SHORT COMMUNICATION

Crani kinesis facilitates quick retraction of stuck woodpecker beaks

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ABSTRACT
Much like nails that are hammered into wood, the beaks of woodpeckers regularly get stuck upon impact. A kinematic video analysis of pecking by black woodpeckers shows how they manage to quickly withdraw their beaks, revealing a two-phase pattern: first a few degrees of beak-tip-down rotation about the nasofrontal hinge causes the tip of the upper beak to be retruded while its proximal end is lifted. Next, the head is lifted, causing beak-tip-up rotation about the nasofrontal hinge while the lower beak starts retruding and initiates the final freeing. We hypothesise that these consecutive actions, taking place in about 0.05 s, facilitate beak retraction by exploiting the presumably low frictional resistance between the upper and lower beak keratin surfaces, allowing them to slide past each other. It also demonstrates the counter-intuitive value of maintaining cranial kinesis in a species adapted to deliver forceful impacts.

KEY WORDS: Birds, Pecking, Kinematics, Biomechanics, Functional morphology

INTRODUCTION
Repeated pecking into trees to excavate cavities and to remove bark while searching for food is essential for many woodpecker species (e.g. Martin, 2015). To do so, they forcefully bore into wood with their chisel-like beaks, a behaviour they perform several hundreds of times per day (May et al., 1976). Woodpeckers prefer softer wood to excavate their nests, including trees showing decay or dead trees (Martin, 2015; Puverel et al., 2019), which suggests a selective pressure to minimise the energetic costs and time investment in pecking.

But how do woodpeckers avoid the potential problem of having their beak stuck into trees? The deformation caused by a sharp object that penetrates a softer, porous and fibrous tissue such as wood, will not be entirely plastic, but also partly elastic (i.e. will tend to take back its original form). As a result, wood will clamp around the penetrated sharp object and, when that object is being pulled back, exert shear forces that resist this movement. This is the way nails become firmly anchored after being hammered into wood (Salem et al., 1975). If this happened to the beak of a woodpecker, it would strongly compromise the bird’s pecking performance.

While studying slow-motion videos of pecking by the black woodpecker, Dryocopus martius, we noted that the beak regularly became markedly immobile right after the time of impact, suggesting that the beak frequently gets stuck. Interestingly, this is typically followed shortly afterwards by a peculiar movement of the beak, after which the head is retracted (Movie 1). In order to unravel how woodpeckers deal with stuck beaks, we describe below the movement of the beak during the phase of unclamping, and hypothesise how this movement is generated and how it contributes to an effective freeing of the beak.

MATERIALS AND METHODS
High-speed videos of Dryocopus martius (Linnaeus 1758) in lateral view during pecking were recorded in an uncompressed 10-bit monochrome format using a Mikrotron Eosens TS3 camera (Mikrotron GmbH, Unterschleissheim, Germany). One adult (individual 1) was filmed in Alpenzoo Innsbruck (Austria) at 500 frames s⁻¹ at 1280×1024 pixels. A second (individual 2) was filmed in Tierpark Goldau (Switzerland) at 1500 or 1533 frames s⁻¹ at 704×564 pixels. Both individuals originated from the central Alpine region, and were pecking at hardwood tree trunks of about 0.3 m diameter. Head size, defined as the distance between the tip of the beak and the back of the head following the centreline of the beak, was measured from pictures of the head at the level of a reference grid and was 116.4 mm and 123.0 mm for individual 1 and 2, respectively. Out of a large number of videos, 10 beak retraction events were selected based on view perspective and image sharpness, and analysed. These included five acts from individual 1 and five from individual 2. As no differences were noted between individuals in the overall displayed movement pattern, and given their small size difference, data from the two individuals were treated conjointly.

