

Age-specific decline in take-off flight performance in a small passerine



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Age-specific differences in individual performance are reported in a number of taxa and are particularly well documented in humans. However, such data are generally lacking for birds, the taxon showing exceptionally long life in relation to body size. Here, we studied differences in vertical flight performance among three distinctive age classes (0.5-, 2- and 4.5-year-old birds) in laboratory-kept zebra finches, *Taeniopygia guttata*. We found that take-off flight speed differed significantly between the age classes with the oldest birds being ca. 10% slower than the youngest birds. Age classes also differed significantly in flight motivation, with old birds tending to be less motivated to fly than young ones. Thus, the age-specific decline in flight performance is clearly visible in zebra finches. In a broader perspective, poorer flight performance may impair foraging efficiency, social interactions and, most importantly, take-off speed when escaping predators. This may help elucidate age-specific decline in reproductive and survival rates commonly observed in natural populations.

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Senescence is an age-related progressive, irreversible decline in organismal performance. It has been widely documented at different levels of organization, including physiology, behaviour and physical performance (Rose, 1991). More importantly, age has been shown to determine survival and reproductive rates (Rose, 1991). Ageing has attracted considerable attention of researchers from different fields, as it has become an important issue in modern human society. Age-specific decline in individual physical performance is apparent among humans (Brown, Ryan, & Brown, 2007; Chamari, Ahmaidi, Fabre, Massebiron, & Prefaut, 1995; Dodds et al., 2014; Runge, Rittweger, Russo, Schiessl, & Felsenberg, 2004), and has been documented in domesticated (e.g. horses; Adamu, Noraniza, Rasedee, & Bashir, 2013; McKeever & Malinowski, 1997) and laboratory animals such as rats (Carter, Sonntag, Onder, & Pahor, 2002; Dehaan, Vandoorn, & Sargeant, 1988). There is growing evidence of age-related decline in individual performance in invertebrates (Anotaux et al., 2012; Liu et al., 2013; Miller et al., 2008; Ridgel & Ritzmann, 2005; Ridgel, Ritzmann, & Schaefer, 2003), but only very few studies have considered this issue among nonmammalian vertebrates (Catry, Phillips, Phalan, & Croxall, 2006; Elliott et al., 2015; Gilbert,

Zerulla, & Tierne, 2014; Lecomte et al., 2010; Møller & De Lope, 1999).

Most bird species rely on flight for foraging and predator avoidance, making this locomotion mode an ideal target to study age specificity of physical performance. Because flight may constitute a key determinant of the likelihood of surviving a predator attack, its performance may represent an important mortality factor (Møller, 2010). However, despite high predatory pressure in the wild, age-dependent components of mortality seem not to differ between captive and free-living birds (Ricklefs, 2000). This led Ricklefs to suggest that birds maintain high physical fitness until old age. This interesting hypothesis, to our knowledge, has never been tested. Here we used captive zebra finches, *Taeniopygia guttata*, to test the prediction that physical performance should not decline with advancing age among birds.

Since flight performance seems to be a critical trait determining survival of small passerine birds, we focused on determining whether birds of different age perform equally well in take-off flights. We studied the take-off vertical flights as they appear particularly costly and seem to be vital for predator escape (Kullberg, Fransson, & Jakobsson, 1996; Kullberg, Jakobsson, & Fransson, 2000). To better understand potential age-specific differences in flight performance we considered flight motivation and wing morphometrics. We also calculated the aerodynamic power of the flight.

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METHODS

Zebra finches live up to 5 years in the wild (Zann, 1996), up to 8 years in captivity (Heidinger et al., 2012), and show some signs of ageing such as decrease in basal metabolic rate in old age (Moe, Rønning, Verhulst, & Bech, 2009). Birds used in our study belonged to three distinct age classes: young birds (0.5 years old; 20 males and 17 females), middle-aged birds (2 years old; 17 males and 17 females) and old birds (4–5 years old; 17 males and 16 females). Middle-aged and old birds originated from the University of Bielefeld (Germany). They were transferred to the Jagiellonian University in Kraków (Poland) 8 months prior to the flight performance tests. After transfer birds from both older age groups were randomly paired to reproduce, thus fathering the youngest age class. Birds from all age groups were ringed at birth, so their exact age was known. After breeding, all the birds were kept in single-age and single-sex aviaries measuring 90 × 70 cm and 80 cm high, in a climate chamber at 30 °C, under a 12:12 h light:dark photoperiod. Birds were fed ad libitum with a standard mixture of seeds (Blattner no. 140104, Ermengerst, Germany) and had constant access to water.

