorer camouflage (Camacho et al., 2022; Gluckman & Cardoso, 2010; Solonen, 2021). Poorer plumage quality or structure can also lead to reduced insulation, decreasing over-winter survival (Dawson et al., 2000; Nilsson & Svensson, 1997). Finally, feathers of higher quality are stronger and more durable, thus lasting over a longer period of time until the next moult (Kiat & Sapir, 2018). As a consequence of all of the above, ageing or senescence of feather quality can lead to lower survival and reproductive success. Therefore, understanding how feather quality deteriorates with age may provide us with insight into mechanistic explanations of avian senescence.

To the best of our knowledge, there are very few studies on within-individual age-related declines in feather quality. In captive zebra finches (*Taeniopygia guttata*) primary wing feather length and feather mass declined with age (Śliż, 2022), while in alpine swifts (*Tachymarptis melba*) tail length showed strong decline with age in both sexes, and there was selective disappearance of males with longer tails in swifts and in barn swallows (*Hirundo rustica*) (Moullec, Reichert & Bize, 2023, Adámková, Tomášek & Albrecht, 2022; Balbontín & Møller, 2015). In contrast, sand martins (*Riparia riparia*) demonstrated improvements in a range of tail feather quality indices with age (Szép et al., 2019). Two of the studies above use feather length, with little studies using a range of feather quality indices (Szép et al., 2019; Śliż, 2022). As a result, whether patterns of feather quality ageing are uniform across multiple indices remains unknown since the studies above that measured ageing across multiple feather quality indices within individuals showed contrasting findings. Furthermore, most studies on feather quality ageing were conducted on migratory species. Migratory birds may allocate different amounts of energy in maintaining flight apparatus compared to sedentary birds (De La Hera, Pérez-Tris & Tellería, 2009), which may lead to different ageing patterns. Finally, few studies investigate how feather quality declines with age in bird species where moult timing and reproduction overlap, where there may be stronger trade-offs in resource allocation (Foster, 1975). The lack of studies in sedentary species presents a gap in our understanding of how feather quality ageing leads to avian senescence.

The Seychelles warbler (*Acrocephalus sechellensis*) population on Cousin Island provides an excellent longitudinal study system in which to investigate ageing. As this is a closed population with almost non-existent inter-island dispersal (<0.1%; Komdeur et al., 2004), intense biannual monitoring of the population from 1997 onwards provides accurate survival and reproductive success data (Hammers et al., 2013). We obtain repeated measures of the same individuals across their lifespan, which allows us to disentangle within and between individual effects of ageing (Nussey et al., 2013). Seychelles warblers have low extrinsic mortality (Komdeur, 1996), high annual survival probability (0.84 ± 0.04 in adults, 0.61 ± 0.09 in juveniles - (Brouwer et al., 2006)), and – with a mean lifespan of c.a. 4 years and maximum lifespan of 19 years are relatively long-lived compared to other passerine species (Hammers & Brouwer, 2017). Past studies have shown that warblers demonstrate reproductive senescence at ages 6 and 7.8 for males and females respectively (Hammers et al., 2012; Raj Pant et al., 2020), and survival senescence at age 6 (Hammers et al., 2013).

In this study we specifically investigate whether three indices of feather quality: mass-to-length ratio, rachis width and barbule density, which indicate feather durability, stiffness and insulation property (Kiat & Sapir, 2018). As moulting is one of the most energetically expensive events for birds (Dietz, Daan & Masman, 1992; Murphy & King, 1992), we expect all measures of feather quality to initially increase until prime age, then decline with age in later life similarly due to life-history trade-offs associated with moulting.

Methods

Study system

The Seychelles warbler is a facultatively cooperative passerine endemic to the Seychelles archipelago. The population on Cousin Island (29 ha; 04°20'S, 55°40'E) has been monitored as part of a long-term study since 1985 (Komdeur, 1992), and more than 96% have been ringed and DNA-sampled since 1997 (Richardson et al., 2001; Lee et al., 2026). The island has a carrying capacity of ~300 adult individuals, and is split into c.a. 110 territories each containing one breeding group that includes a dominant breeding pair, and can include helper or non-helper adult subordinates of either sex, and offspring (Richardson, Burke & Komdeur, 2002).

Fieldwork was carried out twice a year during the minor and major breeding seasons (January-March and June-October). New birds were caught either as chicks in the nest or as dependent fledglings on their natal territory using mistnets and song playback and ringed with a British Trust for Ornithology metal ring (BTO rings) and a unique combination of three colour rings. These individuals were aged according to a combination of behaviour, eye colour (based on (Komdeur, Bullock & Rands, 1991)), and nest date if known, thus allowing the exact age of all birds in the population to be accurately monitored. Also, as many as possible ringed birds of know age were recaptured each breeding season using mist nets and playback.

For all birds caught between 2014-2023 (except for the minor breeding season 2017-2019 and 2022) we sampled the right-most tail feather (rectrix). This feather was chosen to reduce the loss of maneuverability from reduction in lifting surface of bird tails (Carbonell & Tellería, 1999; Grubb, 1989; de la Hera, Perez-Tris & Telleria, 2009). These were individually stored in paper envelopes at room temperature until measurements in the laboratory were taken. Feather samples from fledglings and damaged feathers (feathers missing tips or half of the feather vane) were removed from the analysis. Morphological measurements including body mass and tarsus length were measured at the same time as feather sampling. We also scored the presence/absence of tail moult.

