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ORIGINAL ARTICLE

Minimum longevity and age-related male plumage in Darwin's finches on Floreana Island

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Abstract

Several Darwin's finch populations on the Galapagos Islands are declining and/or locally extinct. Acoustic surveys provide useful information about population size, but do not provide information on the age or morphology of birds. This study uses mist netting data collected during 2004–2016 on Floreana Island with the aim of evaluating minimum longevity in Darwin's finches. The study species are the Small Tree Finch (*Camarhynchus parvulus*), hybrid tree finches (*Camarhynchus* spp.), Medium Tree Finch (*Camarhynchus pauper*), and Small Ground Finch (*Geospiza fuliginosa*). In total, 1032 Darwin's finches were mist netted and 86 of 707 males and 14 of 325 females were recaptured across years. We used the proportion of black plumage to age males, and the age at first capture plus the number of years between recapture to estimate minimum longevity. Minimum longevity ranged from 12 to 15 years and was lowest in the critically endangered *C. pauper* (12 years). The average number of years between first capture and last recapture was significantly lower in females than in males. Because long-term mist netting provides information on age structure, recruitment and longevity in males and females, it should be a key component of effective conservation planning.

Keywords *Camarhynchus* · *Geospiza* · Galapagos · Monitoring · Morphology · Recruitment

Zusammenfassung

Mindestlebensdauer und altersassoziierte Männchenbefiederung von Darwin-Finken auf der Insel Floreana.

Einige Arten der Darwin-Finken auf den Galapagos-Inseln weisen rückläufige beziehungsweise lokal ausgestorbene Populationen auf. Akustische Untersuchungen liefern nützliche Informationen über die Populationsgröße, jedoch nicht über Alter und Morphologie. Diese Studie stützt sich auf Fangdaten, die im Zeitraum 2004–2016 mittels Japannetzen auf der Insel Floreana gesammelt wurden. Ziel der Studie ist, die artspezifische Mindestlebensdauer von vier Darwin-Finkenarten zu ermitteln. Die untersuchten Arten sind: Kleiner Baumfink (*Camarhynchus parvulus*), Hybrider Baumfink (*Camarhynchus spp.*), Mittlerer Baumfink (*C. pauper*) und Kleiner Grundfink (*Geospiza fuliginosa*). Insgesamt wurden 1032 Individuen gefangen, wobei 86 der 707 Männchen und 14 der 325 Weibchen über den Untersuchungszeitraum hinweg wiedergefangen wurden. Zur Altersschätzung der Männchen errechneten wir den schwarzen Gefiederanteil, und zur Schätzung der Mindestlebensdauer (ergo des Mindesthöchstalters) die Summe von „Erstfangalter" und „Anzahl der Jahre zwischen Fang und Wiederfang". Die Mindestlebensdauer lag zwischen 12 und 15 Jahren und war am niedrigsten bei *C. pauper* (12 Jahre). Die durchschnittliche Anzahl der Jahre zwischen Erstfang und letztem Wiederfang war bei Weibchen signifikant geringer als bei Männchen. Da langfristige Fang-Wiederfang-Studien Informationen über Altersstruktur, Populationsdynamik und Lebensdauer bei Männchen und Weibchen liefern, sollten sie einen zentralen Bestandteil in der effektiven Naturschutzplanung bilden.

Introduction

Biodiversity loss and species extinctions are at their highest levels in recorded human history (Ceballos et al. 2015; Ducatez and Shine 2017). In birds, currently ~1200 species are at risk of extinction (International Union for

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Conservation of Nature 2016) and ~ 100 of ~ 10,000 species have become extinct since the 1600s (Grant and Grant 1992; Baiser et al. 2018). Island systems are notoriously prone to extinction risk but also harbour many endemic species (Blackburn et al. 2004). Of the endangered bird species, 39% are endemic to island systems (Grant and Grant 1992). Monitoring studies are key to informing conservation approaches for endangered birds (Campbell et al. 2002; Schemske et al. 1994; Tear et al. 1995). Songbird populations are commonly monitored using acoustic surveys (Haselmayer and Quinn 2000; Peters and Kleindorfer 2017); however, little or no information about population age structure can be gleaned from acoustic surveys. Assessing the age and sex composition of a population is critical for predicting its reproductive potential (Nur and Geupel 1993) and recruitment into the breeding population (Grant and Grant 1992). Capture and release methods provide information on the age and sex of individuals at the time of capture and allow researchers to individually monitor uniquely marked birds in space and time. Individual quality can be evaluated on the basis of morphological measurements at the time of handling, but calibration approaches are necessary to ensure the accuracy of the information. Here we examine longevity and measurement reliability using mark and recapture methods in common and endangered island bird species in the Darwin's finch group.

The average adult lifespan of birds varies greatly. For example, Sedge Warblers (*Acrocephalus schoenobaenus*) live for on average 2 years (Zając et al. 2006) and Wandering Albatrosses (*Diomedea exulans*) can live for up to 50 years (Lecomte et al. 2010). One challenge when interpreting lifespan data is that the maximum age of a bird can differ markedly from the average lifespan for the species for a variety of reasons including different survivorship due to individual quality and/or different mortality bottlenecks across age classes (Kirkwood and Holliday 1979; Crone 2001; Møller 2006). Interval sampling across age classes (e.g. juvenile survival, adult survival) is key to understanding mortality bottlenecks and model population persistence (Weimerskirch 1992). In this regard, mark and recapture data provide details on the age and sex of captured individuals. If birds can be aged in hand, then age at capture can be used to sample age class distribution and assess longevity.

