

Seed husking time and maximal bite force in finches

M. A. A. van der Meij* and R. G. Bout

Department of Evolutionary Morphology, Institute of Biology Leiden, PO Box 9516, 2300 RA Leiden, The Netherlands

*Author for correspondence (e-mail: m.a.a.van.der.meij@biology.leidenuniv.nl)

Accepted 12 June 2006

Summary

Many studies on the efficiency of feeding in finches concentrate on husking time in relation to average seed size and bird size. Large species are capable of eating larger seeds and are able to husk large seeds faster than smaller species. It is generally assumed that husking time is related to bite force. However, there are very few studies that investigate the relationship between husking time, seed hardness and bite force directly.

In our experiments we measured the seed husking time and the maximal bite force of two taxa of seed cracking birds. Husking time is related to maximal bite force in a highly non-linear way and differs between estrildids and fringillids. Fringillids with the same bite force as estrildids take less time to crack seeds, but only when the strength of the seed coat is close to their maximal bite force. For seeds

that are relatively soft the difference in husking time becomes very small. A preliminary jaw motion analysis provides evidence that this difference in husking time between estrildids and fringillids is paralleled by a difference in husking technique. This difference in technique does not affect bite force as such, but decreases the chance of failed cracking attempts.

The selective advantage of a small increase in maximal bite force may be related more to the decrease in husking time for seeds with hardness below the maximal bite force, than to the increase in range of seed hardness that the bird is able to crack.

Key words: bite force, feeding performance, seed hardness, jaw movement, finches.

Introduction

Differences in food choice and feeding performance in granivorous birds have been subject of many studies. The evolutionary mechanisms underlying the divergence of feeding habits and beak morphology during adaptive radiation have been studied extensively in the Darwin finches of the Galápagos Islands (Grant, 1986; Grant and Grant, 1989). Variation in food availability and interspecific competition result in natural selection for specific feeding habits and beak morphologies (Grant, 1986). Within species variation in beak size has been directly related to differences in the selection of different proportions of the available range of seed sizes (Grant et al., 1976; Abbot et al., 1977; Boag and Grant, 1984; Grant and Grant, 1996).

Most studies on the efficiency of feeding in finches concentrate on husking time in relation to average seed size and bird size (Kear, 1962; Hespenheide, 1966; Willson, 1971; Schluter, 1982; Diaz, 1990; Read, 1991). Large species are capable of eating larger seed species and are able to husk large seeds faster than smaller species. Benkman and Pulliam (Benkman and Pulliam, 1988) demonstrated that cardueline finches are not only much faster handling large seeds than emberizine sparrows of the same body size, but also eat a

wider range of seed sizes. An increase in the range of a diet with increasing bite force has been reported for a number of vertebrates (Wainwright, 1991; Herrel et al., 1996; Verwaijen, 2002; Aguirre et al., 2003). As seed size is correlated with seed hardness (Abbott et al., 1977; Van der Meij and Bout, 2000) it is generally assumed that husking time is related to seed hardness and bite force. However, there are very few studies that investigated the relationship between husking time and seed hardness. Feeding time in two morphs of *Pyrenestes ostrinus* is longer on plant species with large, hard seeds than for species with small, soft seeds (Smith, 1987), and husking time decreases when hardness is experimentally lowered for the same seed species (Van der Meij et al., 2004).

Just as only a few studies directly investigate the relationship between husking time and seed hardness, the number of studies that measure bite force in birds is limited. Van der Meij and Bout (Van der Meij and Bout, 2004) and Herrel et al. (Herrel et al., 2005a; Herrel et al., 2005b) related bite force to head morphology. In Galápagos finches bite force is not only related to beak size but even more strongly to head width. Such a relationship may be expected since maximal bite force is closely related to the size of the jaw adductor muscles (Van der Meij and Bout, 2004) and head size closely correlates with jaw muscle size (Herrel et al., 2001; Herrel et al., 2002).

In this study we investigate whether bite force is directly related to husking time in two groups of finches, the estrildids (Estrildidae) and fringillids (Fringillidae). From a previous study with various seed species we know that differences in husking performance between these two groups of finches do occur (R.B., personal observation). In the study reported here we offered a single seed species to a number of different species of both families, and husking times are related to bite force measurements of the same individuals.

