PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Cite this article: Andries T, Müller W, Van Wassenbergh S. 2025 Feeding performance, kinematics and skills change with age in a granivorous songbird. *Proc. R. Soc. B* **292**: 20251839.
https://doi.org/10.1098/rspb.2025.1839

Received: 17 July 2025
Accepted: 11 September 2025

Subject Category:
Morphology and biomechanics

Subject Areas:
behaviour, biomechanics

Keywords:
granivory, songbirds, beak kinematics, ageing, skill, feeding performance

Author for correspondence:
Tim Andries
e-mails: tim.andries@hotmail.com; tim.andries@uantwerpen.be

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8047634.

Feeding performance, kinematics and skills change with age in a granivorous songbird

Tim Andries, Wendt Müller and Sam Van Wassenbergh

Department of Biology, University of Antwerp, Antwerpen, Flanders 2610, Belgium

TA, 0000-0001-5167-6690; WM, 0000-0001-7273-4095; SVW, 0000-0001-5746-4621

Changes in neuromuscular performance owing to maturation and ageing affect a wide range of motor behaviours in birds and mammals. The consequences may be especially pronounced during forceful and complex movements, such as feeding on seeds in songbirds, which require well-developed jaw muscles and fast, strongly coordinated beak and tongue movements. We investigated how feeding performance changes with age by filming juvenile and adult domestic canaries repeatedly over a span of two years with high-speed video. We extracted metrics of feeding performance, beak kinematics and seed handling skills of individuals during feeding on seeds with different characteristics. Age significantly affected several feeding metrics on the more challenging hemp seed, but not on the smaller and softer canary seed. Beak-opening frequency displayed a parabolic pattern, increasing early in life and slightly declining at old age, with no sex differences. Seed handling skills improved linearly with age and more strongly in males. The success rate of hemp seed husking also followed a parabolic pattern, improving in juveniles and declining in old age. Our results suggest that while learning and experience enhance feeding efficiency in early life, age-related declines may stem from reduced bite force or sensorimotor control deterioration.

1. Introduction

Ageing is a ubiquitous yet complex process that affects animals in various ways [1], having far-reaching impacts on an animal's physical and cognitive capabilities. Ageing has, therefore, received a lot of attention in relation to a wide variety of performance traits, like running [2], jumping [3], muscle strength [4], mating behaviour [5], vocalization [6–8] and human sports performance [9,10], among others. What makes the effects of ageing on performance special is that they are typically characterized by a period when performance first improves while a young animal develops and matures, followed by a gradual deterioration again as it grows older (i.e. a biphasic process [2,11]), through a process known as senescence [12].

The main underlying causes for ageing effects on performance are generally considered to be changes in muscle physiology and neural function [2,13]. As juveniles grow, their musculoskeletal and nervous systems are still developing, which should allow them to progressively exert more force, move faster and have better coordination as they mature [14–16]. This, in turn, should contribute to an improved feeding performance in early life. Later in life, muscles begin to deteriorate as a result of senescence [2,12]. Physiologically, senescence of muscles is generally associated with two processes: sarcopenia—the gradual decrease of muscle mass, and dynapenia—the size-independent decrease in force that muscles can generate [13,17]. Effects of senescence on muscle function have already been observed in birds: among others, a decrease in bite force has been reported in boobies [18], as

THE ROYAL SOCIETY PUBLISHING

well as a slowing of muscle contraction speed in quail back muscles [19]. Yet mechanical and kinematic biting capabilities change throughout life and can be expected to be especially relevant for granivorous songbirds, whose feeding strategy involves the husking of seeds before consumption, which requires precise, well-coordinated high-frequency movements of the beak [20–22]. It is, therefore, reasonable to assume that the well-developed musculature of granivorous songbirds, which is necessary to generate sufficient force to crack seeds [23–25], will be affected by senescence, and that this could lead to a reduced performance in seed feeding with increasing age. This might be particularly critical because it influences survival by affecting both the efficiency and capacities to process food—and consequently, the rate of food intake—with the risk of predation increasing as the duration of feeding lengthens [26–28]. However, whether and how the mechanical and kinematic capabilities of biting change throughout life in granivorous songbirds have, to our knowledge, not been investigated yet.

Feeding performance in granivorous songbirds is also related to neuromotor control [29], seed handling techniques [21] and skills [30], which are generally considered to be age-dependent too (e.g. [31]). However, in contrast to muscle function, skills are not expected to decline at old age, but instead to keep improving through experience. For example, juvenile cats learn hunting techniques from their mother and improve their hunting efficiency well into adulthood through experience [32]. In oystercatchers, the specific skills required for foraging and feeding on bivalves also improve throughout life [33]. When granivorous songbirds are still young, their feeding performance tends to be low compared with adults, because they fail more husking attempts and drop more seeds [34]. Improvements in feeding performance as juvenile birds grow up and mature have typically been attributed to experience and learning of skills [31,33,35]. For example, juvenile canaries learn seed husking techniques from their parents in early life [36,37]. However, whether seed husking skills keep improving beyond early life is as yet unknown. This knowledge is key to understanding whether older individuals might be able to compensate for their reduced physical capabilities by displaying better feeding skills, or because skills are at least maintained at a certain level.

Finally, effects of ageing on physical performance can differ between sexes. For example, in humans, muscle strength decreases earlier in women than men [38], while performance in team sports shows patterns of senescence in men, but less so in women [10]. Finally, female crickets experience stronger declines in jumping performance with age than males [3]. Sex differences may relate to the fact that males and females are typically differently affected by sexual selection, which arises from males having to attract and compete for females while the females choose their best potential mate [39,40]. As a result, certain traits will be under different selective pressures, and consequently the ageing of these traits might show very different trajectories between males and females [41]. In songbirds, bird song is first and foremost a sexual signal used by males to attract females [42] and is well-known to be subject to ageing effects, with song quality improving at young age and declining at old age [6,7,43]. The beak plays an important role in song production [44], implying that ageing effects on bird song could be related to ageing of the jaw musculature. Since these are the same muscles that are involved in feeding [24], this combined function of the beak in feeding and singing might lead to a higher selection pressure on beak muscle function and performance throughout life in males, while singing should be much less relevant in females. In analogy with the decline in song quality at old age, this could result in stronger declines in feeding performance with age in males than in females.