A life history perspective is useful when interpreting the significance of lifespan in birds (Bennett and Owens 2002). In general, species with higher annual adult survival invest less effort into each reproductive event, whereas species with lower annual adult survival invest more into each reproductive event (Ghalambor and Martin 2001; Møller 2006). There is also an effect of body size on longevity, with greater longevity in larger birds (e.g. Grant and Grant 1989; Møller 2006). Finally, there are well-established latitudinal patterns. For example, north temperate songbird species tend to have larger clutches and shorter longevity compared with tropical songbird species (Ghalambor and Martin 2001; Lloyd et al. 2014). Controlling for latitude, clutch size and environment, a medium-sized songbird in a tropical system is expected to have greater longevity than a smaller-sized songbird.

Individual quality is a predictor of survival and fitness. Body condition has been shown to reflect individual quality with evidence that birds in good body condition have greater annual survival (Bergan and Smith 1993; Blums et al. 2005; Newton 1993), brighter plumage (Silva et al. 2017) and increased pairing success (Yamada and Soma 2016). At the time of mist netting, measuring body condition is therefore useful for understanding individual survival probability. Body condition assessment often relies on the measurement of morphological traits like body size (wing length, tarsus length) that are interpreted in relation to mass. Therefore, identifying the reliability of morphological measurements is key to determining if birds differ in body condition or if different body condition scores are the consequence of error in morphological measurement. Calibration approaches are essential to understanding sources of measurement error. For long-term studies that measure recaptured birds (Chastel et al. 1995; Przybylo et al. 2000), comparing measurement consistency in the same bird is one approach to testing measurement accuracy. For example, if a recaptured bird has the same morphological measurement 1 or 5 years after first capture and is measured by different researchers in different years, then measurement accuracy can be assumed to be relatively high. However, birds can change their morphology with age via growth, beak abrasion or feather wear. Therefore, as a first step, comparing measurements of recaptured birds can provide insights into the consistency of measured values.

The geological and biological characteristics of the Galapagos Islands were transformational for Charles Darwin's articulation of evolutionary theory by means of natural selection (Darwin 1837; cited in Sulloway 1984). While no Darwin's finch species has yet become extinct, two Darwin's finch species are critically endangered (Mangrove Finch *Camarhynchus heliobates*, Medium Tree Finch *Camarhynchus pauper*) (Dvorak et al. 2012) and six Darwin's finch species have declined within one decade on two inhabited islands (Dvorak et al. 2012; O'Connor et al. 2010a; Peters and Kleindorfer 2017). Within the Galapagos archipelago, Floreana Island has the longest history of human settlement and the greatest number of species extinctions (O'Connor et al. 2010a); the tally for Darwin's finch species is equally grim and only five of nine species persist (Dvorak et al. 2017). The critically endangered Medium Tree Finch (*C. pauper*) is range-restricted to Floreana Island, and its population is declining. Acoustic surveys from 2004 to 2013 showed a 52% decrease in *C. pauper*, and currently it is estimated that there are ~ 2500 male birds (Peters and Kleindorfer 2017) and ~ 3900–4700 territories of this species (Dvorak et al. 2017). Several threatening processes impact the Medium Tree Finch including habitat loss and invasive species (plants, parasites, rodents, cats and dogs) (Fessl et al. 2018; O'Connor et al. 2010b). Recently, it was shown that Medium Tree Finch females frequently pair with Small Tree Finch (*Camarhynchus parvulus*) males, and not vice versa (Kleindorfer et al. 2014a; Peters and Kleindorfer 2017; Peters et al. 2017), which could further exacerbate Medium Tree Finch decline. Here, we focus on understanding key life history traits of the species, which are poorly understood. Specifically, we are interested in assessing maximum age and average longevity to more fully understand if longevity patterns in the Medium Tree Finch deviate from those in sympatric Darwin's finch species on Floreana Island.

Minimum longevity in Darwin's ground finches (*Geospiza* spp.) is known from the long-term study on Daphne Major Island by Grant and Grant (2010). Using data from mist netted, banded, resighted and/or recaptured birds, minimum longevity was 16 years in Cactus Finch (*Geospiza scandens*) and Medium Ground Finch (*Geospiza fortis*) (Grant and Grant 2010).

The aim of this study is to identify minimum longevity, male age, and test measurement accuracy using mist netting data from Darwin's finches on Floreana Island. The study species and their average mass are: Small Tree Finch (*C. parvulus*), 12 g; hybrid finches (*Camarhynchus* spp.), 14 g; Medium Tree Finch (*C. pauper*), 16 g; and Small Ground Finch (*Geospiza fuliginosa*), 14 g. Female Darwin's finches remain grey across their lives, but the colour of crown and chin plumage of males changes with age. For males, we examine (1) age in relation to plumage colour, and (2) maximum age at recapture calculated as the difference between age at first capture and number of years since first capture. For females, we calculate (3) the maximum number of years between captures. We test the following predictions. A previous study on *C. parvulus* on Santa Cruz Island found annual change in the proportion of black plumage in males, which was used to age males (Kleindorfer 2007). Because we are studying the same genus, we predict the same pattern on Floreana Island, whereby *Camarhynchus* males increase the proportion of black plumage on their chins and crowns with each year of moult until attaining a fully black crown and chin by 6 years of age. We predict that maximum age at recapture within Floreana species will be highest in *C. pauper* because it has the largest relative body size. Finally, (5) we will use the recapture data to test measurement reliability for morphological variables across years.

