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Skill rather than beak kinematics affects seed handling performance in a granivorous songbird

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Abstract

1. In granivorous songbirds, feeding is a complex process as seeds need to be dehusked before they can be consumed, making the feeding act a biomechanically challenging endeavour. However, most previous research has focused on how beak morphology affects feeding performance, while the influences of beak kinematics remain largely unknown.

2. In this study, we hence investigated at the individual level how feeding performance (i.e. seed processing time and success rate) relates to both beak kinematics (i.e. beak tip speed, acceleration, frequency) and skill (i.e. seed handling tactics and cracking techniques) in the Canary *Serinus canaria*. To do so, high-speed videos during feeding were recorded and subjected to automated tracking of beak tip movements.

3. Better skills, that is accurate positioning of the seed for being split in half, reduced total seed handling time compared to more random positioning and crushing the husk into multiple, scattering fragments. Surprisingly, individual variation in beak speed, acceleration or frequency generally did not relate to differences in performance.

4. Thus, our data suggest that seed positioning precision, and hence the control of coordinated beak and tongue movement, is critical to minimize feeding durations in songbirds. Further studies are needed to explore whether this develops via a positive feedback between behaviour, learning and increased efficiency or if it relates to intrinsic differences.

KEYWORDS
beak kinematics, feeding performance, feeding skills, granivory, individual variation, songbirds

1 | INTRODUCTION

Natural selection on feeding performance can be a major driver of adaptive radiation and speciation. A well-known example is the diversification of bird beaks as occurred during the adaptive radiation of finches on the Galápagos Islands (Abzhanov, 2010; Boag & Grant, 1981; Darwin, 1845; Grant et al., 1976; Grant & Grant, 2002, 2006; Herrel et al., 2005). Songbirds such as the Darwin's finches typically feed on seeds which they need to dehusk before they can

be properly digested. Seed dehusking performance is potentially a significant driver of beak evolution, since increasing seed shell hardness is a common defence strategy in plants (Fricke & Wright, 2016). However, it is often overlooked that feeding on seeds demands complex actions from the beak. Granivorous birds need to be able to exert considerable forces on the seed's shell, ideally combined with the technically challenging dexterity to manipulate and crack seeds precisely on their weakest spots (Nuijens & Zweers, 1997; van der Meij & Bout, 2006, 2008). Additionally, time constraints could be

of importance too, as birds benefit from processing seeds as fast as possible to reduce the risk of predation, since birds often have to forage away from cover and cannot always keep watching out for predators whilst feeding (Lima, 1985, 1994).

Due to the complexity of the seed-eating act, and our limited mechanical understanding of this process in granivorous songbirds, identifying adaptations to granivory remains difficult. Among other factors, maximal bite force affects which seeds can still be dealt with effectively (Herrel et al., 2005, 2009). This will be reflected in beak morphology and tissue mechanics to resist bite forces (Soons et al., 2015), and head size to accommodate bite muscles (Herrel et al., 2009). In addition, birds might try to concentrate force on a specific area to locally crack the seed shell in an efficient way that minimizes time or energy demands. However, agile motions of the beak can also be important to enable the quick, successive processing of large amount of seeds, as was shown for Darwin's ground finches after a rainy period (Grant & Grant, 2003). Previous studies also indicated that small-billed Darwin's finches deal with rice grains quicker than do large-billed species (Abbott et al., 1975; Grant et al., 1976). The importance of beak movement implies that the force–velocity trade-off in lever systems will become relevant (Herrel et al., 2009). Seed-eating performance will thus depend on many factors related to the mechanical capabilities and constraints of beak movement (Herrel et al., 2009; Mielke & Van Wassenbergh, 2022). Here, we use beak kinematics to refer to basic metrics of beak movement capacity such as maximal speed, acceleration and frequency.

Relatively, limited research has been done thus far on the kinematics of granivory in songbirds. Research has mostly been limited to measuring overall performance metrics like feeding rates (Abbott et al., 1975; Benkman & Pulliam, 1988; Grant et al., 1976), seed handling/husking times (van der Meij & Bout, 2006), bite force (van der Meij & Bout, 2006, 2008) or some qualitative descriptions of feeding and seed husking techniques (Nuijens & Zweers, 1997; van der Meij et al., 2004; van der Meij & Bout, 2006). While these metrics are ecologically important, they do not reveal much about the mechanical capabilities of the cranial musculoskeletal system of bird beaks (e.g. how fast they can move or which movements they can make). One notable exception is Corbin et al. (2015), who included maximum closing velocity in their study, but no other kinematic variables. However, with the technological advancements in high-speed videography, automated tracking software (Knörlein et al., 2016) and machine learning (Mathis et al., 2018), such studies have recently become more feasible. An example thereof is the study by Mielke and Van Wassenbergh (2022), who recently analysed the three-dimensional movements of canary beaks during feeding in a few individuals.