Thus, as it stands, a holistic understanding of how age affects the feeding performance of granivorous songbirds appears to be lacking. Therefore, in this study, we investigated how feeding performance, the kinematics of beak movement and associated feeding skills, change from the juvenile stage until well into adulthood in the domestic Fife fancy canary (*Serinus canaria* (Linnaeus)). The usage of domestic animals is especially advantageous in ageing research, since many causes of mortality such as predation and food limitations are largely excluded, increasing the likelihood of observing ageing effects. We hypothesize that beak kinematics will show parabolic patterns with increasing age, where capabilities first increase in juveniles and decrease again in older individuals owing to senescence. In contrast, we expect feeding skills to keep improving with age, since skills typically improve through experience. Consequently, we expect feeding performance to show a shifted parabolic pattern where performance decreases less at old age than it increases at young ages owing to the compensatory effects of improved feeding skills that are maintained later in life. Lastly, we expect ageing effects on beak kinematics and feeding performance to differ between males and females, given that their effects on feeding performance are likely linked with effects on singing performance.

2. Material and methods

(a) Study species and experimental setup

In this study, we used 50 individuals (25 males and 25 females) of a captive population of Fife fancy canaries (*Serinus canaria*) in a longitudinal approach. This is a subset of birds from an earlier study where feeding performance, seed handling skills and beak kinematics were measured [30]. In order to gather data over as much of the canary's lifespan (4–6 years on average in our population) in a feasible timespan, our sample consisted of two groups: 20 juveniles between 3 and 7 months old and 30 adults between 2 and 3 years old at the start of the experiment. Birds were housed in single-sex aviaries (1.0 × 2.0 × 2.3 m) at a room temperature of 19–24°C and a day : night cycle that varied from 14 h : 10 h (summer) to 10 h : 14 h (winter), with food and water ad libitum.

In order to measure the birds' feeding performance, skills and beak kinematics throughout their life, we recorded individual birds during feeding on two seed types (canary seed and hemp seed) using high-speed video cameras (Fastec IL5, Fastec Imaging), following the procedure described in Andries *et al.* [30] (figure 1A). Individuals were recorded roughly every six months for a total of four times. Four adults and one juvenile died before the third recording session, and eight more adults and two more juveniles died before the last recording session, resulting in a total sample size of 50 individuals for the first

two recording sessions, 45 individuals for the third recording session and 35 individuals for the last session (table 1). Ethical approval for this experiment was granted by the Ethical Committee of Animal Testing of the University of Antwerp (approval number 2021-35).

Video analysis and data collection were done as described in Andries *et al*. [30] for each recording session. Feeding performance (seed handling time and success rate of seed husking) and metrics of feeding skill (proportion of seed husks being split into both halves as opposed to being crushed indiscriminately and average head position during seed husking; see [30]) were calculated from manual video analysis. Metrics of beak kinematics (maximum and minimum gape distance, maximum and minimum velocity, maximum and minimum acceleration, average opening–closing frequency and average amplitude) were obtained through automated tracking of beak tips using the machine learning software DeepLabCut [45] in conjunction with XMAlab [46], according to the workflow of Laurence-Chasen *et al*. [47] (figure 1B).

(b) Statistical analyses

To test for the effects of age on feeding performance, beak kinematics and seed handling skills, we constructed linear mixed models with age as independent variable. We expected ageing patterns to differ between males and females, so we also used sex and its interactions with age as independent variables. For the dependent variables, we used both performance metrics (seed handling time and husking success rate), both skill metrics (proportion of seed splitting and head position) and maximum closing velocity and average frequency to represent beak kinematics, since the other kinematic metrics are strongly correlated with one of the aforementioned [30]. Based on general patterns of ageing and particularly the effects of ageing on birdsong [6,43], which is also related to beak function, we expected age to have parabolic effects on feeding performance and beak kinematics and thus fitted a quadratic regression for age on seed handling time, husking success rate, maximum closing velocity and average frequency. We expected seed handling skills to improve throughout life and decided to take a conservative approach, hence we fitted a standard linear regression for age on the proportion of seed splitting and head position. To facilitate the interpretation of the results, we decided to construct separate models for feeding on the two seed types: canary seed and hemp seed. Since we have repeated measurements per individual, we also added individual bird identity as a random effect to each model.

In summary, we had 12 linear mixed models: six for the six response variables during feeding on canary seeds and another six for the same response variables during feeding on hemp seed. Models for seed handling time, husking success rate, maximum closing velocity and frequency were of the form:

$$\sim \text{Age} + \text{Age}^2 + \text{Sex} + \text{Age}^*\text{Sex} + \text{Age}^2{}^*\text{Sex}\,.$$

Models for the proportion of seed splitting and head position were of the form:

$$\sim \text{Age} + \text{Sex} + \text{Age}^*\text{Sex}\,.$$

All models were checked for assumptions of normality and heteroscedasticity using QQ-plots and residual plots, respectively. All statistical analyses were done in R (v. 4.3.3) [48]. The packages 'lme4' [49] and 'lmerTest' [50] were used for the construction of linear mixed models.

3. Results

We observed several significant effects of age on feeding performance, beak kinematics and skills during feeding on hemp seed (electronic supplementary material, table S1), but none of the response variables were significantly affected by age or sex when feeding on canary seed (electronic supplementary material, figures S1 and table S1). There was a significant interaction effect of sex and age^2 on the success rate of seed husking ($p = 0.017$), indicating that success rate increased at young age and decreased again at old age. This effect was more pronounced in males, where success rate first increased by about 25–30% until reaching a peak around the age of three years, and afterwards decreased by about 10–15% at the oldest ages we investigated. In females, success rate only increased by about 5–10%, until reaching a peak at three years old, after which the decrease was close to zero (figure 2B).

The average frequency of beak opening and closing was significantly affected by age ($p = 0.004$). This effect was independent of sex ($p > 0.05$), indicating that frequency shows a parabolic pattern with increasing age that is similar for males and females. Average frequency increased by about 2–3 Hz as young individuals grew older, reaching a peak at around 3–4 years old, followed by a minor decline of around 0.5 Hz (figure 2D).