Materials and methods

Study site and study species

This study was done in the Cerro Pajas *Scalesia* forest (~ 300–400 m a.s.l.) on Floreana Island from 2004 to 2016. We used mist nets to capture birds (described below). The focal species for analysis are Small Tree Finch (*Camarhynchus parvulus*), Medium Tree Finch (*Camarhynchus pauper*), Small Ground Finch (*Geospiza fuliginosa*), and a newly described group of *Camarhynchus* hybrid birds [identified from the analysis of nine microsatellite loci (Kleindorfer et al. 2014a)] that are the result of pairings between females of the critically endangered *C. pauper* and males of the common *C. parvulus* (Peters and Kleindorfer 2017; Peters et al. 2017). While the Small Tree Finch and hybrid birds can reasonably be described as having formed a hybrid swarm (Peters and Kleindorfer 2017), we analyse data for each group separately to explore possible differences in recapture pattern and/or annual change in moulting. The mist netting data analysed here are an integral component of our long-term nest monitoring that is done in the last remnant *Scalesia* forest (3.71 km^2) on Floreana Island (Peters and Kleindorfer 2017) at the base of the Cerro Pajas volcano (Fig. 1).

Mist netting and recapture data

A total of 1032 Darwin's finches were mist netted in 2004, 2005, 2006, 2008, 2010, 2012, 2013, 2014 and 2016. To capture birds, we placed six 12-m mist nets adjacent to each other along a 2.4-km track (Fig. 1). The mist nets were set up from 6 to 11 a.m. daily for around 2 weeks during February of each year. February is generally the peak breeding period for Darwin's finches on Floreana Island. Each captured bird was fitted with an aluminium leg band with a unique band number that allows identification if recaptured.

At the time of banding, we measured the morphology of birds using callipers (0.1-mm accuracy) and rulers for wing and tail length (0.5-mm accuracy). We measured the following morphological traits: bill length (head), bill length (naris), bill depth, bill width, tarsus length, wing length and tail length. Morphological measurements were done by multiple researchers (Kleindorfer, Christensen, O'Connor, Peters); during all years, at least two researchers were in the field at the same time and hence we calibrated measurement both within and across years (all researchers calibrated against Kleindorfer). We considered two researchers to have made field-calibrated measurements if their measurements differed by less than 5% for any trait. Here we compare accuracy across years in recaptured birds.

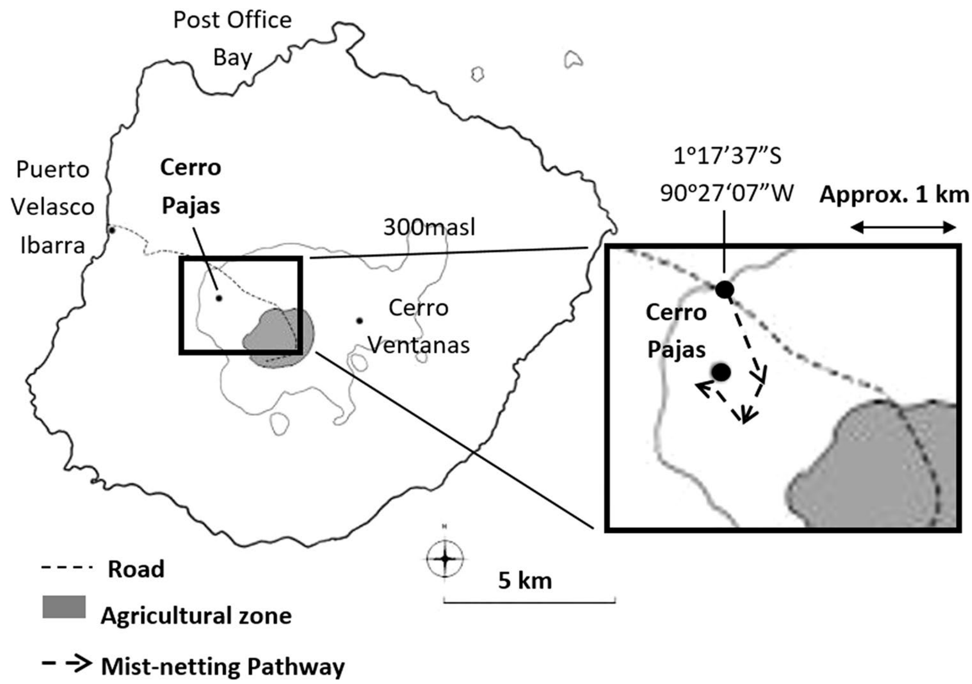

Fig. 1 Map and inset of the mist netting area situated along a 2.4-km path leading to the Cerro Pajas volcano on Floreana Island. Global Positioning System coordinates indicate the start of the trail

The sample size for recaptured birds is 100, with 86 males recaptured and 14 females recaptured (Table 1). The sample size for recaptured birds per Darwin's finch group is 26 *C. parvulus,* 24 hybrids, 17 *C. pauper*, and 33 *G. fuliginosa*. For the analysis, we compare first capture and last recapture. The recapture of the same bird within the same year was not included in the total captures or total recaptures. The recapture data were used to assess minimum longevity and/or number of years between capture, and to compare morphological variables to assess measurement reliability.