Individual territories were visited every two weeks to carry out a population census and to check for breeding activity and occupants. As a result of intense monitoring and very low inter-island dispersal (Komdeur et al., 2004), individual resighting probability per season on Cousin Island is very high ((0.92 ± 0.02 in the first 2 years of life, 0.98 ± 0.01 for older birds, (Brouwer et al., 2010)) therefore we can assume that individuals not seen for two consecutive seasons were dead (Hammers et al., 2013). We determined breeding status (dominant breeder, helper, subordinate) of birds via observations of behavioural interactions and conducting nest watches during breeding seasons (Hammers et al., 2021). Dominant breeders were defined as the primary pair-bonded male and female in a territory. Helpers were defined as resident birds seen helping the primary pair breed, while subordinates were non-helping residents (van Boheemen et al., 2019).

Seychelles warblers are insectivorous and obtain prey from the undersides of leaves (Komdeur, 2006). To determine seasonal food availability, we assessed monthly insect abundance by counting the number of insects on the undersides of 50 leaves of the most abundant plant species from 14 fixed locations on the island (Komdeur, Bullock & Rands, 1991; Spurgin et al., 2018). The monthly insect abundance was then averaged across the locations and over the duration of the breeding season to obtain food abundance estimates across the season (Spurgin et al., 2018).

Feather quality measures

We measured three indicators of feather quality: feather mass-to-length ratio, rachis width, and barbule density. Mass-to-length ratio serves as a proxy for feather quality and durability (Carbonell & Tellería, 1999). This metric reflects feather bending stiffness and resistance to wear (Kiat & Sapir, 2018), and it is positively correlated with barbule density and rachis width. Feathers were weighed using a Mettler Toledo AG-245 digital balance (instrumental repeatability: 0.01 mg ± 0.02 mg) (Carbonell & Tellería, 1999; de la Hera, Perez-Tris & Telleria, 2009). Total length of the feather (distance from the calamus base to the distal feather tip; Figure 1, arrow a) was measured using a digital caliper (± 0.01 mm). The ratio was then calculated by dividing the mass of the feather by the length of the feather.

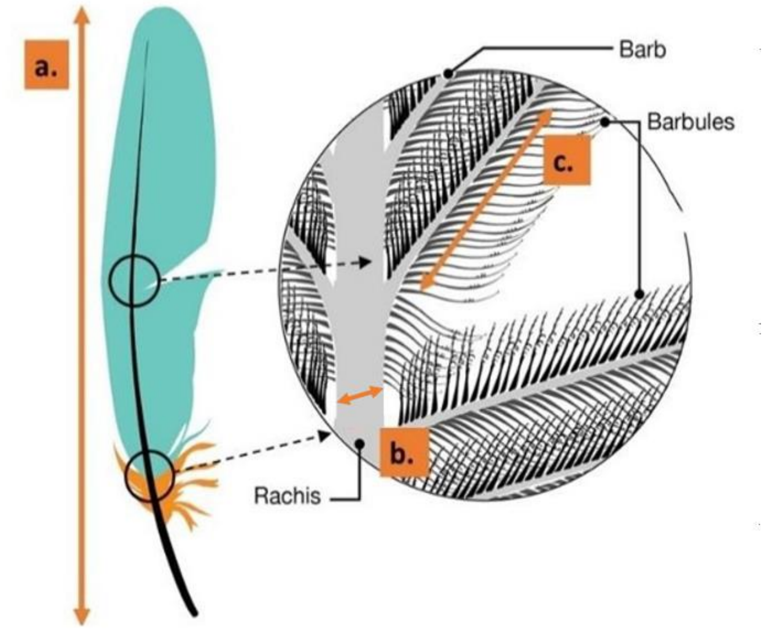

Figure 1. The three metrics of feather structure used in this study: a) length, b) rachis width and c) barbule density.

Rachis width is positively related to stiffness and hardness of the feather structure, on which both durability and aerodynamic properties depend (Dawson et al., 2000). To quantify this, we measured the maximum dorsiventral width of the rachis at the base of the feather vane (Aparicio, Bonal & Cordero, 2003; Dawson et al., 2000) with a digital caliper (± 0.01 mm Figure 1, arrow b.).

Barbule density is positively correlated with the strength, durability and aerodynamic properties of the feather vane (DesRochers et al., 2009). Barbule density also determines the amount of air feathers can trap, determining insulation property (Broggi et al., 2011). Barbule density was examined using a microscope (x40 magnification), counting the number of feather barbules (Pap et al., 2020) across three barbs, 10 repetitions of a 0.375mm section along the barb (Figure 1, arrow c.). As we developed this protocol, we tested the repeatability of the measurement method using the package *rptR v 0.9.23* (Stoffel, Nakagawa & Schielzeth, 2017). The protocol repeatability was 0.738, 95%, CI 0.517-0.866, p<0.01.