Both skill metrics, proportion of seed splitting and average head position were affected by the interaction of age and sex (seed splitting $p = 0.020$; head position $p = 0.044$). In both cases, skills improved with age in males (seed splitting proportion increased by 10–15% and the proportion of feeding in head-up position increased by 35–40% between the youngest and oldest ages), while such effects were negligible in females (figure 2E,F). Seed handling time and maximum closing velocity of the beak were not significantly affected by age, and this was also not modulated by sex (figure 2A,C). See electronic supplementary material, figure S2, for a representation of individual age trajectories during feeding on hemp seed.

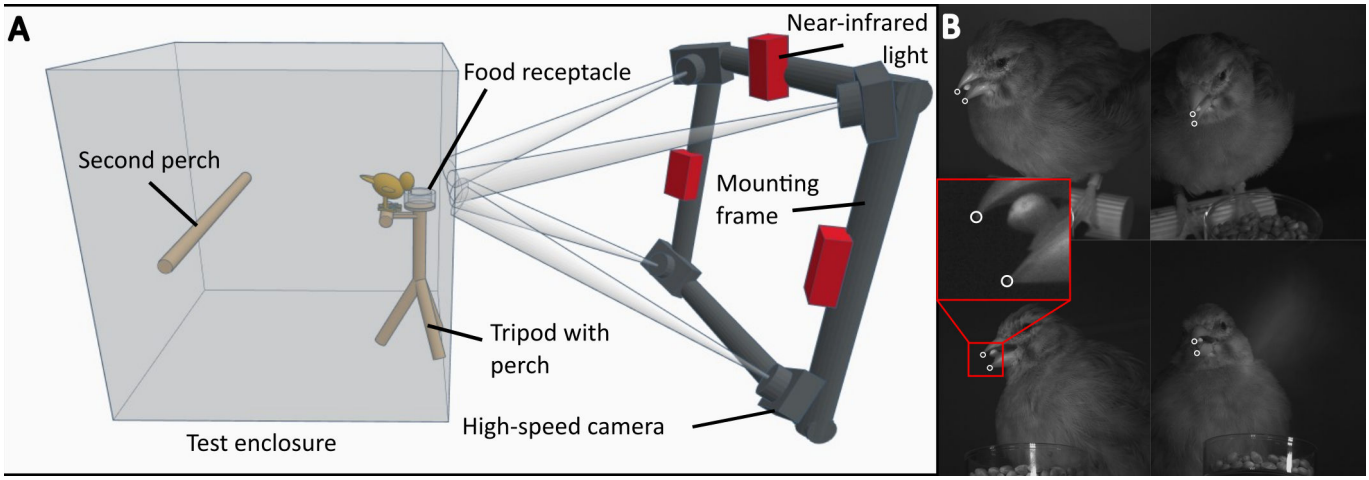

Figure 1. (A) Illustration of the quadroscopic camera setup. Note the four cameras—one on each corner of the mounting frame—and the three rectangular near-infrared lights. (B) Example of the quadroscopic view of a canary whilst positioning a hemp seed for cracking, including a close-up of the beak. Upper and lower beak tips are annotated by white dots. Figure taken from Andries *et al.* [30], with permission.

Table 1. Overview of sample sizes for each recording session, shown for adults (2–3 years old at start of experiment), juveniles (3–7 months old at start of experiment) and the sum of both. The figures in parentheses show the numbers of females and males, respectively.

	session 1	session 2	session 3	session 4
adults (F + M)	30 (15 + 15)	30 (15 + 15)	26 (14 + 12)	18 (9 + 9)
juveniles (F + M)	20 (10 + 10)	20 (10 + 10)	19 (10 + 9)	17 (10 + 7)
totals (F + M)	50 (25 + 25)	50 (25 + 25)	45 (24 + 21)	35 (19 + 16)

4. Discussion

Individuals of most species, particularly birds, appear to maintain high behavioural and motor competence throughout their lives until near their death. However, after an initial improvement early in life through learning and maturation, they supposedly experience reduced performance in most physiological traits. This age-related decline in performance may vary among individuals depending, e.g. on the sex, but this has only received little attention so far. This study is the first to investigate the effects of age on feeding performance, beak kinematics and seed handling skills in a granivorous songbird species, over nearly their entire lifespan. Our longitudinal study conducted over the course of two years showed that age affected seed handling skills, and some aspects of beak kinematics and feeding performance (figure 2). Additionally, ageing patterns of skills and performance differed between males and females. As the performance limits of ageing canaries were more evident when feeding on the seed type that presented the greater challenge for the birds (hemp seed), we will focus our discussion on the results for this seed type.

(a) Age affects average frequency, but not maximum closing velocity

Muscle action is widely known to be affected by age (e.g. [4]), where muscles generally become stronger and faster during maturation at young age, but weaker and slower again during senescence as processes such as sarcopenia and dynapenia set in [13,17]. We expected that jaw muscles would show similar patterns with age, which should become evident when feeding. In line with these expectations, we did find a parabolic effect of age on average beak opening–closing frequency (figure 2D), where young individuals first move their beaks at increasingly higher frequencies as they grow older, for this to level off and slightly decrease again at old age. Interestingly, despite there being a parabolic effect of age, it is remarkable how little frequency decreases at higher age, compared with physical traits in other animals [2,4]. This might reflect that birds experience delayed senescence, where individuals tend to perform remarkably well until shortly before death [51].

Interestingly, in songbirds, average beak opening–closing frequency could also be under sexual selection. In canaries, for example, beak frequencies during feeding are similar to those during peak trill rates, a typical sexually selected song feature in this species [20,52]. Since bird song is quite strongly affected by senescence [6], one would thus expect to observe similar effects of senescence on frequencies during feeding in males, but less so in females, which sing considerably less. However, we did not find that ageing patterns of frequency differed between males and females (figure 1D). Even though the beak plays a role in song production [44], this does not mean that senescence of song is necessarily driven by deterioration of the jaw muscles. Cooper *et al.* [7] have already theorized that deterioration of the vocal muscles and neural degradation might be causing declines in song quality at old age as well. Thus, if the ageing of bird song, which predominantly affects males, is not related to the jaw muscles, ageing patterns of jaw muscle action during feeding are probably not sex-specific either.