Age assessment

Previous studies on different islands found that *Camarhynchus* tree finches can be aged by the proportion of black in the crown and chin feathers (Kleindorfer 2007) and *Geospiza* finches can be aged by the proportion of black in the body feathers (Price 1984). Specifically, on Santa Cruz Island, *C. parvulus* males have brown plumage as yearling males but the proportion of black in their crown and chin increases with each annual moult until ~ 6 years of age when the crown and chin are completely black (Kleindorfer 2007).

Table 1 Summary of mist netted and recaptured male and female Darwin's finches on Floreana Island sampled from 2004 to 2016

Species	Total no. mist netted	No. recaptured	% Recaptured	Maximum years between capture[a]	Minimum longevity (years)
Males					
Camarhynchus parvulus	192	20	10.4	11	15
Hybrids	116	23	19.8	8	14
Camarhynchus pauper	116	16	13.8	10	12
Geospiza fuliginosa	283	27	9.5	9	15
Females					
C. parvulus	97	6	6.2	7	
Hybrids	28	1	3.6	3	
C. pauper	40	1	2.5	2	
G. fuliginosa	160	6	3.8	8	

C. parvulus Small Tree Finch, *Hybrids Camarhynchus* spp., *C. pauper* Medium Tree Finch, *G. fuliginosa* Small Ground Finch

[a]Maximum number of years between first capture and last recapture is shown for males and females, whereas minimum longevity is only shown for males; males can be aged based on chin and crown plumage whereas females cannot be reliably aged at first capture

On Daphne Major Island, *Geospiza* males have streaky grey/brown plumage as yearling males but the proportion of black plumage increases with each annual moult until the males become fully black-bodied by ~6 years of age (Price 1984). We used the established categories to assign a plumage category at the time of mist netting. The proportion of black plumage was categorized as: black 0 (no black plumage present), black 1, black 2, black 3, black 4, and black 5 (totally black plumage) (described in Kleindorfer 2007; Price 1984). For males first captured at black 5, we conservatively assigned them an age of 6 years at first capture. Minimum longevity at recapture was calculated as the age at first capture plus the number of years between recapture.

Female Darwin's finches remain grey across their lives and therefore cannot be aged using plumage colour. For female recaptures, we calculated the number of years between capture. We do not estimate female longevity, but rather report maximum number of years between capture for females.

Statistical analysis

All statistical analyses were done using IBM SPSS Statistics 23.0; graphs were produced using the SigmaPlot 13.0. To test if the change in black plumage category increased linearly with number of years between capture, we used multiple regression analysis; we included bill length head as a covariate. One-way ANOVA was used to test for species differences in male age at first capture and male maximum recapture age with Tukey post hoc comparisons of species pairs. The difference in morphological measurements across years was examined between and within species. Multivariate ANOVA (MANOVA) was used to test the difference in morphological measurements (year 2 minus year 1) as the dependent variable (a value close to zero indicates high measurement reliability) against species as the fixed factor. Within each species, we used a paired *t*-test to compare morphological measurement (year 1 versus year 2) per recaptured bird. The results were Holm adjusted to account for multiple comparisons and reduce the probability of a type II error.

Results

Annual change in plumage colour and age

In general, the proportion of black plumage in male birds increased per year of capture. We compared the variables change in black plumage category and number of years between capture using regression analysis. We restricted the analysis to 33/59 *Camarhynchus* males with black 0–4 plumage at first capture; we compared their rank plumage colour across year of recapture until black 5. There was a statistically significant linear association between number of years between capture and change in plumage category ($r=0.74$, $n=33$, $p=0.001$). The regression equation for annual change in male plumage was $y=0.75 \times \text{year} - 0.91$. If the same male was recaptured across 1 year then it tended to increase its plumage category by ~1 (e.g. B2–B3) and if the same male was recaptured across 5 years, then it tended to increase its plumage category by ~5 (e.g. B0–B5) (Fig. 2). However, there were exceptions (Table 2). While the plumage of 17/33 birds (51.5%) changed by one category per year, in 4/33 (12.1%) the colour stayed the same, in 8/33 (24.2%) increased black plumage was shown in one category less than expected, and in 2/33 (6.1%) increased black plumage was found in one category more than expected. In addition, two birds showed increased black plumage by only two categories instead of four (both B0 and B2 across 2006–2010). We explored this further in relation to the *Camarhynchus* genetic group, and the data shown in Table 2 suggest that hybrid finches may have more erratic patterns of annual plumage change, but the difference across groups was not statistically significant (Likelihood Ratio 14.55, $p=0.069$).