To study the kinematics of the beak, the pixel coordinates of eight anatomical landmark were recorded by frame-by-frame tracking using either XMAlab 1.5.5 (B. Knörlein, Brown University; https://bitbucket.org/xromm/xmalab/src/master/; Knörlein et al., 2016) or Progressive Tracker (gitlab.com/falkm/progressivetracker; Mielke et al., 2020) (Fig. 1A): two separated landmarks on the tree (landmarks 1 and 2), two on the cranium (3, eye; 4, posterior region), two on the upper beak (5, posterior region; 6, anterior), and two on the lower beak (7, posterior region; 8, anterior). The beak tip (9) and the back of the head (10) were also digitised on one image from each video (Fig. 1A; red spheres), and used to scale the pixel coordinates to absolute dimensions. Kinematics were expressed relative to one of these two frames of reference: fixed to the tree (tree bound frame or TBF), to quantify motions relative to the initially anchored position of the beak, or fixed to the cranium (head bound frame or HBF) to quantify the motions from an anatomical perspective. Using a constant angle offset, the x-axis of the TBF and HBF was aligned with the beak axis direction in the final video frame. The calculated variables were low-pass filtered using a fourth-order zero phase-shift Butterworth filter with a cut-off frequency of 70 Hz to remove the high-frequency noise.
resulting from manual landmark digitisation. Note that imperfect camera perspective and occasional out-of-plane motions may have introduced some random error in the reported distances and angles.

RESULTS AND DISCUSSION
A consistent pattern of motion of the upper beak, lower beak and cranium characterised the release of the beak, starting about 25 ms after beak impact (Fig. 1; Movie 2). Rotation directions will be described here for birds facing the left, with time zero defined as the instant of peak clockwise rotation of the cranium. Two phases can be distinguished. During the first phase, at times between approximately −25 and 0 ms, the cranium performed a clockwise rotation with respect to the tree by 6±4 deg (mean±s.d.) (Fig. 1B). During this phase, the upper beak translated away from the tree by 1.8±0.9 mm (Fig. 1C), translated posteriorly with respect to the lower beak by 1.4±0.5 mm (Fig. 1E), and rotated counterclockwise by 4±3 deg with respect to the cranium (Fig. 1G). The posterior end of the upper beak was lifted up from the lower beak (Fig. 1F) while its tip was still located close to the impact site. The lower beak’s translation with respect to the tree along the beak axis was negligible in this time window (0.4±0.9 mm; Fig. 1D). During the second
phase, between approximately 0 and 45 ms, the cranium rotated counterclockwise in the tree-bound frame by 7.4±2.3 deg (Fig. 1B). Both the upper beak and lower beak now rotated clockwise with respect to the cranium by 8±5 deg (Fig. 1G) and 3±2 deg (Fig. 1H), respectively, passing its starting posture in 7 out of the 10 cases before rotating back counterclockwise to approach the initial posture (Fig. 1G, H). The beak parts translated with respect to each other along the beak axis in the reverse direction compared with phase 1, generally to approach their initial position (Fig. 1E), while the gap between the upper and lower beak was closed (Fig. 1F). During phase 2, a small amount of head rolling was noted in 6 out of the 10 analysed events. The upper and lower beak started their final translation away from the tree at, respectively, 15±9 ms and 13±8 ms.

Our videos show that swiftly retracting a beak that has bored into wood involves more than performing a simple pull-back of the head. The motion pattern described above (Fig. 1; Movie 2) highlights a previously unknown role for cranial kinesis in birds (Bout and Zweers, 2001), as flexion and extension about the nasofrontal hinge plays a central part in it (i.e. prokinesis; Gussekloo and Bout, 2005). Our videos also showed that the observed beak retraction is sufficiently quick to allow bouts of about three pecking cycles per second, in which each cycle included a phase with the beak appearing stuck followed by this characteristic release sequence. Based on our full high-speed video archive, we estimated that beaks got stuck in 103 out of 284 hits (36%) in D. martius. Together, this suggests that managing to retract the beak quickly and with minimal energy investment is important for woodpeckers.