Bite force is influenced by the geometry of the skull and jaw muscles, and the size of the jaw closing muscles. The effect of differences in skull geometry between estrildids and fringillids is relatively small compared to the difference in muscle size (Van der Meij and Bout, 2004). However, it is not clear whether the size of the jaw muscles is the only factor determining husking time. Alternatively, differences in husking time may be the result of differences in husking technique. Ziswiler described two different techniques: crushing and cutting. Estrildids use a crushing technique, whereas fringillids use a forward/backward movement of the lower jaw ('cutting') during the cracking phase (Ziswiler, 1965). We therefore also performed a preliminary analysis of the cracking technique of an estrildid and a fringillid.

Materials and methods

Seeds

To measure husking time, hemp seeds (*Canabis sativa*) were offered to 26 individuals of 18 different species (Table 1) belonging to two different passerine families: the Estrildidae

and Fringillidae. In hemp seed the husks are fused and form a closed shell around the kernel (Van der Meij et al., 2004). In contrast to so-called open-shelled seeds, in which the two husks envelop the kernel only loosely, birds need to apply considerable force on the seed before the husk splits into two parts. In open-shelled seeds the husks can be removed very quickly without actually cracking the seed coat (Kear, 1962). The mean hardness of hemp seeds was 12.16 ± 4.95 N. The hardness of the seeds was measured by stepwise lowering of a force transducer pressing on individual seeds, and recording the peak force at the point where the seed husk cracked (see also Van der Meij and Bout, 2000).

Husking time measurements

All birds in the present study were purchased commercially and kept in the laboratory in separate cages (40×38×38 cm) at 22°C and a 16 h:8 h L:D cycle. The food was removed from the cage the evening before the experiments. The following day a large amount of hemp seeds (approximately 300) was offered to the birds. Trial experiments showed that the period of food deprivation clearly affected husking time. To increase feeding motivation and to measure maximal husking performance the period of food deprivation was maximised and adjusted to the size of the species, i.e. between 20 h for the largest species (*Mycerobas affinis*, 70 g) and 15 h for the smallest species (*Erythrura trichroa*, 13 g). The seeds were offered in a small transparent container hanging in front of the cage for 45 min. During this time the bird was monitored with a standard video camera (25 frames s⁻¹). Husking time was determined from these recordings and taken as the time from the moment a seed

Table 1. Maximal bite force and mean husking time for hemp

Species*	Number of individuals	Number of seeds	Husking time (s)	Bite force at bill tip (N)
Estrildidae				
<i>Padda oryzivora</i> Java sparrow	2	40	4.11±3.41	9.6
<i>Erythrura trichroa</i> blue-faced parrotfinch	1	24	7.86±7.25	5.3
<i>Taeniopygia guttata</i> zebra finch	1	4	16.04±3.20	3.9
<i>Lonchura punctulata</i> spotted munia	1	9	11.56±6.45	3.7
<i>Chloebia gouldiae</i> gouldian finch	1	11	12.53±8.91	4.1
<i>Lonchura fringilloides</i> magpie mannikin	1	6	7.87±3.23	5.0
<i>Amadina fasciata</i> cut-throat finch	1	5	5.43±1.75	5.2
Fringillidae				
<i>Carduelis chloris</i> greenfinch	4	71	2.64±1.04	13.6
<i>Loxia curvirostra</i> common crossbill	2	53	3.74±1.78	8.7
<i>Serinus mozambiques</i> yellow-fronted canary	1	20	12.59±8.67	2.9
<i>Eophona migratoria</i> Chinese grosbeak	2	52	2.11±0.72	36.1
<i>Pyrhula pyrrhula</i> bullfinch	1	25	4.87±3.15	4.9
<i>Carpodacus erythrinus</i> common rosefinch	1	20	3.42±2.27	6.3
<i>Carduelis sinica</i> oriental greenfinch	1	20	2.93±0.82	8.1
<i>Rhodopechys obsoleta</i> desert finch	2	30	3.98±2.02	6.4
<i>Serinus serinus</i> European siskin	1	17	9.23±8.18	3.1
<i>Carduelis flammea</i> common redpoll	2	16	9.75±6.16	2.9
<i>Mycerobas affinis</i> collared grosbeak	1	15	2.38±1.03	38.4

*Taxonomy (see Sibley and Monroe, 1990; Sibley and Monroe, 1993).