Age at first capture

There was no statistically significant difference in average age at first capture (as assessed by black plumage category) in *Camarhynchus* tree finch males (ANOVA: $F=0.34$, $df=2$,

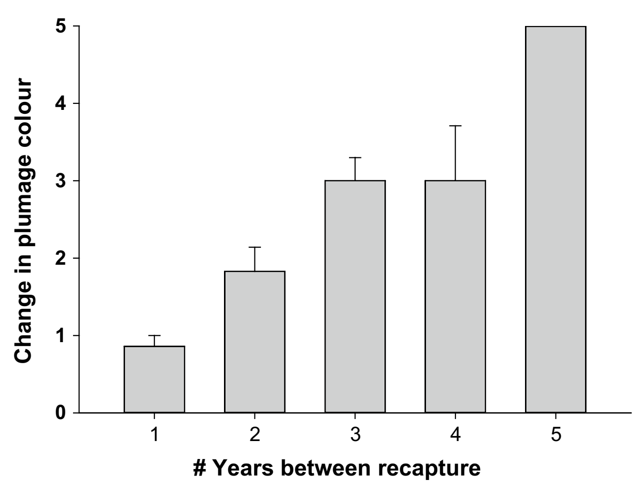

Fig. 2 Difference (mean ± SE) in black plumage category change (rank change from 1 to 5) for a recaptured *Camarhynchus* male in relation to no. (#) of years between recapture. On average, males recaptured within 1 ($n=14$), 2 ($n=6$) or 3 ($n=8$) years showed a change in black plumage by 1, 2 or 3 ranks, as expected, but the pattern of black plumage change did not increase by four when no. of years between recapture was 4, perhaps because of the small sample size ($n=4$). See Table 2 for the percentage of males per genetic group that showed an increase in no. of black plumage categories that was more or less than expected

Table 2 Number and percentage of *Camarhynchus* males for which the black plumage category increased by zero, one, two or more across 1 year

Observed rank change in plumage colour per year	*C. parvulus*		Hybrids		*C. pauper*	
	Number	%	Number	%	Number	%
Increased by one	5	45.5	5	35.7	7	87.5
Stayed the same	2	18.2	2	14.3	0	0.0
Increased by one too few	4	36.4	4	28.6	0	0.0
Increased by one too many	0	0.0	2	14.3	0	0.0
Increased by two too few	0	0.0	1	7.1	1	12.5

The predicted association is that males show one black plumage category increase per year

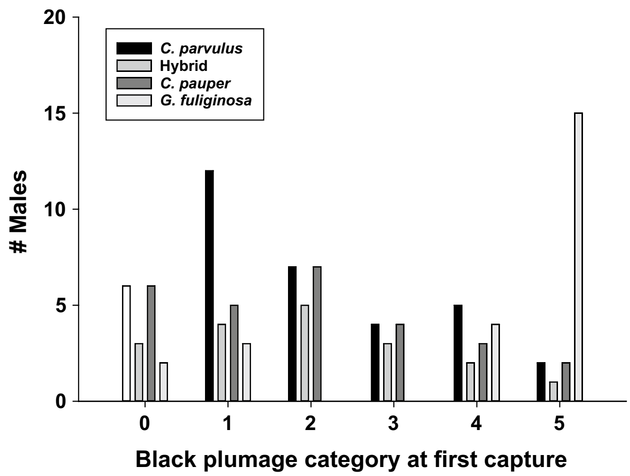

Fig. 3 Number of male Darwin's finches in each plumage category at first year of capture. Data are for Small Tree Finch (*Camarhynchus parvulus*), *Camarhynchus* hybrids, Medium Tree Finch (*Camarhynchus pauper*) and Small Ground Finch (*Geospiza fuliginosa*). Black plumage category generally corresponds with age, whereby black 0 are yearling males and black 5 are 6+years old (see "Materials and methods"). Data are for males captured in the Cerro Pajas region of Floreana Island

$p=0.714$) (Fig. 3). However, there were significantly more *G. fuliginosa* males with plumage category black 5 compared with tree finches (ANOVA: $F=8.61$, $df=3$, $p<0.001$; Tukey post hoc tests $p<0.02$ for all *G. fuliginosa* and *Camarhynchus* comparisons). The mean age at first capture for males was ~3 years in *C. parvulus* (3 ± 0.4 years), hybrid finches (3.1 ± 0.3 years), and *C. pauper* (3.4 ± 0.5 years) and ~5 years in *G. fuliginosa* (5 ± 0.3 years).

Minimum longevity

A total of 707 male and 325 female Darwin's finches were mist netted between 2004 and 2016 (Table 1). Significantly more male ($n=86$) than female ($n=14$) birds were recaptured ($x^2=13.34$, $df=1$, $p<0.001$).

The average number of years between first capture and last recapture was examined in males and females separately. The average number of years between capture was longer in *Camarhynchus* males (4.0 ± 0.5, $n=36$) than in females (2.4 ± 0.8, $n=7$) (multiple regression analysis: sex—$r_{part}=-0.34$, $p=0.030$; bill length head—$r_{part}=-0.88$, $p=0.012$). There was no statistically significant difference in *Geospiza* males (2.9 ± 0.4, $n=27$) or females (2.7 ± 1.1, $n=6$) (regression analysis: sex—$r_{part}=-0.01$, $p=0.979$; bill length head—$r_{part}=0.35$, $p=0.051$).

Minimum longevity ranged from 12 to 15 years in males (Table 1) and was longest in *C. parvulus* and *G. fuliginosa*, and shortest in the critically endangered *C. pauper*.

The maximum number of years between capture was 8–11 years in males and 2–8 years in females (Table 1). Among males, the maximum number of years between capture was 11 years in *C. parvulus*, 10 years in *C. pauper*, 9 years in *G. fuliginosa*, and 8 years in hybrid finches. Among females, the maximum number of years between capture was 8 years in *G. fuliginosa*, 7 years in *C. parvulus*, 3 years in hybrid finches, and 2 years in the critically endangered *C. pauper*.