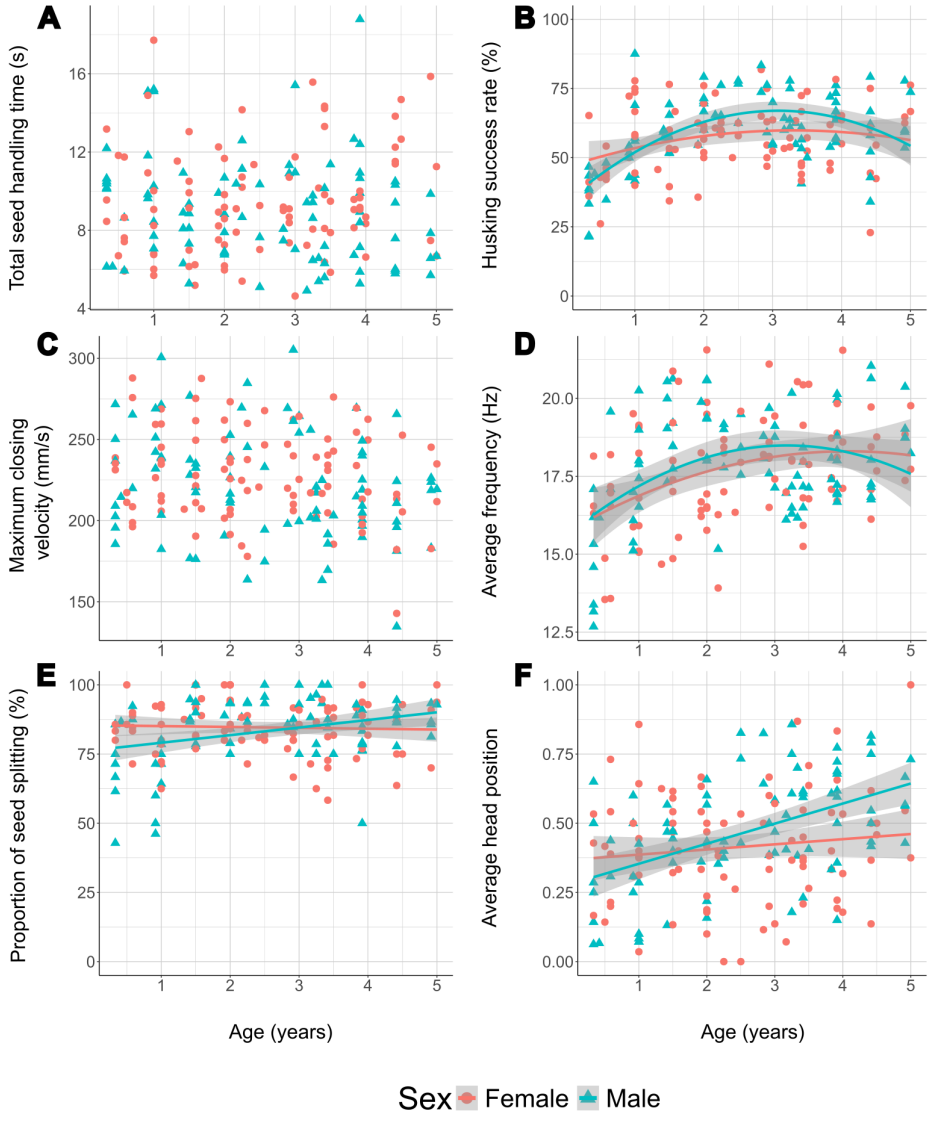

Figure 2. Linear and quadratic relationships of age with feeding performance (A,B), beak kinematics (C,D) and feeding skills (E,F) during feeding on hemp seed. Head position (F) is represented by a value between 0 and 1, where a value of 1 indicates that a bird always keeps its head upright during seed cracking, while a value of 0 indicates that it keeps its head always close to the food recipient (see [30]). Significant relationships are represented by a regression line and its 95% confidence interval shaded in grey. Numerical and statistical results of the regression analyses can be found in electronic supplementary material, table S1.

Curiously, while we found effects of ageing on frequency, maximum closing velocity showed no significant changes with increasing age. Andries *et al.* [53] has already argued that maximum closing velocity might not be a very accurate measure of an individual's maximal physical capabilities. Canaries might not try to move their beaks as fast as possible whilst feeding on seeds, as this comes with a trade-off to accuracy [54,55], i.e. the faster they move their beaks, the more likely they are to make mistakes and drop seeds instead of husking them successfully [30]. As a result, it can be argued that birds aim for an optimal beak speed instead, to balance out speed and accuracy, just as many animals aim for an optimal running speed to avoid tripping [56,57]. This might explain why we did not find effects of ageing. However, how well individuals can approach this optimal speed (i.e. a skill) could in turn be affected by age. In addition, this optimal speed is probably highly context dependent. For example, canaries move their beaks faster while feeding on larger seeds (e.g. 100–250 mm s^{-1} during feeding on canary seed (electronic supplementary material, figure S1C) versus 150–300 mm s^{-1} during feeding on hemp seed (figure 2C), but even seeds of the same plant species can vary considerably in size [58,59]. Hence, determining an optimal beak closing speed (if there is one) might not be feasible.

(b) Skills improve with age

Improvement of feeding skills is generally thought to be a major contributor to increasing feeding performance in juvenile birds [31,35,36]. Here, we confirm that seed handling skills indeed improve with age in canaries, not only in early life, but throughout the entire lifespan (figure 2E,F). Remarkably, however, although these skills improve through life in males, such patterns are much weaker, or even negligible in females. It is possible that feeding skills improve fastest in early life, particularly in females, but that this was not picked up by our analyses since we started experiments at three months of age at the earliest. Cadieu *et al.* [36] demonstrated that juvenile canaries already learn husking techniques from their parents as early as one month after birth,

and Davies & Green [35] reported that reed warblers learn fly-catching skills at even younger ages. In this study, the proportion of juveniles splitting of the seed husk in two halves (which is more efficient, but requires more precise seed positioning than indiscriminate crushing; see [30])is already high at the age of 3 months, and in males, the lifelong improvement in this skill beyond this date is relatively limited (figure 2E). Hence, it is likely that this skill is learnt very early in life, and that females possibly become proficient slightly earlier than males.