On top of the mechanics, the fast and precise action of seed manipulation relies on integrated tactile and visual feedback control (Demery et al., 2011), which, in turn, will depend on an individual's skill. Skill is, in broad terms, defined as the ability to perform a challenging behaviour well (Briffa & Lane, 2017; Byers et al., 2010)

and encompasses many qualities such as accuracy, precision, patience, risk assessment, etc., which are distinct from of the animal's kinematic capacities like maximal speed, acceleration or maximal bite force. The impact of skill on performance has extensively been studied in human sports (Williams & Hodges, 2005; Wilson et al., 2017). In an animal ecological context, it has to a more limited extent been studied for courtship behaviour (Byers et al., 2010; Manica et al., 2017), fighting (Lane & Briffa, 2020), and tool use during feeding in crows (Rutz et al., 2011). Apart from the latter study, the role of skill in feeding performance of birds is largely ignored aside from being invoked as a general cause for age-based differences in performance (e.g. Hand et al., 2010). Yet, in these aforementioned studies, skill was often found to be a good predictor of performance (irrespective of a potential role of kinematics), which warrants studying the role of skill in seed-eating performance as well.

To better understand how natural selection can drive the evolution of bird beaks, it is hence important to know how both the beak kinematics and skill affect feeding performance. Ideally, individual variation in feeding performance should be taken into account, as this is where ultimately natural selection will act on. In this study, we used a granivorous songbird, the Domestic Canary *Serinus canaria*, as model system to investigate the relationships between performance (i.e. seed handling time and success rate), beak kinematics (i.e. speed and acceleration) and skill-related aspects of seed eating (i.e. seed handling tactics). We hypothesize that both affect feeding performance, since dehusking seeds is a complex and delicate process involving precisely controlled three-dimensional movements of the beak and tongue (Nuijens & Zweers, 1997; van der Meij & Bout, 2006). More specifically, we expect that faster beak movements lead to shorter seed handling times, and better seed handling skills improve the success rate of seed husking by reducing the chances of dropping the seed. As seeds can vary greatly in size and shape, and granivorous birds usually feed on a number of different seed types (Camín et al., 2015; Kear, 1962), feeding performance was tested for different seed types.

2 | MATERIALS AND METHODS

2.1 | Study species

In this study, we used a total of 87 individuals (47 males and 40 females) of the Domestic Canary *S. canaria*, Fife Fancy breed, from an outbred population kept at the laboratory. All birds were between 3 months and 4 years old at the time of the experiments. Birds were housed in single-sex aviaries ($11 \times 2 \times 2.3$ m) at a room temperature of 19–24°C and a 12 h/12 h day–night cycle with food and water ad libitum. During the night prior to the experiment individuals were kept alone in the test enclosure (see Figure 1a) for habituation, with access to water ad libitum, but deprived of food to standardize the hunger level and maximize willingness to feed during the recordings.
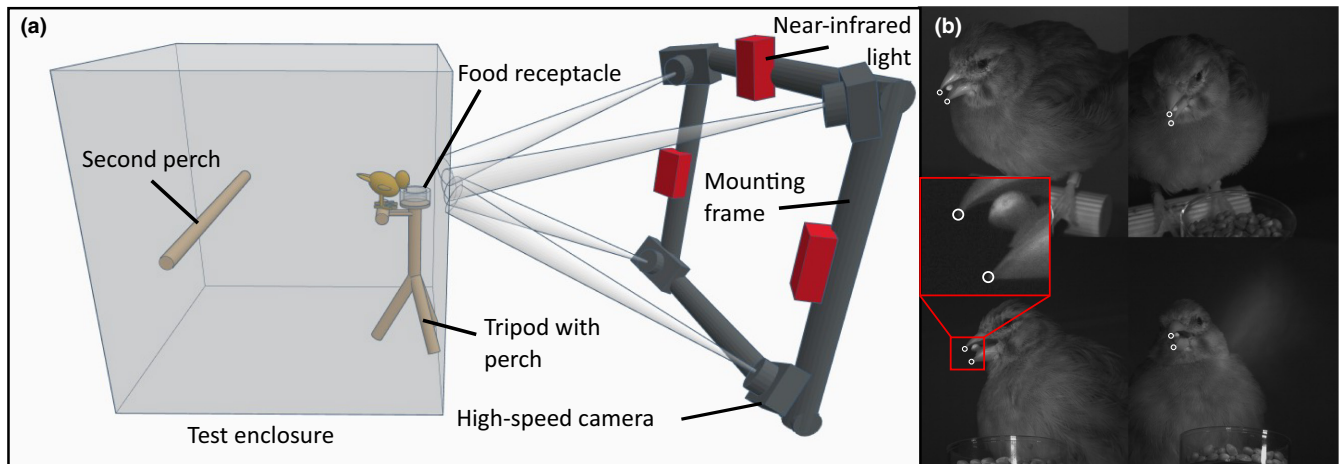
FIGURE 1 (a) Illustration of the quadroscopic camera setup. Note the four cameras on each corner of the mounting frame and the three rectangular near-infrared lights. (b) Example of the quadroscopic view of a canary whilst positioning a hemp seed for cracking, including a close-up of the beak. Upper and lower beak tips are annotated by white dots.