Values for husking time (s) are means ± s.d.

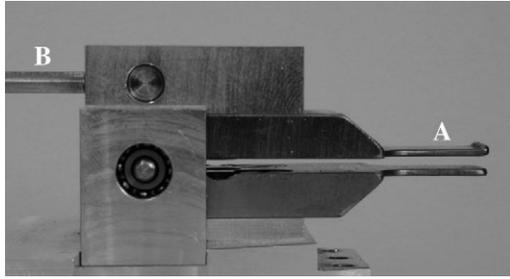


Fig. 1. Tool for bite force measurements. Rigid metal plates (A) that are slightly pressed together by the bill as a bird bites on the plates (notice the rounded ridge to prevent pressure of the rest of the bill). B, connection to the force transducer.

is picked up until the moment the first half of the split husk fell out of the beak, with an accuracy of 0.04 s (1 frame).

Before and after the experiments, water and a standard commercial seed mixture with hemp seeds added were available *ad libitum*. Between consecutive experiments on the same bird there was an interval of at least 3 days.

Bite force

To measure the maximal bite force we used a force transducer (Aikoh, Osaka, Japan; 9000 series) mounted with two flat metal plates (Fig. 1). The birds were held by hand and trained to bite the metal plates. The birds only used their beak tips to bite the force transducer and refused to bite at more caudal positions within the beak. Bite force measurements were performed several times in a row at each occasion, and on at least five different days to determine the maximum bite force at the tip of the bill. The maximal bite force for a bird is the highest value measured, but in all cases at least two other bite forces were recorded that differ less than 0.2 N of the maximal value.

Jaw movements

To study the cracking technique high-speed video recordings (color high-speed video; S-VHS; Nac, Beringen, Belgium, 250 fr s^{-1}) of the Java sparrow (estrildid) and the greenfinch (fringillid) were made. Up to 16 markers were placed on both sides of the bill and on top of the head. The birds were offered hemp seeds on a small plateau surrounded by three mirrors (left, right and overhead; Fig. 2) at an angle of 45° to the frontal plane. The co-ordinates of markers on the head and of markers visible in the mirrors were digitised and the three-dimensional (3D) position of the markers was reconstructed using the direct linear transformation technique (DLT) (Woltring and Huiskes, 1990). The DLT transformation was based on a 3D-calibration object with 15 spherical markers.

Data analysis

Most statistical tests were performed in SPSS 8.0 (SPSS Inc. Chicago, IL, USA). For the analysis of average husking time the standardized major axis routine (S)MATR (v1) (Falster et

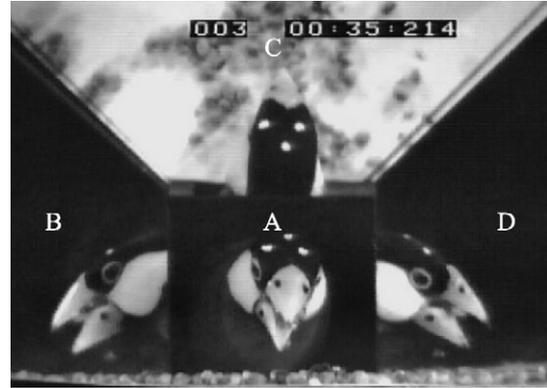


Fig. 2. Image of Java sparrow during seed cracking in experimental setup. The head is recorded directly and in three mirrors: frontal (A, direct view), left lateral (B), dorsal (C) and right lateral (D).

al., 2003), was used. This routine implements the algorithms developed by Warton and Weber (Warton and Weber, 2002).

Results

Husking time and bite force

The average husking time, the number of hemp seeds eaten and the maximal bite force for the different bird species are shown in Table 1. The husking times for both the averages per species and within a single species are distributed exponentially. Fig. 3 shows the average husking time *versus* bite force for each species.