We measured the rachis width and mass-to-length ratio of 395 tail feathers from 219 adult birds. Barbule density was measured in a subset of the tail feathers and the sample size for barbule density was 128 feathers across 58 individuals. All measurements for rachis width and mass-to-length ratio were carried out by one observer (EL). For the barbule density, to account for observer effects (two observers used: EL & FN), the measurements were scaled to the means for each observer.

Statistical analyses

All statistical analyses were completed in R 4.4.1 (R Core Team, 2024). We used Linear Mixed-effects Models (LMMs) to analyse whether feather quality varied with age. We fitted a model per feather quality trait including linear and squared age terms. For the rachis width and mass-to-length ratio models, we controlled for selective disappearance by fitting lifespan as a fixed effect and individual bird identity as a random effect (Nussey et al., 2008; van de Pol & Verhulst, 2006). As most individuals included in the barbule density dataset were still alive at the time of the analysis, and so did not have a value for lifespan, we accounted for selective disappearance using the within and between individual centering method of van de Pol & Wright (2009; see also Fay, Martin & Plard, 2022). To account for any sex differences in ageing, we fitted sex as a fixed effect and an interaction term for both sex by linear and squared age.

Individual differences in resource availability and allocation trade-offs may influence ageing rates (Kirkwood, 1977), therefore we fitted the following variables, as fixed effects to account for this: body mass to tarsus ratio to control for differences in body condition, as birds in better condition may be able to produce higher quality feathers (Vágási et al., 2012); reproductive status (classed into dominant breeders, helpers and non-breeding subordinates) to control for variation in feather length caused by energetic differences resulting from differing reproductive investment; Food abundance, as it corresponds to energy acquisition in the warblers (Hammers et al., 2012), and birds with food shortages grow poorer quality feathers (Hammers et al., 2012; Murphy, King & Lu, 1988); presence of tail moult (1 and 0), to account the effect of moult stage on feather quality. Finally, birth year was fitted as a random effect to account for cohort effects in ageing. Bird identity was included in all models to account for individual variation in feather quality and selective disappearance.

We removed interactions and square terms that were not significant from the model in a negative stepwise order to test for the first-order effect of age with feather quality. All models were tested for collinearity, ensuring that VIF < 4 (Kalnins & Praitis Hill, 2025). The fit of the final models were checked via inspecting the residual plots generated using *DHARMa 0.4.6* (Hartig & Hartig, 2017).

Results

Feather mass-to-length ratio increased with age within-individual, albeit with a small effect size (table 1 & Figure 1). Males had a higher tail feather mass-to-length ratio than females (table 1).

Rachis width decreased with age (Table 2 & Figure 2). We observed selective disappearance of individuals for mass-to-length ratio from the lifespan term (table 1), and selective appearance of individuals with rachis width (table 2). However, the effect sizes of the selective disappearance terms for both feather quality indices are very small (Tables 1 & 2), suggesting low biological significance. Males had a higher rachis width overall (Table 2) and a marginally higher mass-to-length ratio (table 1) than females. While both rachis width and mass-to-length ratio differed by sex, there were no sex differences in how these traits changed with age (Tables S1 & S2). Barbule density did not show significant age nor sex differences (table 3).

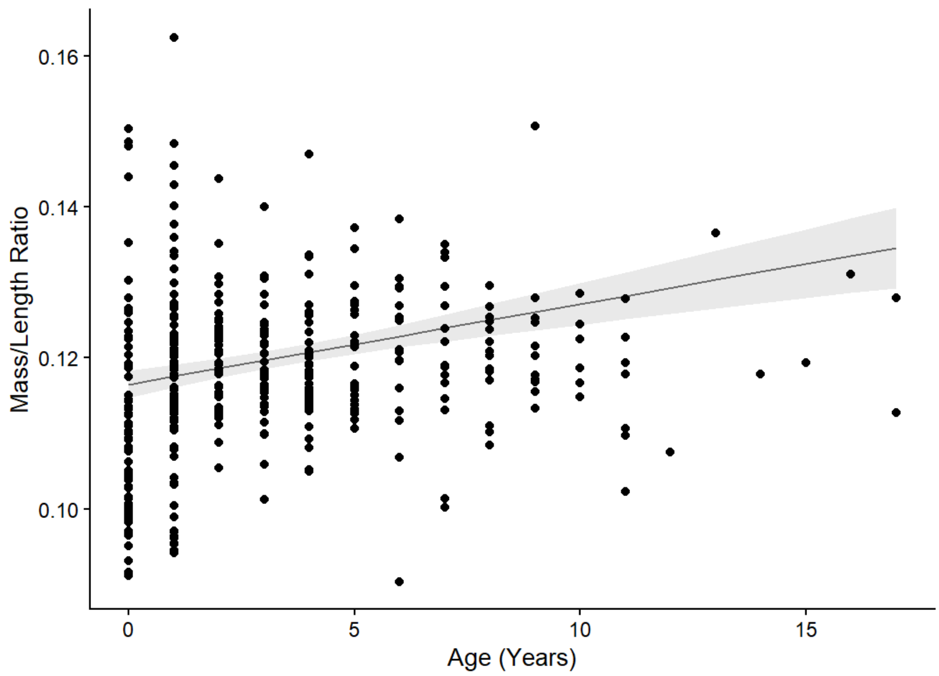

Figure 2. Within-individual changes of tail feather mass-to-length ratio with age (in years) in the Seychelles warbler. Black points correspond to individual data points. The best fit line was plotted from the model estimates using ggpredict and 95% confidence intervals are represented by the grey shaded area.