The test enclosure consisted of a square glass box ($50 \times 50 \times 50$ cm) with the top covered by a metal grating and the floor covered with shell grit. The enclosure contained a tripod with perch and food receptacle attached to it, as well as a second larger perch spanning the width of the enclosure for additional comfort.

2.2 | Experimental setup

Individual birds were recorded during feeding using high-speed video cameras (Fastec IL5, Fastec Imaging) in a synchronized quadroscopic setup, mounted as such that each camera filmed the subject from a distinct angle (Figure 1a). The setup was also equipped with near-infrared (850 nm) spotlights to provide sufficient illumination without hindering the vision of the birds. Recordings were made in 8-bit monochromatic, 936×1024 pixels resolution at 500 frames per second with a sufficiently high shutter speed of $100\,\mu s$ to reduce motion blur. Recording time varied per individual (4–6 min on average) and usually lasted until the subject either refused to continue feeding or had completed sufficient (>30) seed husking attempts. A calibration object consisting of 40 dots at known 3D positions on a 90° corner was also recorded during each session to allow for tracking of the 3D positions of the beak tips (see 'video analysis'). Ethical approval for this experiment was granted by the relevant institutional body (approval number: 2021-35).

Each bird was recorded twice, once feeding on canary seed *Philaris canariensis* and once on hemp seed *Cannabis sativa*. Both seeds are part of the typical diet of domestic canaries, but differ in size (length × width: mean (±SD); canary seed: 4.67 (±0.40) × 1.84 (±0.23) mm; hemp seed: 4.23 (±0.40) × 2.85 (±0.33) mm), shape (canary seed: spindle shaped, hemp seed: oblate spheroid) and strength (hemp seeds are more difficult to crack than canary seeds). As not all birds were willing to feed on both seed types, the resulting number of recorded individuals per seed was 79 for canary seed and 82 for hemp seed.

2.3 | Video analysis

Three types of metrics were procured from the video data: feeding performance, skill and beak kinematics. We define feeding performance as the ability to maximize food intake whilst minimizing the time spent feeding. A high feeding performance is therefore characterized by successfully feeding on many seeds in a short time. Two metrics of feeding performance were quantified: seed husking success rate and seed handling time. Success rate was calculated as the number of successful dehusking attempts divided by total attempts. To calculate seed handling time, up to 10 successful husking attempts were selected. For hemp seed, 29 individuals did not successfully dehusk 10 seeds, so in these cases we had to use fewer attempts (minimum 5). Seed handling time was further subdivided in its distinct phases. In theory, five feeding phases can be discerned: seed picking (and associated head righting), seed positioning, seed cracking, husk removal and seed swallowing. In practice, positioning and cracking are continuously alternated until the dehusking attempt is either successful or the seed is lost, so both phases were combined in the analysis. Similarly, as the husk removal phase is very variable (beak movements can be very irregular depending on which and how many parts of the seed husk are left in the beak) or sometimes practically absent, this phase was combined with the swallowing phase. Thus, we ended up with four metrics for seed handling durations: (1) seed picking (including head righting), (2) cracking (including positioning), (3) husk removal (including swallowing) and as an integrative measure we calculated (4) the total seed handling time.

To quantify skill, we analysed variation in techniques that could consistently be observed: the way in which a seed was cracked and the position of the head during cracking. Consequently, highly skilled individuals are characterized by cracking seeds in a specific orientation whilst keeping their head upright to maximize vigilance. Seeds can be cracked generally in two ways (Nuijens & Zweers, 1997; Zweers et al., 1994): seed husks are split in both their halves or they

are crushed into several irregular pieces. Splitting the seed husk requires a specific orientation of the seed, that is with the seam parallel to the bird's sagittal plane, which causes the seed to split open at the seam upon being compressed during biting. Meanwhile, crushing the husk can be achieved by applying enough force regardless of seed orientation. Therefore, the proportion of seeds that are split in both their halves can be seen as a proxy for accuracy and precision. Example videos of splitting and crushing can be found in the Supporting Information (Videos S1 and S2). Additionally, birds typically keep their head upright during most of the feeding act to scan their surroundings (Cowlishaw et al., 2004; Glück, 1987; Lima, 1994), but from personal observations it appeared that some individuals have a tendency to lower their heads down to the food receptacle at the moment of cracking, presumably to avoid that the seed drops on the ground in case the cracking attempt fails. Therefore, the position of the head relative to the food receptacle during cracking can be seen as a precautionary measure, which implies that individuals with poorer skills will keep their head lower during cracking attempts so they can find the seed back easier, should the cracking attempt fail. Ideally, head position would be calculated as the distance between beak and food receptacle, but it was not feasible to do this in a standardized manner. So we instead chose for a categorical assessment of head position, with the position being either low, medium or high. These categories were given a score (low = 0, medium = 0.5 and high = 1), so an 'average head position' could be calculated.