On the other hand, that ageing patterns of average head position height during seed husking differ between males and females (figure 2F) might be more related to differences in priorities between both sexes. Andries *et al.* [30] considered head position to be a proxy for seed handling skill since it signifies a trade-off between efficiency and vigilance. Granivorous songbirds typically aim to keep their head upright during seed husking to allow them to keep track of their surroundings [27,60], but this increases the chances of losing the seed if they drop it [30]. Hence, the more skilled an individual is, the more they can afford to prioritize vigilance and keep their head upright. Since our experiments were done in a captive population, vigilance for predators is not required, so that only leaves vigilance for intraspecific competitors. Male canaries are generally more territorial and aggressive than females [61,62], which could translate into males prioritizing vigilance for intraspecific competition more than females. However, this remains speculative at the moment.

(c) Age affects husking success rate, but not seed handling time

While age can affect beak kinematics and feeding skills, its effects on the actual performance of seed feeding are what is ultimately most ecologically relevant. In line with our expectations, we did find a shifted parabolic effect of age on the success rate of seed husking, which was more pronounced in males than in females (figure 2B). The increase in husking success rate as young individuals grow older is in line with previous research [31,34], but here we now show that it decreases again at old age as well.

The underlying causes for this pattern are still unclear, however. The traditional explanation is that feeding performance increases through experience and learning of skills in juveniles [31,35,36], but this does not explain why it decreases again at old age. Muscle deterioration might be plausible. Although kinematic capabilities seem to deteriorate little at old age (figure 2C,D), and Andries *et al.* [30] found no positive relations between beak kinematics and feeding performance either, it is still possible that bite force decreases comparatively more at old age (e.g. [31]). This could then result in a decrease in husking success rate at old age since hemp seeds are relatively tough and thus require sufficient bite force to crack [22,63]. The parabolic ageing patterns on feeding performance that we found in granivorous songbirds are largely in line with ageing patterns on motor performance that are found in many other animals (e.g. [2]). Whether caused by loss of muscle mass or reduction of muscle strength, deterioration of muscle performance in ageing individuals has been observed in various muscle groups in a wide range of animals, including birds [18,19], rodents [64], seals [65], primates [4] and humans [13,17], among others. Particularly, the age-related deterioration of masticatory muscles in humans leads to a reduced performance in consuming mainly tougher foods [66,67], very similar to our finding that canaries experience reduced feeding performance when feeding on the tougher hemp seed.

Aside from declines in muscle mass or strength, age-related declines in motor performance have also been attributed to a decline in muscle control and fine coordination. For example, ageing mice become slower at tasks that require fine motor skills [68]. Neural deterioration at old age that results in worse motor control could also decrease the ability to properly execute certain seed handling techniques and consequently lower seed husking success in granivorous songbirds. Moreover, this could explain why we see a stronger ageing effect in males than females (figure 2B), since neural deterioration has also been proposed as a cause of senescence in song [6,7]. The motor skills needed for singing and feeding might be overlapping [20], and may thus affect males more strongly than females, even if the two sexes do not experience differing ageing patterns in kinematics of the jaw muscles themselves (figure 2D). However, granivorous songbirds do appear to maintain a high degree of fine beak coordination late in life, since we found no age-related decline in the performance of feeding on canary seeds, which still require skilled handling to feed on efficiently [30]. While songbirds might retain good beak coordination at old age, their ability to properly exert adequate bite forces might decline. Similar declines in neuromotor control have already been documented in humans, where ageing individuals struggle more to accurately apply and release precise grip forces [69,70]. This could suggest that senescence affects different aspects of neuromotor control at different rates in different animal groups, potentially shaped by their ecology and evolutionary history.

Interestingly, canaries do not seem to become faster or slower at handling individual seeds with age (figure 2A). Granivorous songbirds appear to be rather unique in this regard among birds [34], since food handling time does decrease with age in many other bird species with different diets [31,35,71,72]. A plausible explanation for this might be that the diet of juveniles consists of a higher proportion of easier-to-crack seeds compared with adults. This could reduce their seed handling times on average, even if juveniles would be slower than adults at processing a seed of a given size and toughness.

5. Conclusions

Our study demonstrates that kinematic metrics exhibit an early-life increase followed by a decrease in old age, particularly in the frequency of open–close movements of the beak. However, other kinematic variables remained stable throughout life. In terms of skills, we also found improvements with age but this continued through life. Regarding performance, we observed the expected pattern in the husking success rate. This suggests that the early enhancements can be attributed to learning and experience, while the declines observed in old age may be owing to reduced bite force or deterioration of sensorimotor

control. We found indications of earlier maturation in feeding performance and skills in females compared with males, while males experienced more pronounced ageing effects on performance than females. While our findings overall concur with broader patterns of age-related motor and behavioural changes observed across birds and mammals, they also emphasize the importance of detailed kinematic analyses in identifying the consequences of maturation and senescence. Future research should focus on identifying which motor control programmes or sensory performance could underlie these age-dependent changes in husking success rate, for example through more in-depth kinematic analyses of beak movements during feeding comparing juvenile, adult and senescent life stages.

Ethics. Ethical approval for the experiments described in this manuscript was granted by the Ethical Committee of Animal Testing of the University of Antwerp (approval number: 2021-35)

Data accessibility. Data and code for statistical analysis are archived on the Dryad Digital Repository: [73]. Raw video data size is too large to feasibly archive on an online repository (±180 TB), but can be accessed upon request by contacting the corresponding author Tim Andries.

Supplementary material is available online [74].

Declaration of AI use. Beak kinematics were calculated from beak tip coordinates generated by the machine-learning tracking software DeepLabCut [45]. Further details can be found in §2. No AI tools were used for the writing of this paper.