To test whether there is a significant difference in the time used to crack hemp seeds between estrildids and fringillids we performed two analyses: a standardized major axis analysis on the average husking time per species and a survivorship analysis on the husking times for all individual seeds. The model II regression analysis for the ln transformed average husking time and the inverse of bite force showed a significant positive correlation for both finches ($r=0.978$, $P=0.000$) and estrildids ($r=0.914$, $P=0.004$). However, the slope of the relationship between average husking time and the inverse of bite force differed ($P=0.033$). Husking times were lower for the fringillids (slope 5.09, 95% CI 4.35–5.96) than for estrildids (slope 8.56, 95% CI 5.45–5.96) for the same bite force.

$$\text{Estrildids: husking time} = 1.43e^{8.56/\text{bite force}} \quad (R^2=0.835)$$

$$\text{Fringillids: husking time} = 1.83e^{5.09/\text{bite force}} \quad (R^2=0.956)$$

The curves converge for high bite force to a theoretical minimum time necessary to crack a seed. This is the time necessary to process a seed with one single, successful cracking attempt. The minimum husking time is the same for the two families. Fringillids require a minimum time of 1.8 s to crack a hemp seed; the extrapolated prediction for estrildids is 1.4 s. From the baseline representing minimum husking time there is a rapid increase in husking time with decreasing bite force.

The survivorship analysis (Cox regression) on the husking times for all seeds, with family and maximal bite force as

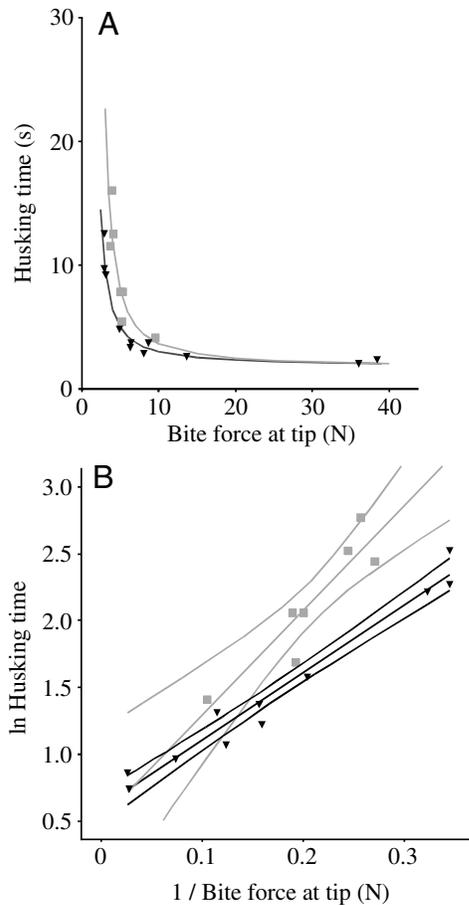


Fig. 3. (A) Exponential decrease in husking time with increasing bite force for estrildids (grey squares) and fringillids (black triangles). The data are fitted with an S-curve for each family. (B) Ln-transformed husking time vs inverse bite force for estrildids (grey squares) and fringillids (black triangles), to show 95% confidence intervals.

covariates gives similar results. There is a significant difference in husking time between estrildids and fringillids ($P=0.002$) as well as for different maximal bite forces ($P=0.000$). The estimated function for husking time is very similar to the one found for the model II regression on average husking time. The cumulative hazard function of the survival function estimates the change of a successful cracking attempt as a function of time. Fig. 4 shows that the chance that a hemp seed cracks within a certain amount of time is much higher in the fringillids than in the estrildids, irrespective of the difference in maximal bite force.

Seed cracking technique

In both the fringillids and the estrildids a seed is picked up and transported to the back of the beak and placed between the rims of the beak. This often requires only limited number (approx. 3) of beak movements. Once the seed is placed correctly between the rims of the beak a cracking attempt is made. This can be recognised by depression of the elevated upper jaw onto the lower jaw. If the cracking attempt is

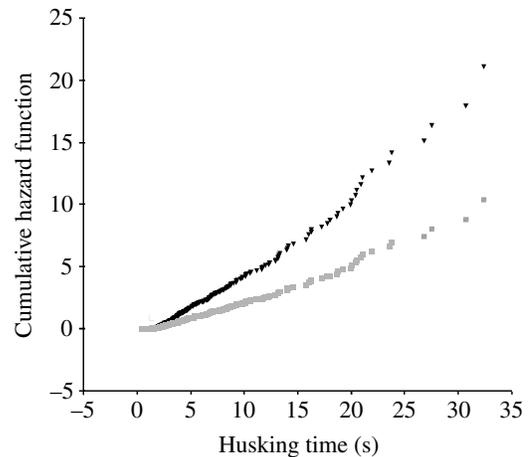


Fig. 4. Cumulative hazard function at the mean of bite force for estrildids (grey squares) and fringillids (black triangles).