Table 1. Summary of the Generalized linear mixed model testing the effect of age (years) on tail feather mass-to-length ratio with age in the Seychelles warbler.

	Mass-to-length ratio		
Predictors	Estimates	95% CI	p
Intercept	0.0853	0.0613 – 0.1094	**<0.001**
Age	0.0011	0.0003 – 0.0018	**0.006**
Lifespan	-0.0000	-0.0000 – -0.0000	**0.034**
Sex estimate	0.0049	0.0016 – 0.0082	**0.004**

Body mass/tarsus	0.0559	0.0155 – 0.0964	**0.007**
Reproductive status (Helper)	-0.0045	-0.0098 – 0.0008	0.098
Reproductive status (Subordinate)	-0.0036	-0.0076 – 0.0004	0.077
Insect availability	-0.0006	-0.0011 – 0.0000	0.063
Tail moult presence	0.0008	-0.0024 – 0.0040	0.632
Rachis width (centred)	-0.0006	-0.0021 – 0.0009	0.436
Random Effects			
σ^2	0.00		
τ_{00} BirdID	0.00		
τ_{00} BirthYear	0.00		
N_{BirdID}	116		
$N_{BirthYear}$	19		
Observations	209		
Marginal R^2 / Conditional R^2	0.228 / NA		

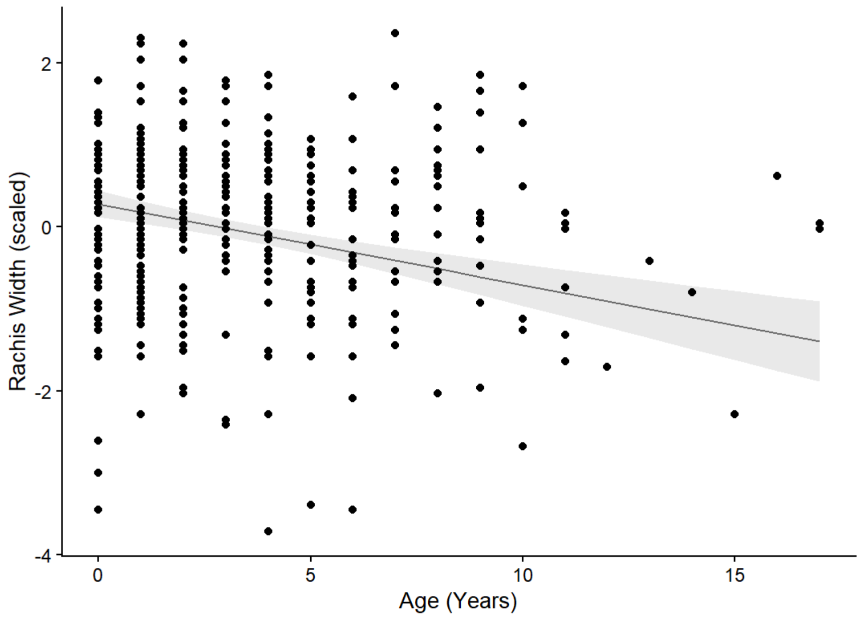

Figure 3. Within individual relationship of tail feather rachis width with age in the Seychelles warbler plotted from model predictions using the package *ggpredict*. The raw individual data is represented by black points, and the grey areas correspond to the 95% confidence intervals

Table 2. Generalized linear mixed model (GLMM) summary for the final model for ageing in tail feather rachis width in the Seychelles warbler. The 95% CI is given in the table. P-value for significant terms are in bold.

Rachis Width (Centred)			
Predictors	Estimates	CI	p
Intercept	-1.4528	-3.8992 – 0.9936	0.243
Age	-0.0989	-0.1686 – -0.0293	**0.006**
Lifespan	0.0002	0.0000 – 0.0003	**0.031**

Sex estimate	0.5882	0.2923 – 0.8841	**<0.001**
Body mass/tarsus	3.0020	-0.7383 – 6.7423	0.115
Reproductive status (Helper)	-0.5067	-0.9907 – -0.0226	**0.040**
Reproductive status (Subordinate)	0.0268	-0.3402 – 0.3938	0.886
Invertebrate availability	-0.0150	-0.0690 – 0.0390	0.583
Mass-to-length ratio	-5.0503	-17.8117 – 7.7111	0.436
Tail moult presence	-0.4527	-0.7405 – -0.1648	**0.002**
Random Effects			
σ^2	0.88		
τ_{00} BirdID	0.00		
τ_{00} BirthYear	0.00		
N BirdID	116		
N BirthYear	19		
Observations	209		
Marginal R^2 / Conditional R^2	0.178 / NA		

Aside from age, other factors influenced feather quality in the Seychelles warbler. Birds with a higher body mass to tarsus ratio, had a higher feather mass-to-length ratio (Table 1). Rachis width was influenced by reproductive status (table 2): helpers had a lower rachis width compared to dominant breeders table 2), however non-helping subordinates did not differ in rachis width from dominant breeders (table 2). The presence of tail moult was negatively related to rachis width (table 2).