Authors' contributions. T.A.: conceptualization, data curation, formal analysis, investigation, methodology, software, validation, visualization, writing—original draft, writing—review and editing; W.M.: conceptualization, formal analysis, methodology, resources, supervision, validation, writing—review and editing; S.V.W.: conceptualization, formal analysis, funding acquisition, methodology, project administration, supervision, validation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This work was supported by the Special Research Fund of the University of Antwerp (grant numbers DOCPRO4-TTZAPBOF FFB210025, SEP BOF FFB190380) and the Research Foundation—Flanders (grant number 1505819N).

Acknowledgements. We thank Maja Mielke for installing the quadroscopic camera setup and providing practical advice on high-speed videography. We also thank Jan Scholliers for building the experimental test enclosures. Finally, we thank Peter Scheys and Clara Garcia i Co for continuous animal care.

References

1. West GB, Bergman A. 2009 Toward a systems biology framework for understanding aging and health span. *J. Gerontol. A* **64**, 205–208. (doi:10.1093/gerona/gln066)
2. Marck A *et al*. 2017 Age-related changes in locomotor performance reveal a similar pattern for *Caenorhabditis elegans, Mus domesticus, Canis familiaris, Equus caballus* and *Homo sapiens*. *J. Gerontol.* **72**, 455–463. (doi:10.1093/gerona/glw136)
3. Lailvaux SP, Zajitschek F, Dessman J, Brooks R. 2011 Differential aging of bite and jump performance in virgin and mated *Teleogryllus commodus* crickets. *Evolution* **65**, 3138–3147. (doi:10.1111/j.1558-5646.2011.01358.x)
4. Hämäläinen A, Dammhahn M, Aujard F, Kraus C. 2015 Losing grip: senescent decline in physical strength in a small-bodied primate in captivity and in the wild. *Exp. Gerontol*. **61**, 54–61. (doi:10.1016/j.exger.2014.11.017)
5. Perrot C, Béchet A, Hanzen C, Arnaud A, Pradel R, Cézilly F. 2016 Sexual display complexity varies non-linearly with age and predicts breeding status in greater flamingos. *Sci. Rep*. **6**, 36242. (doi:10.1038/srep36242)
6. Berg ML, Beebe SC, Komdeur J, Cardilini APA, Ribot RFH, Bennett ATD, Buchanan KL. 2020 Senescence of song revealed by a long-term study of the Seychelles warbler (*Acrocephalus sechellensis*). *Sci. Rep*. **10**, 20479. (doi:10.1038/s41598-020-77405-3)
7. Cooper BG, Méndez JM, Saar S, Whetstone AG, Meyers R, Goller F. 2012 Age-related changes in the Bengalese finch song motor program. *Neurobiol. Aging.* **33**, 2010. (doi:10.1016/j.neurobiolaging.2010.04.014)
8. Doupe AJ, Kuhl PK. 1999 Birdsong and human speech: common themes and mechanisms. *Annu. Rev. Neurosci*. **22**, 567–631. (doi:10.1146/annurev.neuro.22.1.567)
9. Careau V, Wilson RS. 2017 Performance trade-offs and ageing in the 'world's greatest athletes'. *Proc. R. Soc. B* **284**, 20171048. (doi:10.1098/rspb.2017.1048)
10. Lailvaux SP, Wilson R, Kasumovic MM. 2014 Trait compensation and sex-specific aging of performance in male and female professional basketball players. *Evolution* **68**, 1523–1532. (doi:10.1111/evo.12375)
11. Levitis DA, Martínez DE. 2013 The two halves of U-shaped mortality. *Front. Genet*. **4**, 31. (doi:10.3389/fgene.2013.00031)
12. Nussey DH, Froy H, Lemaitre JF, Gaillard JM, Austad SN. 2013 Senescence in natural populations of animals: Widespread evidence and its implications for bio-gerontology. *Ageing Res. Rev.* **12**, 214–225. (doi:10.1016/j.arr.2012.07.004)
13. McGregor RA, Cameron-Smith D, Poppitt SD. 2014 It is not just muscle mass: a review of muscle quality, composition and metabolism during ageing as determinants of muscle function and mobility in later life. *Longev. Heal*. **3**, 9. (doi:10.1186/2046-2395-3-9)
14. dit Durell SEA. 2000 Individual feeding specialisation in shorebirds: population consequences and conservation implications. *Biol. Rev.***75**, 503–518. (doi:10.1111/j.1469-185x.2000.tb00053.x)
15. Herrel A, O'reilly JC. 2006 Ontogenetic scaling of bite force in lizards and turtles. *Physiol. Biochem. Zool.* **79**, 31–42. (doi:10.1086/498193)
16. Marchetti K, Price T. 1989 Differences in foraging of juvenile and adult birds: the importance of developmental constraints. *Biol. Rev* **64**, 51–70. (doi:10.1111/j.1469-185X.1989.tb00638.x)
17. Mitchell WK, Williams J, Atherton P, Larvin M, Lund J, Narici M. 2012 Sarcopenia, dynapenia, and the impact of advancing age on human skeletal muscle size and strength; a quantitative review. *Front. Physiol*. **3**, 260. (doi:10.3389/fphys.2012.00260)
18. Rebol EJ. 2020 Weaker bite force in elderly Nazca Boobies. M.S. thesis, Wake Forest University Graduate School of Arts and Sciences. Winston-Salem, NC, USA.
19. Alway SE. 1995 Slowing of contractile properties in quail skeletal muscle with aging. *J. Gerontol. A* **50**, B26–B33. (doi:10.1093/gerona/50A.1.B26)
20. Mielke M, Van Wassenbergh S. 2022 Three-dimensional movement of the beak during seed processing in domestic canaries. *J. Exp. Biol*. **225**, b244360. (doi:10.1242/jeb.244360)
21. Nuijens FW, Zweers GA. 1997 Characters discriminating two seed husking mechanisms in finches (Fringillidae: Carduelinae) and estrildids (Passeridae: Estrildinae). *J. Morphol*. **232**, 1–33. (doi:10.1002/(sici)1097-4687(199704)232:13.3.co;2-7)
22. van der Meij MAA, Bout RG. 2006 Seed husking time and maximal bite force in finches. *J. Exp. Biol.* **209**, 3329–3335. (doi:10.1242/jeb.02379)