As opposed to the seed-eating techniques listed under skill, we also measured the kinematics of beak movement. To extract these metrics, we tracked the 3D positions of the tips of the upper and lower beak, using the landmark tracking software XMAlab (Knörlein et al., 2016) in conjunction with deep learning software DeepLabCut (Mathis et al., 2018) following the workflow of Laurence-Chasen et al. (2020). First, a training dataset was constructed by randomly selecting video frames of several individuals feeding on both seed types and by manually annotating the tips of the lower and upper beak. Second, after sufficient training, the network was applied to the previously selected trials to automatically track the beak tips frame by frame. Due to the nature of our data, we could not calculate marker-to-marker distance standard deviation as a measure of tracking precision (Knörlein et al., 2016). However, for a similar setup and calibration procedure, Mielke and Van Wassenbergh (2022) reported marker-to-marker distance standard deviations between 0.2 and 0.5 mm and, so we expect tracking precision to be similar here. As beak movements throughout the feeding act can be highly variable and irregular, five fragments of well-tracked and relatively regular high-frequency movements during seed positioning were selected per bird and per seed type for extraction of the kinematic metrics. Distance between the beak tips was calculated and filtered using a fourth-order zero phase-shift Butterworth the filtered distances we calculated the following variables: maximum gape, minimum gape, maximum opening and closing velocity, maximum opening and closing acceleration, average opening-closing frequency and average amplitude (see Figure 2).
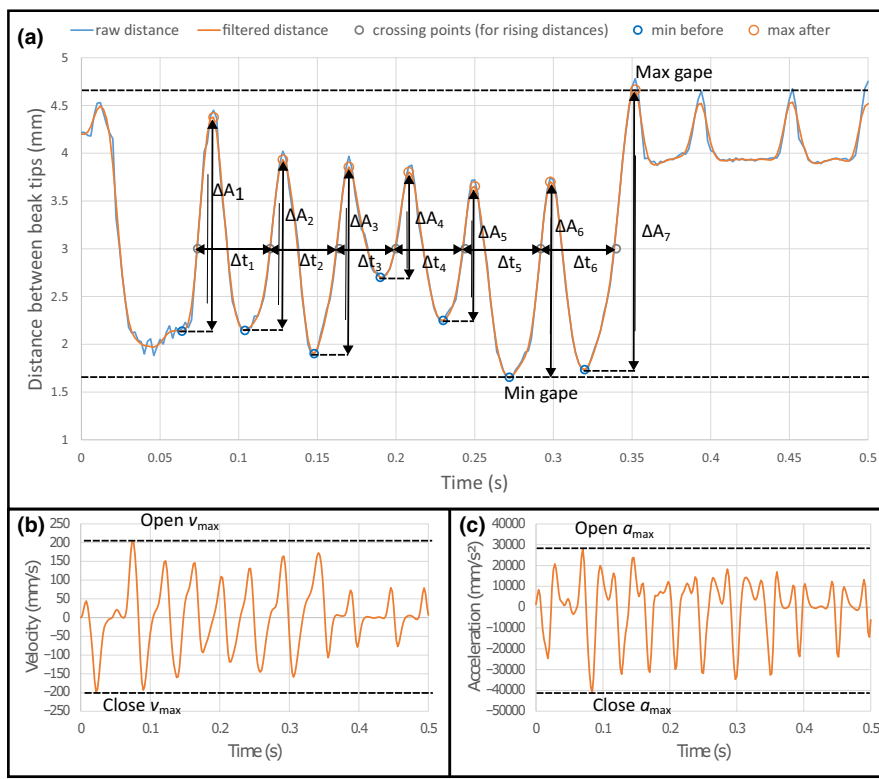

FIGURE 2 Illustration of kinematic metrics calculations. (a) Distance between beak tips of selected fragment after filtering with calculation of maximum gape, minimum gape, average frequency ($f_{avg} = \frac{\sum_{i=1}^{n}(\Delta t_i)}{n}$) and average amplitude ($A_{avg} = \frac{\sum_{i=1}^{n}(\Delta A_i)}{n}$). (b) Velocity of the beak tips (calculated as first derivative of the distance) with calculation of maximum opening (open v_{max}) and closing velocity (close v_{max}). (c) Acceleration of the beak tips (calculated as second derivative of the distance) with calculation of maximum opening (open a_{max}) and closing acceleration (close a_{max}).

2.4 | Statistical analyses

As we want to assess the effects of both beak kinematics and feeding skills, as well as their relative importance, on feeding performance, we constructed multiple linear regression models (ordinary least squares regression) with performance metrics as response variables and kinematic and skill metrics together as predictor variables. All statistical analyses were done in R (version 4.2.1). Individual repeatability estimates were calculated using the R-package RPTR (Stoffel et al., 2017; Supporting Information Table S1). All repeatability estimates were statistically significant, and varied between about 0.1 and 0.4, which is a typical repeatability for behavioural traits in vertebrates (Bell et al., 2009). Hence, average values per individual were used for all metrics to account for dependency of data within individuals. The replication statement is found in Table 1.

