Point-of-View

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Bill sweeping in spoonbills *Platalea*: no evidence for an effective suction force at the tip

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We analysed the hypothesis of Weihs and Katzir (1994) that feeding spoonbills use their broad bills by sweeping it through the water to shed a vortex. This would result in a hydrodynamic suction on the bottom for catching prey immediately or during the next sweep besides providing some extra benefits. The basic assumptions appear to be erroneous. (1) A spoonbill does not mainly feed on small, benthic invertebrates, but mainly on nekton such as fish and shrimps. (2) The inner surface of the upper mandible of a spoonbill is not concave but convex. (3) During feeding, a spoonbill does not keep its bill tip close to the bottom independent of the water depth. The outcomes of the tests supporting the hypothesis do not hold and the suggested benefits are dubious. Therefore, we reject the hypothesis and the claim that the bill of a spoonbill is used as a hydrofoil. The discussed paper tried to give an explanation of the behaviour of a bird with the help of hydrodynamic formulae. The fundamental mistake in the paper is that the use of the formulae is based on wrong assumptions concerning the food of the bird, its feeding behaviour as well as its anatomical details. The tests with a bird kept in captivity suggesting a proof of the rightness of the hypothesis lack a proper connection to the situation in the wild.

Spoonbills (Aves: Ciconiiformes: Threskiornithidae, genus *Platalea*) are large wading birds characterised by their extremely flattened bills that are widened in the distal parts. The six species are very similar in shape and behaviour, mainly differing in size, colour of legs, bills and other bare parts, and in distribution (Matheu and del Hoyo 1992). They feed tactilely by walking in shallow water and sweeping their bills from side to side through the water (Kushlan 1978, Hancock et al. 1992, Matheu and del Hoyo 1992). The wider distal part of the bill shows similarity with the bills of some ducks that sieve small prey out of sediments or water, but Allen (1942) showed that the bill of a spoonbill is not suited for sieving because it lacks the necessary lamellae.

Weihs and Katzir (1994) have presented an intriguing hypothesis about the function of the remarkable bill shape. This shape would shed a vortex off the tip of the opened bill tip by the lateral sweeping movements during feeding. The vortex results in hydrodynamic suction, which is used for capturing prey that are stationed on the bottom or buried below the bottom surface, either by direct physical displacement or by triggering escape responses. Prey lifted into the water during one sweep will be grasped during the following sweep. These theoretical considerations are supported by a schematic drawing and hydrodynamic formulae. Weihs and Katzir (1994) suggested as benefits: (a) The method will allow feeding on benthic prey without grazing the solid bottom surface with the bill thus in this way minimising the probability of damage to the bill tip. (b) The lift force will also act to push the bill forward, helping to reduce the effort required to move the submerged bill as the bird walks forward during feeding. To achieve this the bill has to be used as a hydrofoil.

On the basis of three predictions, Weihs and Katzir (1994) have tested if spoonbills indeed use the bill as a hydrofoil for capturing submerged prey. A live Eurasian spoonbill *Platalea leucorodia* from a zoological garden and a skull with intact bill were used for the tests. The predictions were: (1) The bird should attempt to keep the tip of the bill close to the bottom while sweeping it through the water (i.e. bill immersion depth should increase in proportion to water depth). It was found that the spoonbill increased its bill immersion depth as the water was increased from 9 to 23 cm, so that the tip of the bill was always kept at less than 3 cm from the bottom. This fits with the first prediction. (2) Sweeping speed may be reduced with increased bill immersion. This was also found although the average reduction was less than predicted. (3) That prey items on the bottom are indeed lifted into the water by the bill-tip vortex was shown with a mechanical device. A skull with intact bill was fastened to the outside of a bicycle wheel (60 cm diameter) which closely simulated the observed sweeping radius. The wheel was mounted horizontally on a vertical stand placed in a shallow water pool in which prey items were simulated by empty (water-filled) snail shells of 8–12 mm diameter on the bottom. In this way the effect was checked that a sweep of a bill has on benthic prey items. The result was that most of the small empty shells were swirled up and displaced over distances of up to about 6 cm in forward direction after the bill tip had passed over them. Weihs and Katzir (1994) were satisfied with their results and claimed that this was the first reported case of an avian bill being used as a hydrofoil.

We came to a more prosaic, opposite hypothesis while studying the feeding structures of the black-faced spoonbill *Platalea minor*. We deduced that the rounded edges and the extreme flatness of the mandibles would just minimise drag and turbulence during the sweeping movements. This would mainly be intended to avoid disturbing the nektonic prey in advance, because tactile feeding means that prey has to be touched by the bill and caught at once. A disturbed prey will flee from the source of disturbance and will be difficult to locate again without visual clues (Swennen and Yu 2004). These deductions were strengthened by field studies concerning the food and feeding behaviour of the black-faced spoonbill (Swennen and Yu 2005). The conflicting hypotheses forced us to study also the bill and the feeding of the Eurasian spoonbill, the species on which Weihs and Katzir (1994) based their hypothesis. The feeding of Eurasian spoonbills *P. leucorodia* was studied in China and The Netherlands and found to be basically similar, but step length and sweeps were larger than those of the black-faced spoonbill. The present paper reviews the basic assumptions and their supporting tests of the hypothesis of Weihs and Katzir (1994) and compare them with our results as well as statements in the literature.

Results and discussion

(1) Weihs and Katzir (1994) assumed that benthic prey are the main food source of spoonbills. However, the food of all spoonbill species mainly consists of fish and shrimps (Cramp and Simmons 1977, Matheu and del Hoyo 1992). Stomach analysis of shot birds show that a variety of other animals and even plant fragments can be swallowed, but fish and shrimps contribute most to the general energy intake even when other items are numerically important (Allen 1942, Lowe 1982, Aguilera et al. 1996, Swennen and Yu 2005, Ueng et al. 2006). The kind of prey and direct observations of feeding spoonbills indicate that the prey are caught in the water column (Hsueh et al. 1993, Swennen and Yu 2005). It seems unlikely that the bill shape and feeding movements have just been adapted for catching or disturbing small benthic items while nekton is the main food.