Flight performance was measured using a vertical flight tube as described by Kullberg, Metcalfe, and Houston (2002). The transparent tube (height 185 cm, diameter 40 cm) had a release hole at the bottom and a collecting cage at the top. Each bird was released into the tube three times, with approximately 1 h of rest between each trial. Most birds flew into the collecting cage within a few seconds after being released. Those that did not fly into the collecting cage immediately were 'encouraged' by the experimenter placing a hand into the releasing hole every 20 s. If the bird did not fly into the collecting cage after six such 'encouragements', the trial was terminated. Flight trials were performed on 2 consecutive days to which birds were assigned in semirandom manner. Individuals with similar body condition (calculated as residuals from the regression of body mass and tarsus length) that belonged to the same sex/age group were split between the 2 days. The birds were tested in random order from 0830 to 1300 hours and they were food deprived until experimental flights were completed.

Flights were recorded with a digital camera (Samsung VP-D361). Flight time between two marks on the tube at 20 cm and 160 cm height (for video examples see the [Supplementary material](#)) was quantified by counting the video frames (each frame covering 0.033 s). The two-dimensional flight trajectory within the tube was traced using EthoVision XT9 (Noldus Information Technology, Wageningen, The Netherlands) and the actual distance covered by the birds during each flight was measured. There were no differences between the age classes in actual distances flown (see [Appendix tables](#)). Flight speed was calculated as actual distance divided by time. All individuals were trained to fly in the tube prior to the tests and flew at least five times. The trial flights were performed approximately a month prior to the tests.

Birds were weighed immediately before the first flight to the nearest 0.01 g, wing span was measured with a wing ruler to the nearest 0.1 cm ([Table 1](#)) and wing shape was traced on gridded paper and wing area calculated (Pennycuick, 1999). Wing loading was calculated by dividing body mass by wing area. Aerodynamic power of flights was calculated as the sum of kinetic energy and potential energy divided by flight time where kinetic energy = $0.5 \times \text{body mass} \times \text{flight speed}^2$ and potential energy = $\text{body mass} \times \text{gravitational acceleration} \times \text{height difference}$.

The time (s) that took a bird to move between two marks in the tube (vertically the shortest distance = 140 cm) and flight speed

Table 1

Morphometric data for the three age classes of the birds

Variable	Young	Middle-aged	Old	$F_{2,101}$	P
Body mass (g)	11.61±0.15	11.50±0.15	11.56±0.17	0.12	0.88
Wing span (cm)	18.0±0.13	17.8±0.10	17.8±0.10	0.57	0.57
Wing area (cm ²)	63.31±0.77	62.28±0.70	62.87±0.83	0.46	0.63
Wing loading (g/cm ²)	0.184±0.002	0.185±0.002	0.185±0.004	0.05	0.95

Reported values are averages ± SE. Fixed-model analyses including age and sex effects revealed no significant differences and lack of interactions. Presented results are of a minimum model with age class as a single explanatory variable.

(actual distance in cm divided by time in s) were used as proxies of take-off flight performance. All trials during which the birds flew the full height of 140 cm were included in the analyses ($N = 299$). Flight time was log-transformed to meet the criteria of normality. Flight motivation was a binomial variable indicating whether a given flight took place with or without additional 'encouragement' by the experimenter. In this analysis we included all trials ($N = 312$), including those in which birds did not cover 140 cm vertical distance.