We first assessed correlations between all variables, which also allowed us to identify the most relevant response and predictor variables. Correlation matrices containing either Pearson's r or Spearman's rho correlation coefficients (depending on whether the respective variables were normally distributed) were constructed for both response (performance) and predictor (skill and kinematics) variables per seed using the R-package Hmisc. Among response variables, success rate did not correlate strongly with any time metric. Total seed handling time was strongly correlated with the other time metrics, except seed picking time for canary seed and husk removal time for hemp seed (Supporting Information Tables S2 and S3). Ultimately, to limit the number of statistical tests, we omitted seed picking and husk removal time from further analyses as both metrics are less relevant in regards to overall feeding performance. Hence, we kept only total seed handling time and success rate as response variables for our linear models. Many moderate and strong correlations were observed among predictor variables (Supporting Information Tables S4 and S5). Seed splitting proportion, head position, minimum gape and frequency were not strongly correlated with other variables and they might hence explain different aspects of seed handling time and success rate, respectively (Supporting Information Tables S4 and S5). In addition, we chose maximum closing velocity as a representative for the strongly correlated variables (maximum gape, opening velocity, closing velocity, opening acceleration, closing acceleration and amplitude).

We then constructed two linear models per seed type: one with total seed handling time and another with husking success rate as response variable. Both models included seed splitting proportion, head position, minimum gape, maximum closing velocity and frequency as predictor variables.

TABLE 1 Replication statement.

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Population	Individuals	87 individuals

3 | RESULTS

Variation among individuals in the measured variables was substantial in our population and generally higher for hemp seed than canary seed. Average total seed handling time varied between 1.6 and 8.6 s for canary seed and between 3.2 and 17.9 s for hemp seed (Figure 3a,b). The individuals their husking success rate ranged from 62.5% to 100% for canary seed and from 21.4% to 77.8% for hemp seed (Figure 3c,d). The proportion of seed splitting reached a maximum of 100% in some individuals for both seeds, while a minimum of 23.1% for canary seed and 42.9% for hemp seed was observed (Figure 3a,c). Average head position spanned the entire range from always a low position to always a high position for hemp seed, and from halfway to always a high position in canary seed (Figure 3b,d). Average minimum gape varied between 0.28 and 0.78 mm for canary seed and between 0.39 and 1.76 mm for hemp seed (Figure 4a,d). Average maximum closing velocity ranged from 84.4 to 246.5 mm/s for canary seed and from 152.3 to 291.4 mm/s for hemp seed (Figure 4b,e). Variation in average frequency was similar for both seeds, ranging from 11.6 to 21.5 Hz for canary seed and from 12.7 to 20.5 Hz for hemp seed (Figure 4c,f).

Skill and beak kinematics, together, had a number of significant effects on feeding performance ($p < 0.05$; see Supporting Information Table S6). Our models revealed significant effects on total handling time for both canary seed ($F_{5,73} = 9.56$, adj $R^2 = 0.354$, $p = 4.8*10^{-7}$) and hemp seed ($F_{5,76} = 4.53$, adj $R^2 = 0.179$, $p = 0.0011$). Significant effects on success rate were only found for hemp seed ($F_{5,76} = 4.25$, adj $R^2 = 0.167$, $p = 0.0018$), but not for canary seed ($F_{5,73} = 0.806$, adj $R^2 = -0.0126$, $p = 0.549$). For canary seed, only the proportion of seed splitting significantly reduced total seed handling time (Figure 3a): birds that on average split seeds more accurately had shorter average handling times. For hemp seed, the proportion of seed splitting by an individual also reduced seed handling time (Figure 3a). Interestingly, average head position height extended handling time (Figure 3b), while it increased success rate (Figure 3d). On the other hand success rate was not significantly affected by any variable for canary seed. The effects of the kinematic metrics on handling time and husking success rate were limited, only for hemp maximum closing velocity significantly reduced success rate (Figure 4e). In other words, birds that closed their beak faster, on average, were less successful at processing seeds.