successful part of the split husk becomes visible at the outside of the beak. If the cracking attempt was not successful the seed is repositioned between the rims and another attempt is made. The preliminary analysis of the cracking technique shows that the lower jaw makes a lateral movement just before a cracking attempt. During this movement the tip of the lower jaw moves in a direction opposite to the side where the seed is cracked. Its amplitude is much smaller in the Java sparrow than in the greenfinch. In the Java sparrow the movement is about 1 mm, whereas the movement of the lower jaw of the greenfinch is up to 4 mm (Fig. 5). Note that in both cases the amplitude of the movement is clearly larger than for the rigid upper beak (measurement error).

Discussion

Our results provide direct evidence that in both estrildids and fringillids husking time is directly related to bite force and that husking time decreases exponentially with increasing bite force. To get a good estimate of the relationship between bite force and husking time we aimed to collect data over the whole range of bite forces within the two families investigated. Unfortunately we were not able to find an estrildid species large enough to crack hemp very easily, and to confirm experimentally the estimate of minimum husking time. For a few species only one individual was measured. However, the interspecific variation in husking time is much larger than the intraspecific variation. This is illustrated by the analysis of the data according to a nested ANOVA design (individuals nested within species, and species within family). For the species for which more than one individual was measured it shows that intraspecific variation of the ln transformed data is only 4% of the total variation (restricted maximum likelihood estimate), and that variation between species is 13 times larger than intraspecific variation.

Unlike the Darwin's finches in the study by Herrel et al. (Herrel et al., 2005a; Herrel et al., 2005b) the birds in our study

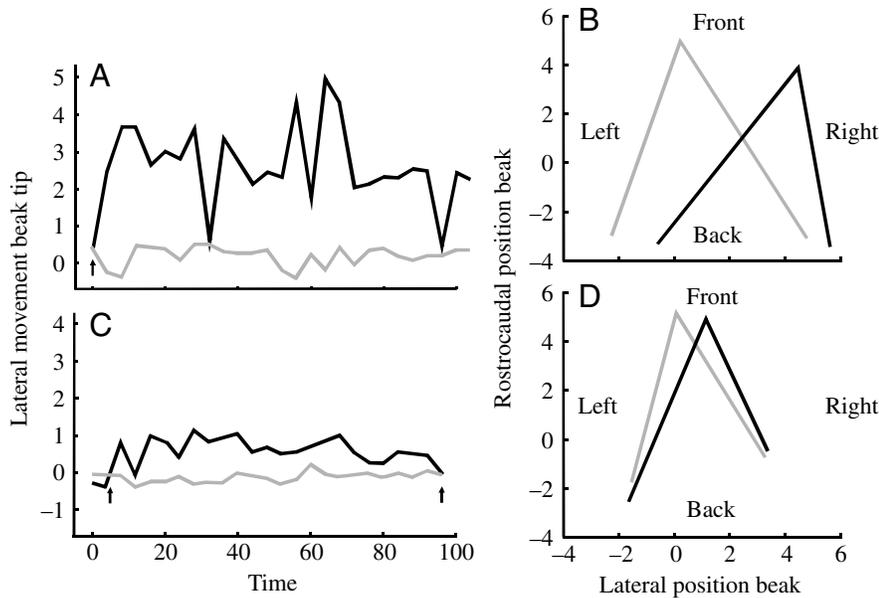


Fig. 5. Movement of the upper (grey) and lower jaw (black) in the greenfinch (A,B) and Java sparrow (C,D) during a cracking attempt. A and C show the lateral movement (in mm) vs time (frames). While the lower jaw moves sideways during opening of the beak, the tip of the upper jaw does not move in the horizontal plane. Arrows indicate positions with closed beaks (opposing beak tips). B and D show graphically the most extreme positions of the lower jaws in the horizontal plane. The beak tips are pointing upward. On the x axis, zero coincides with the medial plane. On the y axis the position of zero is arbitrary.