Variation in flight time, flight speed and flight power were analysed with linear mixed models, variation in flight motivation with a generalized linear mixed-effects model and variation in morphometric measures with a fixed-effect model using R ([R Development Core Team, 2008](#)). In all models sex, age class and the day of the trial were fixed effects and, additionally, in mixed models individual ID was a random effect, to account for multiple flights of the same bird. In the analyses of flight time, speed and motivation, wing loading was included as a covariate. Because flight motivation could affect flight time, speed and aerodynamic power, it was included as a covariate in the analyses of these variables. In most models, interactions of the third and second order were not significant so they were excluded from the final analyses, but results of full models are presented in the [Appendix](#).

The study was performed according to the agreement from the First Local Ethical Committee on Animal Testing at the Jagiellonian University in Kraków (decision 146/2013).

RESULTS

Age class was the only factor explaining variation in flight time ([Table 2](#); raw mean ± SE: young: 0.82 ± 0.02 s; middle-aged: 0.85 ± 0.02 s; old: 0.94 ± 0.03 s). The oldest birds took significantly longer to fly the vertical distance of 140 cm than the young ones and longer than the middle-aged ones, although not significantly in the latter case (post hoc Tukey test: young: $z = -3.00$, $P = 0.01$; middle-aged: $z = -2.33$, $P > 0.05$; [Fig. 1a](#)). A similar pattern was observed for flight speed ([Table 2](#); raw mean ± SE:

Table 2

Results of linear mixed models of variation in flight time and flight speed and of generalized linear mixed models of variation in flight motivation

	df	Flight time		Flight speed		df	Motivation	
		F	P	F	P		χ^2	P
Age class	2, 96	4.94	0.01	4.64	0.01	2	7.68	0.02
Sex	1, 96	1.63	0.20	1.86	0.18	1	1.84	0.18
Day	1, 96	0.66	0.42	1.43	0.23	1	0.001	0.97
Wing loading	1, 96	0.07	0.79	0.02	0.88	1	3.15	0.08
Motivation	1, 196	0.81	0.37	0.51	0.48			

Age, sex and day were introduced as fixed factors. Wing loading was a covariate in all analyses and flight motivation in the analyses of flight time and speed. For the results including interactions (which all appeared nonsignificant) see [Appendix tables](#).

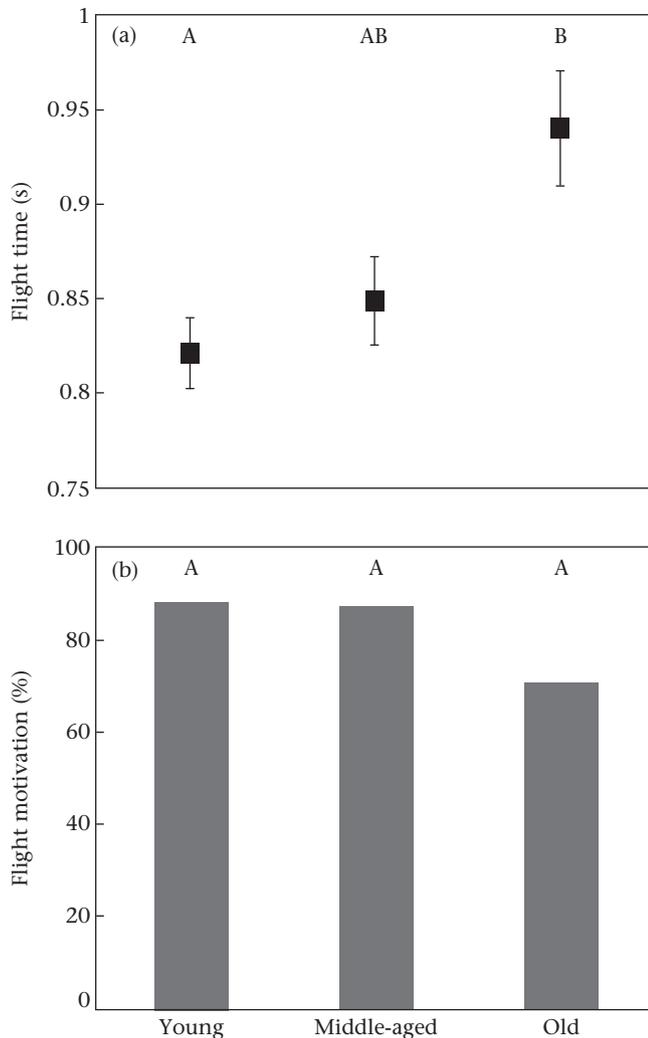


Figure 1. Flight performance in three age classes of zebra finches: (a) time of vertical flight over a distance of 140 cm (mean \pm SE), (b) percentage of flights without additional 'encouragement' by the experimenter. Different letters denote significant differences between the means.