Morphology

We show the association between wing length and beak length for the 59 male *Camarhynchus* finches that were recaptured and analysed in this study (Fig. 4), but do not explore morphological differences across genetic groups as this has already been done by Peters et al. (2017). In this study, our research interest was to assess the reliability of morphological measurement for each bird that was recaptured. First, we compared the difference in the same morphological trait value across years using MANOVA, with a value close to zero indicating high measurement reliability. From this analysis, there was no statistically significant difference in morphological measurement. The *F*- and *p*-values from the MANOVA test for each morphological trait are as follows: bill length (head) $F=1.15$, $p=0.352$; bill length (naris) $F=1.02$, $p=0.370$; bill depth $F=0.67$, $p=0.516$; bill width $F=1.48$, $p=0.240$; tarsus $F=0.03$, $p=0.970$; wing $F=1.16$, $p=0.324$; tail $F=0.03$, $p=0.969$. Table 3 summarises measurement reliability as the percentage difference comparing year 1 (year of first capture) with year 2 (year of recapture). Using the absolute values in measurement

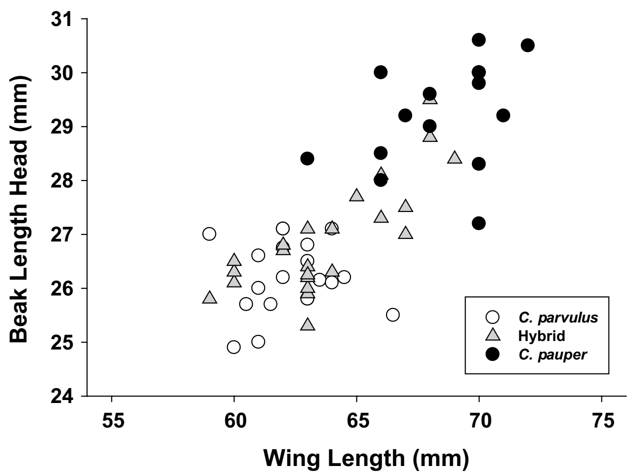

Fig. 4 The association between wing length (mm) and beak length head (mm) in *Camarhynchus* males on Floreana Island. Data are for 20 *C. parvulus*, 23 hybrids, and 16 *C. pauper* that were recaptured as part of this study. We used nine microsatellite loci to assign adult males to a genetic group (Kleindorfer et al. 2014a; Peters et al. 2017). Assignment to each genetic group was based on the individual membership coefficient (*qi*) derived from Bayesian clustering analysis using STRUCTURE, which rates the probability (0–1) of an individual belonging to the *C. parvulus* cluster ($qi \geq 0.80$ for *C. parvulus*, $qi \leq 0.20$ for *C. pauper* and $0.80 > qi > 0.20$ for the hybrid group)

difference, the average difference in measurement reliability across all morphological variables was 3.3%. Next, we examined the difference in morphological variables across years using a paired *t*-test per bird and per species (Table 3). Because we ran a separate *t*-test for each variable, we used the Holm adjustment to reduce the probability of a type II error. After Holm adjustment, morphological measurements did not statistically differ across year of capture, with the exception of longer wing length in recaptured hybrid finches (Holm adjustment $p = 0.049$; see Table 3).

Discussion

This study had three main aims: to measure annual plumage change in males, to identify minimum longevity, and to test the reliability of morphological measurements in Darwin's finches on Floreana Island. The results were generally consistent with a previous study on *C. parvulus* on Santa Cruz (Kleindorfer 2007) whereby male *Camarhynchus* on Floreana also generally showed a change in the proportion of black plumage on the chin and crown annually. Hence male plumage colour category is useful for the assessment of male age. Minimum longevity in male Darwin's finch species on Floreana ranged from 12 to 15 years. Finally, there was high measurement reliability (average difference 3.3%) for morphological variables measured across years.

Our results provide supporting evidence for the use of plumage colour to interpret male age in *Camarhynchus* on Floreana Island. The previous findings of annual plumage change in male *C. parvulus* on Santa Cruz (Kleindorfer 2007), combined with the findings here, suggest that the annual increase in black plumage on the crown and chin of *C. parvulus* and *C. pauper* could follow a general pattern. We restricted our analysis to 33 recaptured birds that were identified as black 0 to black 4 at first capture, and compared plumage rank change over year(s) of recapture until this reached black 5 because this allowed us to track patterns of plumage change across years. Some males changed plumage category across years of capture more quickly than expected, and others took longer than expected. For example, a *C. pauper* categorised as black 0 (2006) at first capture was recaptured 4 years later and re-categorised as black 2; the predicted plumage colour after 4 years was black 4. Conversely, a *Camarhynchus* hybrid categorised as black 2 (2010) at first capture was recaptured 2 years later and re-categorised as black 5; the predicted plumage was black 4. Plumage colour has been shown to be influenced by an individual's body condition (Silva et al. 2017). A Darwin's finch with poor body condition or immune function, for example, may have delayed plumage development. From studies on other songbird systems, there is evidence for an effect of physiology (e.g. increased testosterone, decreased immune response) on the delayed onset of male plumage colouration (Peters 2000; Peters et al. 2000) and a negative association between endoparasite intensity and plumage colour (Colombelli-Négrel and Kleindorfer 2008). Notably, the Darwin's finch with the slower than expected annual moult in the example above was first captured during a drought year (rainfall from January to March was 118 mm) while the bird with the faster than expected annual moult was first captured during a high rainfall year (635 mm) (Peters and Kleindorfer 2015), suggesting that prevailing ecological conditions may also play a role in annual moult patterns.

