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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.

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 × body mass × flight speed^2 and potential energy = body mass × gravitational acceleration × 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 (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).

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.

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.