young: 205 ± 6 cm/s; middle-aged: 200 ± 7 cm/s; old: 184 ± 8 cm/s). The oldest birds were significantly slower than the young ones and slower than the middle-aged ones, but not significantly in the latter case (post hoc Tukey test: $z = 2.88$, $P = 0.01$ and $z = 2.25$, $P = 0.06$, respectively).

Flight motivation differed significantly between the age classes (Table 2). The number of birds that flew without 'encouragement' tended to decline with age (young: 88.3%; middle-aged: 87.3%; old: 70.7%; Fig. 1b), but pairwise comparisons between the groups were not significant (post hoc Tukey test: $P > 0.05$).

Morphometric parameters did not differ between the age classes (Table 1) and did not explain variation in flight time and speed (Table 2 and Appendix). Variation in aerodynamic power of flights was shaped by a significant interaction between the age class and sex (the minimum model: age: $F_{2, 96} = 3.38$, $P = 0.04$; sex: $F_{1, 96} = 0.58$, $P = 0.45$; age*sex: $F_{2, 96} = 3.67$, $P = 0.03$). In analyses performed for each sex separately, there were no differences between the age classes among females, while among males age class was a significant predictor of flight power ($F_{2, 50} = 5.03$, $P = 0.01$) with the oldest males having less power than the middle-aged ones (post hoc Tukey test: $z = 3.14$, $P = 0.005$).

DISCUSSION

We showed that old zebra finches were significantly slower in vertical take-off flight than young and middle-aged ones (Fig. 1a), and that they tended to be less motivated to take off than younger birds (Fig. 1b). To our knowledge, this is the first study reporting age-specific differences in flight performance and thus indicating occurrence of senescence of physical performance in birds. This result clearly contradicts Ricklefs's (2000) suggestion that birds maintain high physical fitness until the very end of their life.

Flight performance may have important consequences for survival, at least among small passerine bird species. Under natural conditions take-off performance can be a vital trait for surviving predator attacks, especially in species living in habitats where predators are detected at close range and surprise attacks are common (Cresswell, 1993; Kenward, 1978; Van den Hout, Mathot, Maas, & Piersma, 2010). We suggest that age-related decline in flight performance should contribute to mortality patterns among birds. The disparity between our result and Ricklefs's (2000) suggestion that free-living birds should show similarly low ageing as captive birds is likely to be because his data concerned mainly large nonpasserine bird species. In fact, the survival rate of small passerine species might be much more dependent on physical performance than that of large nonpasserine species.

As shown, age-related decline in flight time and speed (actual distance based on trajectory divided by flight time) of zebra finches was accompanied by differences in their behaviour, with older animals being seemingly less motivated to take off. However, the observed differences in motivation do not explain age-specific variation in flight time and speed. Old birds may merely employ an energy-saving strategy or different antipredator strategies. We quantified take-off time and speed in response to a human experimenter, but not in a direct avian predator context. Thus, it is possible that older birds are more accustomed to people, but we think it unlikely that this effect could explain a difference between middle-aged and old birds (Fig. 1). In fact, young birds were probably more accustomed to the conditions of the local colony as they were born there.

Age-related variation in behaviour is very seldom studied in birds, yet a few studies that included behavioural traits in their analyses have shown that traits such as foraging abilities (Catry et al., 2006; Lecomte et al., 2010) and migratory performance (Møller & De Lope, 1999) decline with age. Reduced activity levels in older seabirds have been documented (Catry et al., 2006) and potentially our observation of 'less motivated' older zebra finches may be linked to overall activity levels, which, however, remains to be studied.