We captured more *G. fuliginosa* than *Camarhynchus* males in black plumage in the highland *Scalesia* forest, which is an area considered a stronghold for the *Camarhynchus* tree finches (O'Connor et al. 2010b, c; Galligan and Kleindorfer 2010). While we do not know why this occurred, there are several possible explanations related to maturation, survival, and dispersal. There is some evidence that *G. fuliginosa* males and females have comparable physiological stress profiles in the *Scalesia* forest (Clark et al. 2018), occupy diverse habitats across elevational gradients (Kleindorfer et al. 2006), and sustain *Philornis downsi* parasites for longer compared with *Camarhynchus* finches (Kleindorfer et al. 2014b). Perhaps *G. fuliginosa* is more tolerant of environmental change caused by agricultural activity, introduced predators, and introduced parasites in increasingly human-modified *Scalesia*

Table 3 Morphology measurements (mean ± SE) in recaptured birds comparing year of first capture (*Year 1*) versus year of recapture (*Year 2*)

Morphology variable (mm)	Year 1 (mean ± SE)	Year 2 (mean ± SE)	% Difference	*t*-value (*df*)	*p*-value	Holm *p*-value
C. parvulus						
Beak length head	26.1 ± 0.1	26.6 ± 0.4	1.97 ± 1.6	− 1.26 (24)	0.221	1.11
Beak length naris	7.3 ± 0.0	7.3 ± 0.0	0.14 ± 1	− 0.14 (24)	0.891	0.891
Beak depth	7.1 ± 0.0	7.1 ± 0.0	− 0.64 ± 0.8	0.79 (24)	0.436	1.31
Beak width	6.2 ± 0.0	6.3 ± 0.1	2.25 ± 1.7	− 1.32 (24)	0.200	1.2
Tarsus	20.2 ± 0.2	20.4 ± 0.2	0.69 ± 0.7	− 0.97 (23)	0.343	1.37
Tail	38.3 ± 0.5	38.8 ± 0.8	1.63 ± 2.1	− 0.79 (15)	0.441	0.882
Wing	61.3 ± 0.4	62.2 ± 0.4	1.37 ± 0.7	− 2.08 (24)	*0.049*	0.343
Mass (g)	12.4 ± 0.1	12.2 ± 0.2		2.10 (18)	.069	
Hybrids						
Beak length head	26.9 ± 0.2	26.9 ± 0.2	0.16 ± 0.3	− 0.50 (23)	0.624	1.87
Beak length naris	7.7 ± 0.1	7.7 ± 0.1	0.05 ± 0.7	− 0.08 (23)	0.941	0.941
Beak depth	7.5 ± 0.1	7.4 ± 0.0	− 0.42 ± 1	0.41 (23)	0.685	1.37
Beak width	6.5 ± 0.0	6.6 ± 0.0	0.7 ± 1.3	− 0.55 (23)	0.586	2.34
Tarsus	20.9 ± 0.2	21.0 ± 0.3	0.53 ± 0.9	− 0.57 (23)	0.576	2.88
Tail	40.1 ± 0.3	40.5 ± 0.5	1.08 ± 1	− 1.14 (20)	0.267	1.60
Wing	63.8 ± 0.6	64.8 ± 0.6	1.63 ± 0.6	− 2.95 (23)	*0.007*	*0.049*
Mass (g)	13.7 ± 0.4	13.4 ± 0.4		0.120 (17)	0.906	
C. pauper						
Beak length head	29.4 ± 0.2	29.3 ± 0.2	− 0.35 ± 0.8	0.44 (16)	0.664	2.66
Beak length naris	8.9 ± 0.1	8.7 ± 0.1	− 2.5 ± 1	2.60 (16)	*0.019*	0.114
Beak depth	8.4 ± 0.1	8.2 ± 0.1	− 1.61 ± 0.6	2.67 (16)	*0.017*	0.119
Beak width	7.3 ± 0.0	7.1 ± 0.0	− 2.44 ± 1.1	2.25 (16)	*0.039*	0.195
Tarsus	22.1 ± 0.3	21.9 ± 0.4	− 0.37 ± 1.5	0.26 (16)	0.801	2.40
Tail	42.7 ± 1.1	42.7 ± 0.9	− 0.10 ± 3.2	0.03 (11)	0.975	0.975
Wing	68.7 ± 0.6	68.9 ± 0.9	0.27 ± 1.2	− 0.24 (15)	0.816	1.63
Mass (g)	15.7 ± 0.6	16.0 ± 0.7		0.988 (10)	0.349	
G. fuliginosa						
Beak length head	28.2 ± 0.1	28.2 ± 0.1	− 0.06 ± 0.3	0.22 (31)	0.827	1.65
Beak length naris	8.7 ± 0.0	8.7 ± 0.0	− 0.42 ± 0.8	0.52 (29)	0.606	3.03
Beak depth	7.7 ± 0.0	7.6 ± 0.0	− 0.82 ± 1.1	0.78 (29)	0.443	2.658
Beak width	6.7 ± 0.1	6.7 ± 0.0	− 0.5 ± 1.2	0.44 (29)	0.665	2.66
Tarsus	19.7 ± 0.2	19.7 ± 0.2	0.01 ± 0.8	− 0.01 (28)	0.991	0.991
Tail	40.0 ± 0.4	40.1 ± 0.3	0.35 ± 1.1	− 0.30 (18)	0.764	2.29
Wing	62.8 ± 0.4	63.7 ± 0.4	1.51 ± 0.5	− 2.79 (28)	*0.010*	0.07
Mass (g)	14.1 ± 0.2	14.3 ± 0.2		− 0.584 (20)	0.566	