were not willing to bite the force transducer at a position closely corresponding to that used to crack seeds. In most species the maximal bite force measured at the tip of the beak is lower than the average hardness of hemp, except in the greenfinch and the Chinese grosbeak. Static force modelling (R.B., unpublished data) shows that maximal bite force increases approximately linearly towards the base of the bill and is about two times higher close to the rictus than at the tip of the beak. hemp seeds are usually cracked about halfway between rictus and beak tip in species that easily eat hemp, but are moved more caudally in species with a relatively low bite force. In the smallest estrildids (e.g. *Poephila*, *Lonchura*) maximal bite force is clearly less than the average hardness of hemp and only a small amount of seeds at the lower end of the hardness range are available for the birds. Note that this underestimates husking time in these species compared to more powerful biters, because the average hardness of the seeds eaten is less. The low number of husking times recorded in these species result from a lack of motivation to continue searching for seeds that they are able to crack. This mechanism of avoiding seed species that are too difficult to eat has been reported in field studies as well (Newton, 1967) (see also Van der Meij and Bout, 2000).

Husking time and bite force

Seed hardness together with maximal bite force determines which part of the available food resources a bird is able to use. Species with a maximal bite force that is higher than the seed hardness range are able to eat all seeds. When maximal bite force falls within the range of seed hardness a bird will also pick up seeds that are too hard to crack. Time spent handling seeds that have to be rejected because they are too hard leads to a decrease in food intake rate. High percentages of rejection of seeds occur in the field (Grant, 1981; Greig-Smith and Wilson, 1985). Laboratory experiments with Java sparrows

showed that birds do use size cues as an indicator for seed hardness to avoid picking up seeds that are too hard to crack, even when the correlation between seed size and hardness is very low (Van der Meij and Bout, 2000). Selective uptake of seeds has been reported for other species as well (Hespenheide, 1966; Willson, 1972).

Our data show that maximal bite force does not simply put an upper limit on the hardness of the seeds that can be cracked and eaten, but that with increasing bite force, less time is needed to crack seeds with hardness just below the maximal bite force. This suggests that the selective advantage of a small increase in maximal bite force may not only be related to the increase in range of seed hardness available to the bird, but also to the decrease in husking time for seeds with hardness just below the maximal bite force. Any new seed available at the top of the range will require very large husking times, while already available seeds just below the top of the hardness range will be husked much faster than with a lower bite force. Which effect will be more beneficial is not clear and may depend on the availability of seeds in the environment. A similar relationship between maximal bite force and feeding performance (handling time) may exist in lizards (Verwaijen et al., 2002). The increase in accessibility of seeds and faster husking times with increasing bite force raises the question of why low bite force may be adaptive in some species (cf. Grant et al., 1976). Bite force increases positive allometrically with body mass (Van der Meij and Bout, 2004). However, large species seem to have problems manipulating relatively small seeds and may have longer husking times on soft seeds than smaller species with less bite force (M.A.A.M. and R.G.B., unpublished observation). This would give small, less powerful biters an advantage over large species at the low end of the range of accessible seeds. Whether this would also explain differences in bite force between species of the same body size, for instance because powerful biters have larger beaks, remains to be seen.

Seed cracking technique

Fringillids and estrildids differ in their husking time on hemp seeds, independent of maximal bite force. Fringillids are on average faster than estrildids, especially when their bite force is low (statistically when the bite force is less than 7 N; see Fig. 3). Frame by frame analysis of a limited set of video recordings of the seed cracking process in finches and estrildids showed that husking time comprises two different phases (van der Meij et al., 2004). During the transport phase, the seed is transported to the back of the beak and positioned next to its rims. The number of beak movements (mandibulations) required to transport a seed is the same in finches and estrildids, and seems largely independent of seed size. During the next phase the seed is manipulated to position it between the rims of the beak. This often requires a number of small amplitude opening and closing movements of the beak. Once the seed is positioned correctly, a cracking attempt is made. If the cracking attempt fails, the whole process is repeated until the cracking attempt is successful. The number of positioning movements per cracking attempt increases with seed size, reflecting the difficulty in manipulating large seeds. The number of cracking attempts clearly increases with seed hardness and the largest contribution to differences in husking time comes from the number of cracking attempts (Van der Meij et al., 2004). In birds that use a long time to crack a seed, many cracking attempts fail and the seed is often squeezed from between the rims of the beak into the oral cavity. The difference in husking time between estrildids and fringillids may therefore be related to a difference in the way the two groups handle the seed during cracking attempts.