The effects of seed splitting on seed handling time were substantial. Birds that split 100% of their seeds in both halves spend about 3.3 s less to process seeds whilst feeding on canary seed and 4.3 s less whilst feeding on hemp seed than birds that split the least seeds relatively, which translates in a relative reduction in handling time of roughly 50% and 33% for canary seed and hemp seed, respectively. Effects of head position height were also rather strong as birds that always keep their head high spend 4.2 s longer to process hemp seeds and are successful in 18% more of their husking attempts on average than birds that always keep their head low. Lastly, the effect of maximum closing velocity is important as well as birds that close their beak the fastest on average successfully husk about
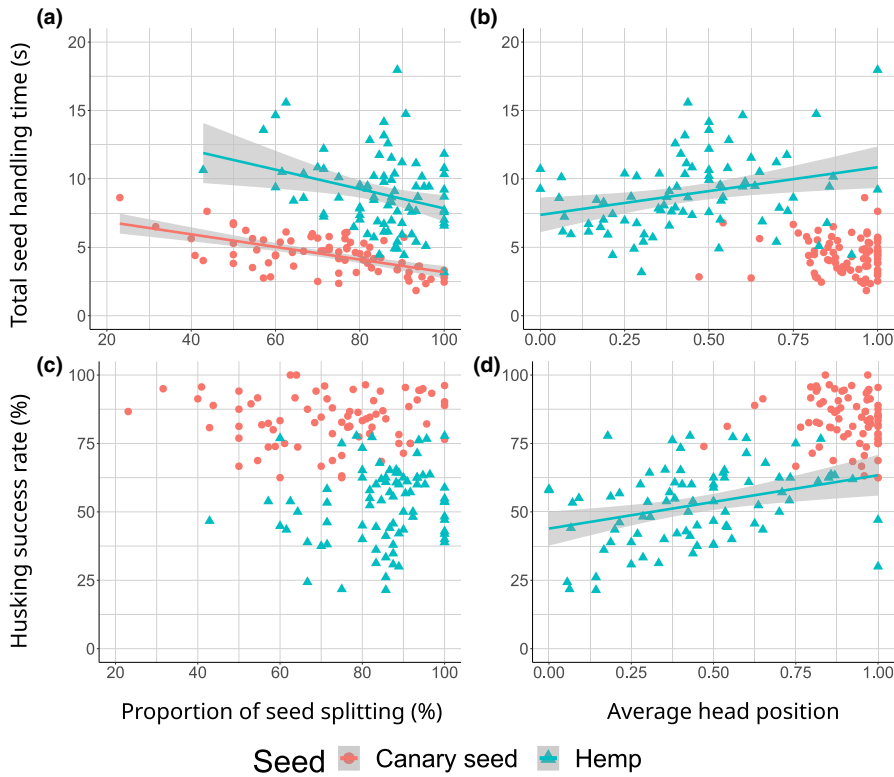
FIGURE 3 Linear relationships of skill variables with seed handling time (a, b) and husking success rate (c, d). Head position is represented by a value between 0 and 1, where a value of 1 indicates that a bird always keeps its head upright during seed cracking, while a value of 0 indicates that it keeps its head always close to the food receptacle. Significant relationships are represented by a regression line and a 95% confidence interval shaded in grey. Numerical and statistical results of the regression analyses can be found in Table S6.
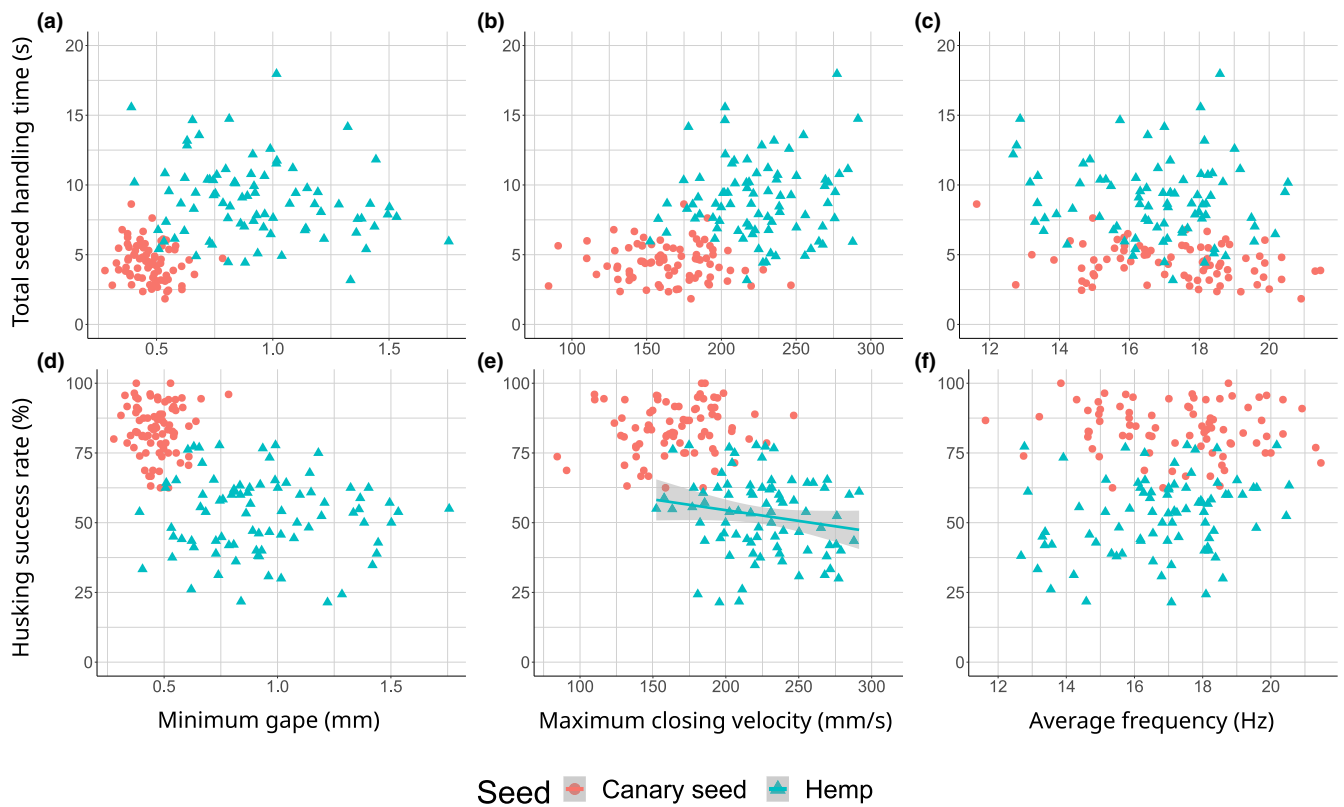