Statistical results are shown for a paired *t*-test, including Holm-adjusted *p*-values (Aickin and Gensler 1996) for the morphological variables excluding mass

Statistical significance indicated by *italic*

forest (Kleindorfer and Dudaniec 2016), and perhaps colonist *G. fuliginosa* have accelerated maturation and/or survival compared with resident *Camarhynchus* finches? The interpretation of higher survivorship is supported by findings from Santa Cruz Island, where *G. fuliginosa* showed high gene flow between lowland and highland habitats (Galligan et al. 2012) and highland *G. fuliginosa* had 15% increased annual survival compared with lowland birds (Sulloway and Kleindorfer 2013).

Because female Darwin's finches remain olive green/grey throughout their lives, we could not use plumage colour to age female finches. Instead we compared the number of years between capture. Importantly, the average number of years between first capture and last recapture was significantly lower in females (~ 2.4 years) than in males (~ 4 years). We caught many more males (707 total, 86 recaptured) than females (325 total, 14 recaptured), therefore this difference could be an artefact of low sample size. Mist netting was done at the onset of the breeding season when males were actively defending their territories and females were preparing for egg-laying. The lower number of female recaptures is striking; for example, only one female *C. pauper* was recaptured across 2 years (2012 and 2014) during the entire 12-year mist netting period. It is possible that the sex difference in years between recapture is an indication that females experience higher annual mortality compared with males. This possibility requires study given that egg-laying females are essential for population persistence.

According to life history theory, larger body size is associated with lower extrinsic mortality and later onset of reproductive maturity (Ricklefs 2000; Møller 2006). In this study, *C. pauper* (~ 17 g) had 30% larger body mass than *C. parvulus* (~ 12 g) and 18% larger mass than *G. fuliginosa* (~ 14 g), but *C. pauper* had the shortest minimum longevity (12 years), which contradicts the life history prediction. Minimum longevity was 15 years in *C. parvulus* and *G. fuliginosa*, and therefore *C. pauper* had 22.2% shorter longevity. Why would *C. pauper* be an exception to the expected pattern of longer lifespan in larger birds? Long-term nest monitoring on Floreana Island from 2004 to 2014 identified significant in-nest mortality in *C. pauper* from the introduced fly *P. downsi* whose larvae parasitise developing birds (Fessl et al. 2001). Adult *P. downsi* oviposit eggs in bird nests; the eggs hatch and the larvae feed internally and externally on the blood and flesh of nestlings causing on average ~ 55% mortality in infested nests (Fessl et al. 2006; Kleindorfer and Dudaniec 2016; Fessl et al. 2018). Compared with other sympatric finch species, *C. pauper* had the most *P. downsi* larvae per nest (Kleindorfer et al. 2014b; O'Connor et al. 2010b). Larger-bodied finches tend to have more *P. downsi* (Dudaniec et al. 2007) and nests placed higher in the canopy, such as those built by *C. pauper*, tend to have more *P. downsi* (Kleindorfer et al. 2016). During the nestling phase, *P. downsi* consume the beak tissue of developing birds in the nest, which results in an enlarged naris (Kleindorfer and Sulloway 2016). In *C. pauper*, surviving adults had greater naris deformation compared with *C. parvulus* and *G. fuliginosa* (Kleindorfer and Sulloway 2016). It is possible that extreme naris deformation in adult *C. pauper* negatively impacts its foraging success or mating success, although this remains to be studied.

There was high measurement reliability for all morphological variables in recaptured birds. On average, the measurement difference was only 3.3%. Irrespective of the number of years between capture, the same values were measured for birds that were measured across two time periods. This finding is useful for several reasons. First, it shows that the calibration approach for measurement between researchers is effective across time. Second, the measurement consistency can be used to assess body condition and interpret individual quality (Blums et al. 2005; Silva et al. 2017; Yamada and Soma 2016).

This study highlights the utility of long-term mist netting data to inform recovery plans for target species under the threat of extinction. Investigation into the age structure of the critically endangered *C. pauper* is a case in point because its longevity assessed from mist netting data is less than expected when compared with that deduced from life history theory (Ricklefs 2000; Møller 2006), and the only recaptured female was recaptured across 2 years. In males, we confirmed that annual change in plumage colour can be used to age Darwin's tree finches on Floreana Island, though there are exceptions to the general pattern. Our data suggest that female longevity may be significantly shorter than male longevity based on the number of years between recapture. This finding underscores the urgent need to sample females and not just singing males in studies of critical conservation concern. Lastly, we confirmed measurement reliability for morphological traits in birds measured across years. Information from long-term mist netting of males and females can complement information from acoustic surveys that typically only sample singing males. With these combined insights, we should take greater steps to implement a recovery plan for *C. pauper* so that it does not become the first Darwin's finch species that we observe going extinct.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in the studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. This study was approved by the Flinders University Animal Welfare Committee (E270, E393). This publication is contribution no. 2218 of the Charles Darwin Foundation for the Galapagos Islands.

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