In a preliminary analysis we show that during a cracking attempt the tip of the lower jaw moves sideways from its medial position opposite the upper jaw, to a position left or right from the tip of the upper jaw. The amplitude of this mediolateral movement differs in the greenfinch, a fringillid, and in the Java sparrow, an estrildid. The mediolateral movement of the lower jaw is four times larger in the greenfinch than in the Java sparrow. Although the number of lower jaw movements analyzed was very limited, they may be representative for most

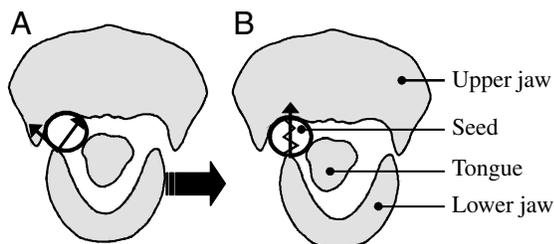


Fig. 6. Schematic representation of a cross section through the upper and lower beak of the Java sparrow. (A) In the resting position the lower jaw would press just off centre onto a 2.5 mm seed, generating a force along the surface of the seed. (B) Biting force might be directed more efficiently perpendicular to the surface of the seed by moving the lower jaw in a direction opposite to the side where the seed is cracked (large arrow in A).

movements, because the difference in amplitude is often clearly visible in video recordings.

Ziswiler studied the husking technique of estrildids and fringillids and described two different techniques: crushing and cutting (Ziswiler, 1965). Crushing is used by the estrildids and is characterised by opening and closing (dorsoventral) movements of the jaws, restricted to the vertical plane. Fringillids, however, are believed to use a forward/backward (rostrocaudal) lower jaw movement ('cutting') during the cracking phase and mediolateral movements of the lower jaw during the husking phase. A morphological analysis of the jaw apparatus (Nuijens and Zweers, 1997) and our preliminary analysis of 3D kinematics of the lower jaw suggest that the rostrocaudal movement may be an artefact of the 2D analysis made by Ziswiler. In projection the large mediolateral movements of the lower jaw present during seed cracking and husking in fringillids appear to be 'rostrocaudal' movements.

We suggest that the lateral movement of the lower jaw does contribute to the shortening of husking time. When the lower beak is in its rest position it is not pressing against the centre of the seed, which is fixated in a groove of the upper beak, and there is a force component along the surface of the seed (Fig. 6A). When during a cracking attempt there is not enough friction between the lower beak and the seed, it is squeezed into the beak and another cracking attempt is needed. However, when the lower jaw moves in a lateral direction to a position right under the seed (Fig. 6B), the bite force is directed in such a way that chance of squeezing the seed from between the beaks becomes much smaller.

We have no reason to believe that the tongue plays a different role in the two groups of finches during seed cracking. It prevents the seed from falling into the beak in the same way that the most lateral ridge of the upper jaw prevents the seed from falling out of the beak. Lateral jaw movement may therefore decrease the number of cracking attempts and increases husking performance on closed-shelled seeds.

The difference in amplitude of lateral lower jaw movement between estrildids and fringillids may be related to a difference in preferred seed type. Estrildids are generally believed to feed mainly on open shelled seeds, and remove the husks without actually cracking the seed coat (Kear, 1962). Although the force with which open-shelled seeds are dehusked cannot be measured directly it is very probably low. Husking times for open-shelled seeds are low in comparison to husking times for closed shelled seeds and very similar in estrildids and fringillids of various sizes (R.G.B., personal observation). Fringillids, on the other hand, feed primarily on closed-shelled seeds that need to be cracked. As the number of failed cracking attempts may be expected to be lower when biting forces are low, small amplitude lateral movements are not necessary for species that feed mainly on open-shelled seeds.

The authors are thankful to Mirjam Griekspoor and Richard Verbeek for collecting part of the husking time data, the people of the technical department of our institute for

constructing the bite force equipment and to Jim Vanden Berge for his comments on the manuscript.

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