Table 3 Summary of the generalized linear mixed model testing the effect of age (years) on tail feather barbule density in the Seychelles warbler. 'Within age' represents the within-individual ageing component, while 'between age' is the among-individual component. The 95% CI is reported in the table. Significant terms have p-values in bold (p<0.05).

	Centred Barbule Count		
Predictors	Estimates	95% CI	p
(Intercept)	-0.56	-3.73 – 2.62	0.73
Within age	0.01	-0.09 – 0.11	0.83
Between age	-0.0002	-0.07 – 0.07	0.99
Sex estimate	0.22	-0.22 – 0.67	0.32
Body mass/ tarsus	0.63	-4.48 – 5.75	0.81
Reproductive status (Helper)	0.17	-0.71 – 1.06	0.70
Reproductive status (Subordinate)	-0.21	-0.73 – 0.29	0.39
Invertebrate availability	-0.01	-0.17 – 0.14	0.85
Tail moult presence	0.13	-0.26 – 0.53	0.51
Random Effects			

σ^2	0.79
$\tau_{00\ BirdID}$	0.18
$\tau_{00\ BirthYear}$	0.02
ICC	0.21
N_{BirdID}	58
$N_{BirthYear}$	15
Observations	128
Marginal R^2 / Conditional R^2	0.034 / 0.236

Discussion

We investigated how three tail feather quality indices (rachis width, mass-to-length ratio and barbule density) changed with age in a closed population of Seychelles warblers. We found that the patterns of change with age across the three feather quality indices were not consistent. Within-individual age-related increases in mass-to-length ratio suggested birds produced feathers with higher quality as they grow older, since higher mass-to-length ratio is associated with feathers that are more resistant to wear and have better bending stiffness (Kiat & Sapir, 2018; Muñoz, Aparicio & Bonal, 2011). In contrast to mass-to-length ratio, rachis width showed within-individual reduction with age, suggesting that feather quality declined with age. Finally, barbule density was not observed to improve or decline with age. Together, these contrasting patterns suggest that different components of feather quality may age differently, and there is no unified pattern of ageing in tail feather quality in the Seychelles warblers.

When compared to existing research, our results both aligned and differed from existing patterns in the literature. The majority of studies found age-related declines in feather length or mass, suggesting deterioration in feather quality with age (tail feather: Moullec, Reichert & Bize, 2023; Adámková, Tomášek & Albrecht, 2022; Balbontín & Møller, 2015; wing feather Śliż, 2022), while only one study found increases of tail feather length with age (Szép et al., 2019). Compared to the aforementioned studies, our study differs by using mass-to-length ratio, a more direct indicator of feather quality than either feather mass or feather length. Thus, may present a more accurate measure of feather quality than those used in the prior studies. There are very few studies on rachis width ageing. The only study using rachis width to our knowledge found that increases in rachis width arises from selective appearance than within-individual ageing (Szép et al., 2019). Evidence for age-related changes in barbule density remains limited and inconsistent. House sparrows (*Passer domesticus*) and ten species of new world warblers displayed age related improvements in barbule density due to trade-offs with growth before fledging (Butler, Rohwer & Speidel, 2008; Vágási et al., 2011). Our lack of trend in barbule density could be due to the much lower sample size compared to the other two metrics in our study, and thus lower statistical power. However, compared to our study, inferences for late life changes in barbule density are limited for the prior studies, as both did not investigate older age declines but rather compared between juvenile and adult age classes.

Additionally, the opposite ageing patterns of mass-to-length ratio and rachis width (Figure 2 & 3) were unexpected, as mass-to-length ratio is expected to be positively correlated with rachis width and barbule density (Kiat & Sapir, 2018). These inconsistent patterns may indicate potential trade-offs between different feather quality aspects, or that certain aspects of feather quality are more important for flight and feather function in the warbler. As Seychelles warblers demonstrate moult breeding overlap (De Ruyck & Koper, 2025), and we do not have constant year round data collection, we could not control for the amount of feather wear and time since previous moult. As feather wear increases with feather age and use, this may have impacted the measurement of feather quality (Kiat et al., 2025), and may have caused noise or variation in the measurements. Without investigating how direct flight performance correlates with age, it is difficult to understand the combined impact of the age-dependent changes in the feather quality indices we observe. Overall, the lack of consistent ageing pattern across our results and past studies makes it difficult to conclude whether age-related changes in feather quality is a potential mechanistic explanation for reproductive and survival senescence in the warbler, and whether they influence flight ability.

Other variables apart from age were observed to affect feather quality in the Seychelles warbler. Warblers in better body condition produced feathers with higher mass-to-length ratio (Table 1). Similarly, the only study to our knowledge on House sparrows found that mass-to-length ratio was condition dependent (Vágási et al., 2012). However, we did not find this to be true for both rachis width and barbule density in the warbler. Additionally, barbule density might be a better quality indicator in body feathers than in tail feathers since feather density is shown to be an important factor to insulation (Pap et al., 2017), thus may be less important to maintain in tail feathers. This may indicate that feather mass-to-length ratio may be more costly to maintain than the other metrics, or mass-to-length ratio may be more instrumental to good feather quality, thus warblers invest more energy into improving mass-to-length ratio than rachis width and barbule density.