23. Genbrugge A, Herrel A, Boone M, Van Hoorebeke L, Podos J, Dirckx J, Aerts P, Dominique A. 2011 The head of the finch: the anatomy of the feeding system in two species of finches (*Geospiza fortis* and *Padda oryzivora*). *J. Anat*. **219**, 676–695. (doi:10.1111/j.1469-7580.2011.01437.x)
24. Herrel A, Podos J, Vanhooydonck B, Hendry AP. 2009 Force–velocity trade-off in Darwin's finch jaw function: a biomechanical basis for ecological speciation? *Funct. Ecol*. **23**, 119–125. (doi:10.1111/j.1365-2435.2008.01494.x)
25. van der Meij MAA, Bout RG. 2008 The relationship between shape of the skull and bite force in finches. *J. Exp. Biol*. **211**, 1668–1680. (doi:10.1242/jeb.015289)
26. Lima SL. 1985 Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. *Oecologia* **66**, 60–67. (doi:10.1007/BF00378552)
27. Lima SL. 1994 On the personal benefits of anti-predatory vigilance. *Anim. Behav*. **48**, 734–736. (doi:10.1006/anbe.1994.1293)
28. McNamara JM, Houston AI. 1992 Risk-sensitive foraging: a review of the theory. *Bull. Math. Biol.* **54**, 355–378. (doi:10.1007/BF02464838)
29. Demery ZP, Chappell J, Martin GR. 2011 Vision, touch and object manipulation in Senegal parrots *Poicephalus senegalus*. *Proc. R. Soc. B* **278**, 3687–3693. (doi:10.1098/rspb.2011.0374)
30. Andries T, Müller W, Van Wassenbergh S. 2023 Skill rather than beak kinematics affects seed handling performance in a granivorous songbird. *Funct. Ecol*. **37**, 2677–2686. (doi:10.1111/1365-2435.14402)
31. Wunderle JM. 1991 Age-specific foraging proficiency in birds. *Curr. Ornithol*. **8**, 273–324.
32. Caro TM. 1980 Effects of the mother, object play, and adult experience on predation in cats. *Behav. Neural Biol*. **29**, 29–51. (doi:10.1016/s0163-1047(80)92456-5)
33. Hand CE, Sanders FJ, Jodice PGR. 2010 Foraging proficiency during the nonbreeding season of a specialized forager: are juvenile American oystercatchers 'Bumble-Beaks' 1 compared to adults? *Condor* **112**, 670–675. (doi:10.1525/cond.2010.100031)
34. Greig-Smith PW. 1985 Winter survival, home ranges and feeding of first-year and adult Bullfinches. In *Behavioral ecology: the ecological consequences of adaptive behaviour* (eds RM Sibley, RH Smith), pp. 387–392. Oxford, UK: Blackwell Scientific Publ.
35. Davies NB, Green RE. 1976 The development and ecological significance of feeding techniques in the Reed Warbler (*Acrocephalus scirpaceus*). *Anim. Behav.* **24**, 213–229. (doi:10.1016/S0003-3472(76)80118-2)
36. Cadieu JC, Cadieu N, Lauga J. 1995 Local enhancement and seed choice in the juvenile canary, *Serinus canarius*. *Anim. Behav*. **50**, 793–800. (doi:10.1016/0003-3472(95)80139-1)
37. Cadieu N, Winterton P, Cadieu JC. 2008 Social transmission of food handling in the context of triadic interactions between adults and young canaries (*Serinus canaria*). *Behav. Ecol. Sociobiol* **62**, 795–804. (doi:10.1007/s00265-007-0505-0)
38. Doherty TJ. 2001 The influence of aging and sex on skeletal muscle mass and strength. *Curr. Opin. Clin. Nutr. Metab. Care* **4**, 503–508. (doi:10.1097/00075197-200111000-00007)
39. Andersson M, Iwasa Y. 1996 Sexual Selection. *Trends Ecol. Evol*. **11**, 53–58. (doi:10.1016/0169-5347(96)81042-1))
40. Lailvaux SP, Irschick DJ. 2006 A functional perspective on sexual selection: insights and future prospects. *Anim. Behav.* **72**, 263–273. (doi:10.1016/j.anbehav.2006.02.003)
41. Bonduriansky R, Maklakov A, Zajitschek F, Brooks R. 2008 Sexual selection, sexual conflict and the evolution of ageing and life span. *Funct. Ecol*. **22**, 443–453. (doi:10.1111/j.1365-2435.2008.01417.x)
42. Eriksson D, Wallin L. 1986 Male bird song attracts females? A field experiment. *Behav. Ecol. Sociobiol.***19**, 297–299. (doi:10.1007/BF00300645)
43. Zipple MN, Nowicki S, Searcy WA, Peters S. 2019 Full life course analysis of birdsong reveals maturation and senescence of highly repeatable song characteristics. *Behav. Ecol.* **30**, 1761–1768. (doi:10.1093/beheco/arz146)
44. Podos J. 2001 Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature* **409**, 185–188. (doi:10.1038/35051570)
45. Mathis A, Mamidanna P, Cury KM, Abe T, Murthy VN, Mathis MW, Bethge M. 2018 DeepLabCut: markerless pose estimation of user-defined body parts with deep learning. *Nat. Neurosci*. **21**, 1281–1289. (doi:10.1038/s41593-018-0209-y)
46. Knörlein BJ, Baier DB, Gatesy SM, Laurence-Chasen JD, Brainerd EL. 2016 Validation of XMALab software for marker-based XROMM. *J. Exp. Biol*. **219**, 3701–3711. (doi:10.1242/jeb.145383)
47. Laurence-Chasen JD, Manafzadeh AR, Hatsopoulos NG, Ross CF, Arce-McShane FI. 2020 Integrating XMALab and DeepLabCut for high-throughput XROMM. *J. Exp. Biol*. **223**, b226720. (doi:10.1242/jeb.226720)
48. R Core Team. 2025 R: A language and environment for statistical computing. R Foundation for Statistical Computing. See https://www.R-project.org/.
49. Bates D, Mächler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using lme4. *J. Stat. Softw* **67**, 1–48. (doi:10.18637/jss.v067.i01)
50. Kuznetsova A, Brockhoff PB, Christensen RHB. 2017 lmerTest package: tests in linear mixed effects models. *J. Stat. Softw* **82**, 1–26. (doi:10.18637/jss.v082.i13)
51. Ricklefs RE. 2011 Insights from comparative analyses of aging in birds and mammals. *Aging Cell* **9**, 273–284. (doi:10.1111/j.1474-9726.2009.00542.x)
52. Drăgănoiu TI, Nagle L, Kreutzer M. 2002 Directional female preference for an exaggerated male trait in canary (*Serinus canaria*) song. *Proc. R. Soc. B* **269**, 2525–2531. (doi:10.1098/rspb.2002.2192)
53. Andries T, Müller W, Van Wassenbergh S. 2025 Beak dimensions affect feeding performance within a granivorous songbird species. *J. Exp. Biol.* **228**, jeb249681. (doi:10.1242/jeb.249681)
54. Fitts PM. 1954 The information capacity of the human motor system in controlling the amplitude of movement. *J. Exp. Psychol* **47**, 381–391. (doi:10.1037//0096-3445.121.3.262)
55. Heitz RP. 2014 The speed-accuracy tradeoff: history, physiology, methodology, and behavior. *Front. Neurosci*. **8**, 150. (doi:10.3389/fnins.2014.00150)
56. Nasir AFAA, Clemente CJ, Wynn ML, Wilson RS. 2017 Optimal running speeds when there is a trade-off between speed and the probability of mistakes. *Funct. Ecol.* **31**, 1941–1949. (doi:10.1111/1365-2435.12902)
57. Wynn ML, Clemente C, Nasir A, Wilson RS. 2015 Running faster causes disaster: trade-offs between speed, manoeuvrability and motor control when running around corners in northern quolls (*Dasyurus hallucatus*). *J. Exp. Biol.* **218**, 433–439. (doi:10.1242/jeb.111682)
58. Herrera CM. 2009 *Multiplicity in unity: plant subindividual variation and interactions with animals*. Chicago, IL: Chicago University Press. (doi:10.7208/chicago/9780226327952.001.0001)
59. Michaels HJ, Benner B, Hartgerink AP, Lee TD, Rice S, Willson MF, Bertin RI. 1988 Seed size variation: magnitude, distribution, and ecological correlates. *Evol. Ecol.* **2**, 157–166. (doi:10.1007/BF02067274)
60. Baker DJ, Stillman RA, Smart SL, Bullock JM, Norris KJ. 2011 Are the costs of routine vigilance avoided by granivorous foragers? *Funct. Ecol*. **25**, 617–627. (doi:10.1111/j.1365-2435.2010.01829.x)
61. Parisot M, Tanvez A, Lacroix A, Vallet E, Béguin N, Leboucher G. 2005 Social competition and plasma testosterone profile in domesticated canaries: an experimental test of the challenge hypothesis. *Horm. Behav*. **48**, 225–232. (doi:10.1016/j.yhbeh.2005.02.011)
62. Shoemaker BH. 1939 Social hierarchy in flocks of the canary. *Auk* **56**, 381–406. (doi:10.2307/4078790)
63. Meij MAA, Griekspoor M, Bout RJ. 2004 The effect of seed hardness on husking time in finches. *Anim. Biol* **54**, 195–205. (doi:10.1163/1570756041445164)