Poor flight performance observed among old birds may arise from age-specific deterioration in morphological or physiological properties (Elliott et al., 2015). Older birds could show reduced mass and power output of muscles similar to that reported in humans (Koopman & Van Loon, 2009; Runge et al., 2004). However, our estimation of aerodynamic power of flights does not show clear differences between the age classes. The only significant difference was observed among males, with old males showing lower aerodynamic power than middle-aged ones. Another potential mechanism to explain age-specific changes in flight performance may include possible deterioration in feather quality, a trait known to affect flight performance (Swaddle, Witter, Cuthill, Budden, & McCowen, 1996). Age-specific metabolic capacity may also constitute a potential physiological mechanism for the observed age differences in flight speed, as metabolic efficiency seems to deteriorate with age (Khandelwal, Enno, & Njanoor Narayanan, 1984; Moe et al., 2009).

In conclusion, birds do show an age-related decline in take-off flight time and speed. This proxy of physical performance may

have potentially important consequences for survival prospects, especially in a predator escape context, but the direct link between physical performance and survival remains to be determined. It is still possible that lower physical fitness of old birds does not increase predation rate. So, birds may not maintain high levels of physical fitness in old age as suggested by Ricklefs (2000), but they might still die primarily from age-independent mortality factors.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2015.04.003>.

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Appendix

Table A1

Full model in which flight time was examined in relation to age, sex, day, flight motivation and wing loading

	df	F	P
Age class	2, 89	4.84	0.01
Sex	1, 89	1.14	0.29
Day	1, 89	0.37	0.54
Motivation	1, 196	1.12	0.29
Wing loading	1, 89	0.65	0.42
Age class*Sex	2, 89	2.23	0.11
Age class*Day	2, 89	1.48	0.23
Sex*Day	1, 89	0.57	0.45
Age class*Sex*Day	2, 89	0.20	0.81

Table A2

Full model in which trajectory of flights (actual distance) was examined in relation to age, sex, day, motivation and wing loading

	<i>df</i>	<i>F</i>	<i>P</i>
Age class	2, 89	0.53	0.59
Sex	1, 89	0.22	0.64
Day	1, 89	0.15	0.69
Motivation	1, 196	0.13	0.72
Wing loading	1, 89	1.47	0.23
Age class*Sex	2, 89	1.48	0.23
Age class*Day	2, 89	0.31	0.73
Sex*Day	1, 89	1.74	0.19
Age class*Sex*Day	2, 89	0.62	0.54

Trajectory was log-transformed to fulfil requirements of normality.

Table A3

Full model in which flight speed was examined in relation to age, sex, day, flight motivation and wing loading

	<i>df</i>	<i>F</i>	<i>P</i>
Age class	2, 89	4.69	0.01
Sex	1, 89	1.43	0.24
Day	1, 89	1.01	0.32
Motivation	1, 196	0.78	0.38
Wing loading	1, 89	0.43	0.51
Age class*Sex	2, 89	2.29	0.11
Age class*Day	2, 89	1.48	0.23
Sex*Day	1, 89	1.08	0.30
Age class*Sex*Day	2, 89	0.28	0.76

Table A4

Full model in which flight motivation was examined in relation to age, sex, day and wing loading

	<i>df</i>	χ^2	<i>P</i>
Age class	2	6.15	0.05
Sex	1	0.0001	0.99
Day	1	0.0001	0.99
Wing loading	1	2.87	0.09
Age class*Sex	2	0.20	0.90
Age class*Day	2	0.03	0.98
Sex*Day	1	0.0001	0.99
Age class*Sex*Day	2	0.001	0.99

Table A5

Full model in which aerodynamic power of flights was examined in relation to age, sex, day and motivation

	<i>df</i>	<i>F</i>	<i>P</i>
Age class	2, 90	3.54	0.03
Sex	1, 90	0.54	0.46
Day	1, 90	1.10	0.30
Motivation	1, 196	0.57	0.45
Age class*Sex	2, 90	3.64	0.03
Age class*Day	2, 90	0.80	0.45
Sex*Day	1, 90	0.51	0.48
Age class*Sex*Day	2, 90	0.28	0.75