In the Seychelles warbler, while males tended to have higher feather quality (Table 1 & 2), we did not find sex specific ageing patterns in any of the feather quality measures (Table S1-3). Likewise, the only study to our knowledge on alpine swifts did not observe sex specific patterns for ageing in tail length, but rather sex differences in selective disappearance (Moullec, Reichert & Bize, 2023).

While sex differences in ageing are well documented in many species (Clutton-Brock & Isvaran, 2007), warblers do not demonstrate sex specific differences in survival senescence (Hammers et al., 2013), thus we may also expect no sex differences in feather quality ageing.

One possible reason for the lack of ageing in tail feather quality may be a potential low cost of moult in the Seychelles warbler. Flight apparatus may be less costly to maintain in the sedentary Seychelles warblers compared to long-distance migratory bird species. Although the flight apparatus of Seychelles warbler does not differ from other migratory Acrocephalus warblers (Komdeur et al., 2004), Seychelles warblers do not undertake long flights nor migrate, but rather only use flights for foraging, fighting, or gathering nest material. These usually involve short flights, as warblers are territorial and are mostly active within their territories. The warblers also live in an environment with little to no predation on adults (Hammers et al., 2015; Komdeur, 1996), potentially signifying that flight ability is less important for escaping predation. If warblers rely less on flight ability, survival may not be affected by poorer flight apparatus, thus they may be able to invest less energy in moulting compared to species flying longer distances. Most past studies demonstrating feather quality declines were conducted were on migratory species, where the energetic trade-offs between molting and survival or reproduction may be more pronounced and lead to production of poorer feathers or faster ageing of feather quality (de la Hera, Perez-Tris & Telleria, 2009). Finally, moulting is very energetically costly. Birds with overlapping breeding and moulting produced poorer quality feathers than individuals just moulting (Echeverry-Galvis & Hau, 2013; Tsuru & Tonra, 2026). Thus bird species in general avoid breeding and moulting at the same time (De Ruyck & Koper, 2025). However, Seychelles warblers demonstrate moult-breeding overlap (Komdeur, 1994), further supporting a potential low cost of moult and maintaining feather quality in the warbler.

An alternative explanation to moulting not being of high cost to SW, is birds may be able to trade-off keeping high quality feathers with other life-history traits (Podlaszczuk et al., 2016). The limited evidence for feather quality ageing in the warblers may indicate that given that feathers are vital for bird survival, a bird may allocate more energy to produce high quality feathers instead of investing in other functions or traits. A similar conclusion was drawn by a study on a different trait in common gulls (*Larus canus*), which found that individuals prioritize maintaining an important trait over reproduction in older age where increased lifespan correlates positively with lifetime fitness (Brommer & Rattiste, 2008; Urvik et al., 2019). Great tits (*Parus major*) in lower quality urban areas were also not seen to show differences in tail feather structure compared to great tits in higher quality rural areas, suggesting birds may invest more in tail feather quality to maximize flight and maneuverability (Sándor et al. 2022).

This paper tested for ageing in a feather quality, a morphological trait essential to survival and fitness in birds. To our knowledge, this is the first study investigating ageing in this trait in a tropical, non-migratory wild bird. While we expected ageing in this trait, the lack of consistent ageing patterns across feather quality indices in the Seychelles warbler, and indeed the lack of consensus in feather quality ageing across species, suggests we have limited understanding of processes underlying feather quality ageing such as energy demands and trade-offs involved in plumage maintenance in birds. Our results highlights the need for further research on how energetic trade-offs between morphological traits and life history traits contributes to ageing.

Acknowledgements

We would like to thank Elizabeth Los (EL) and Femke Noorman (FN) for collecting the feather data. We are very grateful to Elizabeth Los for developing the barbule protocol and running the initial analysis. We thank Nature Seychelles, Seychelles Bureau of Standards and the Ministry of Agriculture, Climate Change & Environment for providing permission and facilitating work on Cousin Island. We are also grateful to all fieldworkers, technicians and database managers associated with the Seychelles Warbler Project for their contribution to the long-term data collection and feather sampling.

Author contributions

CLST designed the study with input from HLD. CLST compiled data, performed analysis and wrote the manuscript. HLD, DSR, JK and TAB acquired funding. DSR and HLD provided feedback on the analysis. All authors provided critical feedback and edited the manuscript. DSR, JK, TB and HLD coordinated the long term study.

Ethics statement

Fieldwork was carried out in accordance with local ethical regulations and agreements (UEA ethics approval ID ETH2223-0186). Fieldwork and export of samples were approved by the Seychelles Department of Environment and the Seychelles Bureau of Standards.

Conflict of interest statement

The authors declare no conflict of interest.

Funding statement

This study was funded by various Natural Environment Research Council [NE/P011284/1 and NE/S010939/1 (HLD and DSR), NE/I021748/1 (HLD), and NE/K005502/1 (DSR)] and Dutch Research Council (ALWOP.531 and 854.11.003 to JK; 040.11.232 to JK and HLD) grants. CLST was funded by a double-degree PhD scholarship from the University of Groningen and the University of East Anglia. HLD was funded by a Rosalind Franklin Fellowship from the University of Groningen.