64. Hindle AG, Lawler JM, Campbell KL, Horning M. 2009 Muscle senescence in short-lived wild mammals, the soricine shrews *Blarina brevicauda* and *Sorex palustris*. *J. Exp. Zool.* **311**, 358–367. (doi:10.1002/jez.534)
65. Hindle AG, Horning M, Mellish JAE, Lawler JM. 2009 Diving into old age: muscular senescence in a large-bodied, long-lived mammal, the Weddell seal (*Leptonychotes weddellii*). *J. Exp. Biol.* **212**, 790–796. (doi:10.1242/jeb.025387)
66. Mioche L, Bourdiol P, Peyron MA. 2004 Influence of age on mastication: effects on eating behaviour. *Nutr. Res. Rev*. **17**, 43–54. (doi:10.1079/NRR200375)
67. Sekundo C, Frese C, Alich N, Langowski E, Awounvo S, Wolff D, Zenthöfer A. 2024 Very old age impacts masticatory performance: a study among sexagenarians to centenarians. *Clin. Oral Investig*. **28**, 349. (doi:10.1007/s00784-024-05742-y)
68. Sukoff Rizzo SJ, Anderson LC, Green TL, McGarr T, Wells G, Winter SS. 2018 Assessing healthspan and lifespan measures in aging mice: optimization of testing protocols, replicability, and rater reliability. *Curr. Protoc. Mouse Biol*. **8**, e45. (doi:10.1002/cpmo.45)
69. Lin BS, Kuo SF, Lee IJ, Lu LH, Chen PY, Wang PC, Lai CH, Wang XM, Lin CH. 2021 The impact of aging and reaching movements on grip stability control during manual precision tasks. *BMC Geriatr*. **21**, 703. (doi:10.1186/s12877-021-02663-3)
70. Davidson S, Learman K, Zimmerman E, Rosenfeldt AB, Koop M, Alberts JL. 2024 Older adults are impaired in the release of grip force during a force tracking task. *Exp. Brain Res*. **242**, 665–674. (doi:10.1007/s00221-023-06770-y)
71. Richardson H, Verbeek NAM. 1987 Diet selection by yearling northwestern crows (*Corvus caurinus*) feeding on littleneck clams (*Venerupis japonica*). *Auk* **104**, 263–269. (doi:10.1093/auk/104.2.263)
72. Sutherland WJ, Jones DWF, Hadfield RW. 1986 Age differences in the feeding ability of Moorhens *Gallinula chloropus*. *Ibis* **128**, 414–418. (doi:10.1111/j.1474-919x.1986.tb02691.x)
73. Andries T, Müller W, Wassenbergh S. 2025 Feeding performance, kinematics and skills change with age in a granivorous songbird. Dryad Digital Repository. (doi:10.5061/dryad.bcc2fqzs5)
74. Andries T, Müller W, Van Wassenbergh S. 2025 Supplementary material from: Feeding performance, kinematics and skills change with age in a granivorous songbird. Figshare. (doi:10.6084/m9.figshare.c.8047634)