FIGURE 4 Linear relationships of kinematic variables with seed handling time (a–c) and husking success rate (d–f). Significant relationships are represented by a regression line and a 95% confidence interval shaded in grey. Numerical and statistical results of the regression analyses can be found in Table S6.

16% fewer seeds on average than the birds with the slowest beak closing velocities.

4 | DISCUSSION

Our study is the first to have measured and analysed individual variation in kinematics of granivorous feeding based on data from a large number of individuals. We found considerable variation between individuals in many aspects of granivorous feeding. For example, a two-fold range was observed in both open–close frequency of the beak during seed handling (Figure 4c,f) and beak closing velocity (Figure 4b,e). Such variables were categorized as measures of beak *kinematics*. The capacity to properly execute feeding tactics that are assumed to be beneficial, seed splitting and seed handling in an upright head posture were scored as *skill*. Here also, our laboratory population showed considerable variability: for example, the proportion of seeds that were split in half varied from a minority of the seeds that were handled in some birds to 100% in others (Figure 3). We then evaluated how individual variation within these two categories influenced *performance*, that is, how quickly (total seed handling time) and effectively (husking success rate) the feeding task was executed.

4.1 | Skill significantly affects feeding performance

Feeding tactics as well as the capacity to properly execute them likely varies among individuals. Intraspecific variation in seed cracking techniques has, for example, been described in Darwin's finches which either hold the seed lengthwise in the bill during cracking or brace it against the ground to secure it for a biting and twisting motion (Grant, 1981). Here, we could now show with our laboratory-based experiment, which included repeated video observations per individual, that skill had an overall positive effect on feeding performance in our laboratory population of *S. canaria*.

The ability to consistently split seed husks in both their halves as opposed to crushing them into irregular pieces appears to be correctly classified by us as a valuable feeding skill for a granivorous songbird. As observed in many previous studies, splitting the seed husk is the preferred method of seed cracking for Fringillid finches such as canaries. Possible reasons for this include that splitting requires the least force to crack the seed, that it allows for efficient husk removal and that it avoids crushing the seed itself, thus avoiding loss of edible parts (Mielke & Van Wassenbergh, 2022; Nuijens & Zweers, 1997; van der Meij & Bout, 2006). However, seeds can only be split when held in a specific orientation, so it requires a skilled coordination of beak and tongue movements, not only to position the seed, but also to keep it in place when applying force for cracking. Our results now show the benefit of seed splitting from a functional perspective: birds that manage to proportionally split more seeds are considerably faster at seed handling

(Figure 3a). This indicates that skilled seed positioning precision is critical for improving feeding performance, even if the bird has sufficient bite force to opt for crushing and shatter the seed husk into small pieces.

Head position height during cracking relates to a different kind of skill than the ability to split seeds. Granivorous birds aim at keeping their head upright during seed handling to maximize vigilance (Baker et al., 2011; Cowlishaw et al., 2004; Glück, 1987; Lima, 1994), but some birds move their head down at the moment of cracking. We consider this to be a form of precautionary behaviour, as it reduces the chances that the bird would lose the seed in case it is dropped on the ground. Retrieving dropped seeds is likely advantageous because granivorous birds can sometimes spend a long time manipulating a single seed before giving up, even after dropping the seed (Greig-Smith, 1987). They likely stick to the same seed because previous manipulations might have weakened the seed husk to some extent, also called micro-cracking (Genbrugge et al., 2011; van der Meij & Bout, 2000). In our study, we found that birds keeping their head more often close to the food receptacle show more failed attempts of seed husking and hence a greater chance of dropping and having to retrieve the seeds, than birds that keep their head more often upright. Thus, a tendency to lower the head could be seen as a reflection of poorer seed handling skills.