Data Availability Statement

All data and code are available on the github repository: https://github.com/Clairetls/feather-proj

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Supplementary material

Table S1 Summary statistics for Generalized linear mixed models for mass-to-length ratio with age of tail feathers in the Seychelles warbler. The leftmost is the full model, then the model removing the square interaction, and finally removing both interactions on the rightmost. The reference level for reproductive status is dominant breeders and females for sex.

	Mass-to-length ratio								
Predictors	Estimates	95% CI	p	Estimates	95% CI	p	Estimates	95% CI	p
(Intercept)	0.0874	0.0628 – 0.1121	**<0.001**	0.0868	0.0623 – 0.1113	**<0.001**	0.0865	0.0624 – 0.1106	**<0.001**
Age	0.0014	-0.0008 – 0.0036	0.219	0.0018	0.0002 – 0.0035	**0.027**	0.0019	0.0003 – 0.0034	**0.021**
Sex Estimate (Males)	0.0042	-0.0009 – 0.0092	0.105	0.0049	0.0007 – 0.0092	**0.024**	0.0052	0.0018 – 0.0085	**0.002**
Age^2	-0.0000	-0.0002 – 0.0001	0.822	-0.0001	-0.0002 – 0.0000	0.251	-0.0001	-0.0002 – 0.0000	0.254
Lifespan	-0.0000	-0.0000 – -0.0000	**0.043**	-0.0000	-0.0000 – -0.0000	**0.046**	-0.0000	-0.0000 – -0.0000	**0.046**
Body mass /tarsus	0.0500	0.0080 – 0.0920	**0.020**	0.0497	0.0078 – 0.0917	**0.020**	0.0500	0.0084 – 0.0917	**0.019**
Rachis width (centred)	-0.0005	-0.0021 – 0.0010	0.510	-0.0005	-0.0021 – 0.0010	0.486	-0.0005	-0.0021 – 0.0010	0.483
Reproductive status (helper)	-0.0029	-0.0093 – 0.0035	0.375	-0.0026	-0.0089 – 0.0037	0.421	-0.0025	-0.0088 – 0.0037	0.425
Reproductive status (subordinate)	-0.0023	-0.0070 – 0.0023	0.327	-0.0022	-0.0069 – 0.0024	0.347	-0.0022	-0.0069 – 0.0024	0.341
Insect availability	-0.0005	-0.0011 – 0.0001	0.075	-0.0005	-0.0011 – 0.0001	0.081	-0.0005	-0.0011 – 0.0001	0.077
Tail moult presence	0.0007	-0.0026 – 0.0039	0.687	0.0007	-0.0025 – 0.0040	0.650	0.0007	-0.0025 – 0.0040	0.647
Age × Sex estimate	0.0007	-0.0016 – 0.0029	0.561	0.0001	-0.0008 – 0.0009	0.878			
Sex estimate × Age^2	-0.0001	-0.0002 – 0.0001	0.572						
Random Effects									
σ^2	0.00			0.00			0.00		
τ_{00}	0.00 $_{BirdID}$			0.00 $_{BirdID}$			0.00 $_{BirdID}$		
	0.00 $_{BirthYear}$			0.00 $_{BirthYear}$			0.00 $_{BirthYear}$		
N	116 $_{BirdID}$			116 $_{BirdID}$			116 $_{BirdID}$		
	19 $_{BirthYear}$			19 $_{BirthYear}$			19 $_{BirthYear}$		
Observations	209			209			209		
Marginal R^2 / Conditional R^2	0.231 / NA			0.231 / NA			0.232 / NA		

Table S2 Summary statistics table for 3 Rachis width models. Leftmost model corresponds to the full model with both age and age squared terms and corresponding sex interactions, the middle panel corresponds to the model for removing the non significant sex * age squared interaction, and the third model with both interactions removed. The reference level for reproductive status is dominant breeders and females for sex.