But what mechanism underlies the observed movements? Let us assume the tip of the beak is forcefully clamped by the surrounding wood, and that the woodpecker’s head allows rotation in the sagittal plane at two locations: (1) the nasofrontal hinge and (2) the quadrate bone. The latter includes several joints located relatively close to each other, which for simplicity we assume to act as one hinge at the centre of the quadrate (Fig. 2A). When the neck pulls the head towards the bird’s trunk, and lower beak remains static, a torque will be exerted on the cranium about the quadrate (Fig. 2B). This torque will move the nasofrontal hinge dorsally and posteriorly. As the tip of the beak is still constrained inside the hole in the wood, this action inevitably involves a tip-down rotation of the upper beak about the nasofrontal hinge. The upper beak will translate away from the tree and the beak opens predominantly at its proximal end (Fig. 2B). This corresponds well to the observed kinematics of ‘phase 1’ (Fig. 1; at times <0 ms). During ‘phase 2’, the head is rotated counterclockwise (view on left-facing bird), presumably caused by a pushing force from the neck (Fig. 2C). In the case where the upper beak is still stuck at this time, this would create a beak-tip-up torque about the nasofrontal hinge, which rotates the quadrate dorsally and posteriorly and thereby retrudes the lower beak. The gap between the upper and lower beak will close. Again, this matches the observed kinematics (Fig. 1; at times >0 ms).

We hypothesise that in the case where the initial retraction of the upper beak is insufficient to reduce the clamping pressure to release the beak at once, this will create a new anchor point closer to the exit of the hole in the wood (Fig. 2B). Given the pointed shape of the beak, subsequent retraction of the lower beak will most likely be enough to create sufficient free space surrounding the beak inside the excavated hole, and thereby cancel out the clamping. It may also be possible that the rotations of the beak as a response to force input from the neck help to slightly expand the hole: the beak has the potential to provide crowbar-like leverage to amplify the force input from the neck to push the hole further open. Such forces exerted on the wood must occur as part of the mechanisms described in Fig. 2. In future research, videos focusing on the beak tip from an oblique view on the tree surface could help us to answer whether this technique is used or not.

Why do black woodpeckers use this sequential ‘walking’ of the upper and lower beak instead of a simple pullback of the head? A potential answer could be that frictional resistance to slide two approximately parallel surfaces covered with scales of keratin (upper and lower beak rhamphotheca) relative to each other is lower than that between the beak and the wood under the same normal forces. Sliding friction between two hard materials is known to be considerably smaller than between a hard material and wood (Atack and Tabor, 1958). Interestingly, a study on the microstructure of keratin scales of bird beaks showed a longitudinal elongation of the scales from a red-bellied woodpecker (Melanerpes carolinus), but not in other birds (Lee et al., 2014). This elongated shape may be beneficial for reducing sliding friction during beak retraction.

Woodpecker species other than the black woodpecker can probably also make use of a similar mechanism to withdraw their
beak in case it gets stuck. The cranial skeleton of woodpeckers should generally allow a certain degree of cranial kinesis (Bock, 1999). Hence, the intrinsic capacity to perform the described sequence of beak movements (Fig. 2) should be present. In support of this hypothesis, we have observed a comparable kinematic pattern in a high-speed video of a smaller European species, the great-spotted woodpecker *Dendrocopos major* (Movie 3). However, variation in size and shape of the beak among woodpeckers (Bock, 1999; Donatelli, 2012) may influence both the frequency of the beaks getting stuck and the mechanics of beak retraction.

In conclusion, we quantified the kinematics of a previously unknown behaviour by the black woodpecker in response to a stuck beak: a quick succession of upper and lower beak retraction facilitates the release of the beak. This suggests that efficiently dealing with stuck beaks is important for a successful execution of bouts of short-interval pecks. During this process, the woodpeckers make extensive use of cranial kinesis.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: S.V.W.; Methodology: S.V.W.; Formal analysis: T.A., E.P.; Investigation: S.V.W., A.A.; Writing - original draft: S.V.W.; Writing - review & editing: T.A., E.P., A.A.; Supervision: S.V.W.; Funding acquisition: A.A., S.V.W.

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Data availability
All analysed video frames and raw kinematic data supporting the findings of this study are available from the Dryad Digital Repository (Van Wassenbergh et al., 2022); https://doi.org/10.5061/dryad.866t1g1sd.

References
**Movie 1.** Slow-motion replays of high-speed videos showing the characteristic beak movement pattern during head retraction in *Dryocopus martius*.

**Movie 2.** Animation of the tracked landmarks and rigid body movement inferred from these landmarks during beak retrusion in *Dryocopus martius*. 
**Movie 3.** Slow-motion replay of a high-speed video showing beak movements during beak retrusion in great-spotted woodpecker *Dendrocopos major* which strongly resemble those described for the black woodpecker.