This, however, might be an oversimplification of the relation between head position height and feeding skill since our results show that the effects of head position height on feeding performance are conflicting. While birds that keep their head mostly upright are more successful at dehusking seeds, they also take longer to do so. This increase in seed handling time might be indicative of a trade-off between feeding rate and vigilance (Glück, 1987; Lima, 1994). Baker et al. (2011) showed that, despite their upright head position during feeding, granivorous birds still experience a considerable time cost of vigilance behaviour during foraging. If we assume that birds with a higher average head position prioritize to be more vigilant, then this could explain their longer seed handling times rather than a lack of skill. Taking this into account, the relation between head position height and feeding performance is likely multifaceted.

4.2 | Beak kinematics have no positive effect on feeding performance

Despite the notable amount of individual variation in beak velocity, acceleration, open–close frequency and gape size during feeding in our sample, no significant positive effects of these beak kinematic variables on seed handling duration or husking success rate were found (Figure 4). We even found a negative effect of maximal velocity on success rate (Figure 4e). The seed positioning phase consists of a sequence of (presumably) coordinated actions by the beak and tongue to move the seed. The speed at which the beak is executing these actions during seed positioning should, theoretically, minimize the overall duration of the phase, and hence reduce the overall seed handling time, provided that the seed is not dropped in the process.

Consequently, these results are thus unexpected and puzzling from a mechanical point of view.

A first potential explanation for the lack of effects of beak kinematics on feeding duration could be a trade-off between the speed to complete seed positioning versus cracking. In our data, the duration of seed positioning and cracking was pooled because the instant of transition between these two alternating phases is often unclear. Still, one could argue that a shorter seed cracking phase due to a relatively high bite force may be coupled with a longer seed positioning phase because of a relatively low beak movement frequency. Such a trade-off between biting and beak movement frequency has been observed during singing (Herrel et al., 2009; Podos, 2001). However, it seems improbable that the effects on both phases would precisely equalize the total duration, and would do so for two vastly different seed types.

A second explanation could be a speed-accuracy trade-off. This is a well-known effect in the context of rapid movements (Fitts, 1954; Heitz, 2014). It is possible that as birds move their beaks faster, they have reduced control over the seed, thus leading to more corrective movements that need to be executed and/or more unsuccessful husking attempts. The observed negative relationship between the beak's closing speed and seed husking success rate on hemp seeds in our canaries seems to support the latter (Figure 4e), though no effects on success rate were found for the other kinematic variables. To learn more about this potential speed-accuracy trade-off, more in-depth biomechanical analyses are needed, for example, to test whether the speed of beak movement changes the pattern of seed movement.

4.3 | The mechanistic basis of feeding: From the laboratory to the wild

Captive birds experience different selection pressures due to, among others, the absence of predators or food scarcity (e.g. Price, 1984). Such relaxed selection pressures are thought to increase variability (McPhee & Carlstead, 2010). It should therefore be noted that individual variation in feeding performance, skill and kinematics as measured in our captive population was probably larger compared to wild populations. Yet, a relatively high individual variability likely benefitted our analyses by increasing the probability to detect relationships among these variables. Our model canary breed, the Fife Fancy, has historically been selected for body posture only (Güttinger, 1985), so no directional, artificial selection has occurred on traits promoting beak speed. Hence, the mechanistic basis of feeding should not differ between our captive population and their wild counterparts.

5 | CONCLUSIONS

Our results highlight the complexity of the feeding act in granivorous songbirds from a functional point of view. We show that

skill has an overall positive effect on performance, but unexpectedly, despite the canary's impressively fast beak movements and considerable individual variation in our sample, beak kinematics had no positive effects on performance. Therefore, our study adds to the growing body of research supporting the idea that skill is a critical factor in explaining individual differences in performance during complex actions (Briffa & Lane, 2017; Lane & Briffa, 2020; Wilson et al., 2017). As being skilled in seed husk splitting considerably reduced the feeding time in our canaries, a reduced vulnerability to predation and hence a predation-pressure-dependent selection on seed processing skills can be expected. Since these skills are thought to develop through a positive feedback between behaviour, learning and increased efficiency, and thus will likely improve with age, it still remains unclear how and on which components natural selection will act on. As such, research into the ecological, developmental, sensory and neuromechanical aspects of feeding skills (such as the reported seed splitting ability), and particularly longitudinal studies to incorporate changes over a lifetime, would further improve our understanding of the dynamic aspects of the feeding process of songbirds and how these could be subject to selective pressures.

CONFLICT OF INTEREST STATEMENT
We declare there are no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.1jwstqk09 (Andries et al., 2023). Raw video data size is too large to deposit (±90 TB), but can be accessed upon request by contacting Tim Andries (tim.andries@uantwerpen.be).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Video S1. Bird splitting a seed husk of canary seed.

Video S2. Bird crushing a seed husk of canary seed.

Table S1. Repeatability estimates of performance and kinematic variables of canary and hemp seed.

Table S2. Correlation matrix of performance variables of canary seed.

Table S3. Correlation matrix of performance variables of hemp seed.

Table S4. Correlation matrix of skill and kinematic variables of canary seed.

Table S5. Correlation matrix of skill and kinematic variables of hemp seed.

Table S6. Summary statistics of independent variables per regression model.