Rachis Width

Predictors	Estimates	95% CI	p	Estimates	95% CI	p	Estimates	95% CI	p
Intercept	-1.7014	-4.2062 – 0.8034	0.182	-1.5985	-4.0912 – 0.8942	0.207	-1.5709	-4.0328 – 0.8909	0.210
Age	-0.0908	-0.2956 – 0.1141	0.383	-0.1533	-0.3026 – -0.0040	**0.044**	-0.1560	-0.3009 – -0.0112	**0.035**
Sex (Males)	0.6908	0.2359 – 1.1458	**0.003**	0.5852	0.1970 – 0.9734	**0.003**	0.5659	0.2657 – 0.8660	<**0.001**
Age squared	-0.0014	-0.0168 – 0.0140	0.860	0.0042	-0.0050 – 0.0133	0.371	0.0041	-0.0050 – 0.0131	0.376
Lifespan	0.0002	0.0000 – 0.0003	**0.036**	0.0002	0.0000 – 0.0003	**0.041**	0.0002	0.0000 – 0.0003	**0.040**
Body Mass/Tarsus	3.3439	-0.5231 – 7.2109	0.090	3.4100	-0.4518 – 7.2718	0.083	3.3832	-0.4540 – 7.2204	0.084
Reproductive Status (Helper)	-0.5895	-1.1706 – -0.0084	**0.047**	-0.6363	-1.2075 – -0.0651	**0.029**	-0.6400	-1.2078 – -0.0721	**0.027**
Reproductive Status (Subordinate)	-0.0537	-0.4807 – 0.3733	0.804	-0.0699	-0.4951 – 0.3553	0.746	-0.0681	-0.4916 – 0.3554	0.752
Invertebrate availability	-0.0147	-0.0694 – 0.0399	0.596	-0.0170	-0.0714 – 0.0375	0.539	-0.0167	-0.0708 – 0.0375	0.545
Mass-to-length ratio	-4.3019	-17.1693 – 8.5655	0.510	-4.5518	-17.3992 – 8.2956	0.486	-4.5634	-17.3779 – 8.2511	0.483
Tail moult presence	-0.4353	-0.7259 – -0.1447	**0.004**	-0.4483	-0.7372 – -0.1593	**0.003**	-0.4487	-0.7368 – -0.1606	**0.002**
Age × Sex estimate	-0.0892	-0.2907 – 0.1122	0.383	-0.0060	-0.0822 – 0.0702	0.877			
Age^2 x Sex estimate	0.0073	-0.0090 – 0.0235	0.380						
Random Effects									
σ^2	0.88			0.88			0.88		
τ_{00}	0.00_{BirdID}			0.00_{BirdID}			0.00_{BirdID}		
	$0.00_{BirthYear}$			$0.00_{BirthYear}$			$0.00_{BirthYear}$		
N	116_{BirdID}			116_{BirdID}			116_{BirdID}		
	$19_{BirthYear}$			$19_{BirthYear}$			$19_{BirthYear}$		
Observations	209			209			209		
Marginal R^2 / Conditional R^2	0.182 / NA			0.180 / NA			0.181 / NA		

Table S3. Summary statistics for the generalized linear mixed models for barbule density with age. Leftmost model corresponds to the full model with both age and age squared terms and corresponding sex interactions, the middle panel corresponds to the model for removing the non significant sex * age squared interaction, and the third model with both interactions removed. The reference level for reproductive status is dominant breeders and females for sex.

	Centred Barbule Count								
Predictors	Estimates	95% CI	p	Estimates	95% CI	p	Estimates	95% CI	p
(Intercept)	-0.3560	-3.5071 – 2.7951	0.823	-0.3695	-3.5229 – 2.7839	0.817	-0.3636	-3.4986 – 2.7715	0.819
Within age	-0.4441	-1.0300 – 0.1419	0.136	-0.2442	-0.6174 – 0.1291	0.198	-0.2358	-0.5127 – 0.0412	0.094
Sex estimate (Males)	0.2035	-0.2375 – 0.6445	0.363	0.1684	-0.2658 – 0.6027	0.444	0.1685	-0.2649 – 0.6018	0.443
Within age2	0.0541	-0.0180 – 0.1262	0.140	0.0246	-0.0020 – 0.0511	0.069	0.0246	-0.0013 – 0.0506	0.063
Average age	-0.0122	-0.0793 – 0.0548	0.718	-0.0107	-0.0776 – 0.0563	0.753	-0.0105	-0.0772 – 0.0562	0.756
Body mass/tarsus	0.5343	-4.5334 – 5.6020	0.835	0.5846	-4.4867 – 5.6559	0.820	0.5713	-4.4623 – 5.6050	0.823
Reproductive status (Helper)	-0.2651	-1.2230 – 0.6928	0.585	-0.1914	-1.1395 – 0.7568	0.690	-0.1836	-1.1236 – 0.7565	0.700
Reproductive status (Subordinate)	-0.3540	-0.8706 – 0.1627	0.177	-0.3225	-0.8359 – 0.1908	0.216	-0.3195	-0.8293 – 0.1902	0.217
Insect availability	-0.0331	-0.1861 – 0.1198	0.669	-0.0368	-0.1894 – 0.1158	0.634	-0.0369	-0.1888 – 0.1150	0.631
Tail moult presence	0.1537	-0.2475 – 0.5549	0.449	0.1577	-0.2428 – 0.5581	0.437	0.1584	-0.2376 – 0.5543	0.430
WithinAge × Sex estimate	0.2402	-0.3737 – 0.8540	0.440	0.0094	-0.3064 – 0.3252	0.953			
SexEstimate × WithinAge2	-0.0331	-0.1086 – 0.0424	0.387						
Random Effects									
σ^2	0.81			0.80			0.79		
τ_{00}	0.14 $_{BirdID}$			0.15 $_{BirdID}$			0.15 $_{BirdID}$		
	0.02 $_{BirthYear}$			0.02 $_{BirthYear}$			0.02 $_{BirthYear}$		
ICC	0.17			0.17			0.18		
N	58 $_{BirdID}$			58 $_{BirdID}$			58 $_{BirdID}$		
	15 $_{BirthYear}$			15 $_{BirthYear}$			15 $_{BirthYear}$		
Observations	128			128			128		
Marginal R^2 / Conditional R^2	0.071 / 0.227			0.068 / 0.231			0.068 / 0.235		