(2) Weihs and Katzir (1994) predicted that a vortex at the tip of the bill will occur during the sweeping movement if the inner surface of the upper mandible is concave and the lower mandible is essentially flat. They seem to take for granted that the inner surface of the mandible is indeed concave and show that also in a schematic drawing of the bill of a spoonbill (Fig. 1A). However, the major part of the inner surface of the upper mandible is convex, including at the indicated site (Fig. 1B). The shapes of the bills of the six spoonbill species are basically similar (Swennen and Yu 2004).

(3) A vital premise for the suction effect is that the bill tip is kept on a constant distance of 2–3 cm to the bottom independent from the water depth (Weihs and Katzir 1994). That is also what their test bird did, which has been considered as support for the hypothesis. In the wild, the first phase of a feeding bout is an attempt to locate a prey. Then the behaviour is a stereotypic walking and sweeping the bill. Insertion depth is between below the nostrils and above the spoon. The distance of the head to the water and the angle of insertion usually does not noticeably change with water depth. The second phase is the attempt to catch a located prey. Then behaviour is adapted to the location and behaviour of the prey. Sweeps and steps are irregular in rhythm and length. The angle and

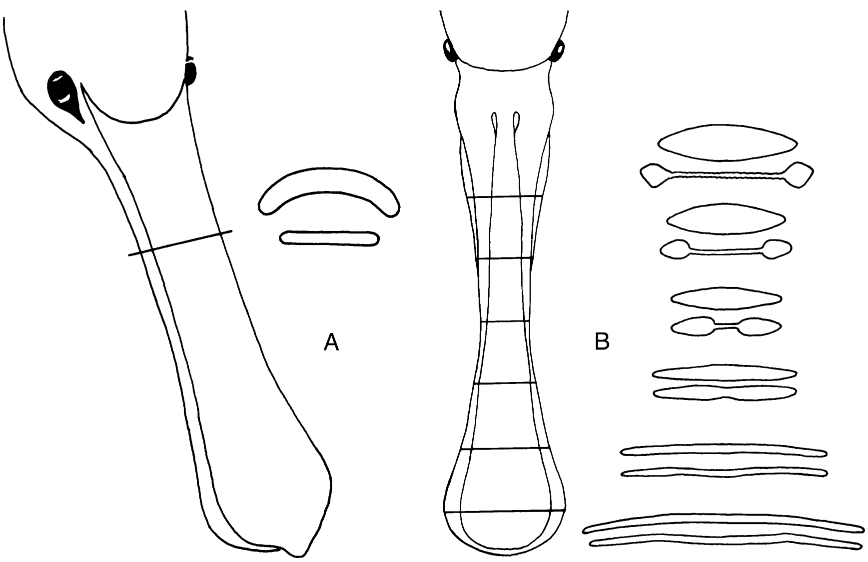

Fig. 1. The bill of an Eurasian spoonbill *Platalea leucorodia* with indication lines where the cross-sections are taken. A. Bill and cross-section according to the schematic drawing of Weihs and Katzir (1994 Fig. 1). B. Bill and cross-section as found in the present study. The main differences are: (1) that the upper mandible is concave in A while it is found convex in B, (2) the upper mandible is wider than the lower in the distal part and narrower than the lower in the proximate part.

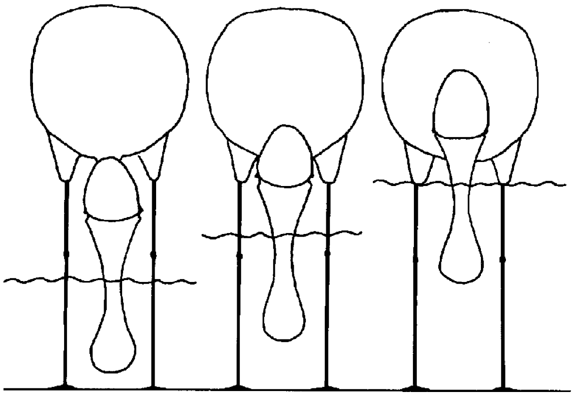

Fig. 2. Position of the head in relation to water depth during feeding of an Eurasian spoonbill showing the differences in distances of the tips of the mandibles to the bottom. The bill is inserted deeper with increasing water depth. Angle of insertion does not vary, and nostrils and neck do not come in the water during searching for prey. Drawings after frontal and lateral photographs. The underwater parts are adjusted to mean lengths of bill and leg parts taken from nine stuffed specimens.

insertion depth of the bill may change by which even the total head can be immersed. The test bird was a zoo specimen that was adapted to feeding on dead fish and chickens on the bottom of its tank (Weihs and Katzir 1994). A constant distance of the bill tip to the bottom is not shown in the field by Eurasian (Fig. 2) and black-faced spoonbills (Swennen and Yu 2005).

(4) Weihs and Katzir (1994) supposed that a lower pressure would occur around the bill tip resulting in suction. However, where spoonbills had been feeding over a soft mud bottom, their footprints could be discovered but not indications of disruption caused by suction of the sweeping bill (Swennen and Yu 2005).

(5) Weihs and Katzir (1994) mentioned as extra benefit of the hypothetical hydrodynamic effect that the lift force would also act to push the bill forward, helping to reduce the effort required to move the submerged bill as the bird walks forward. However, when this passive frontal movement would occur, it would lift the bill to a more horizontal position. This would be a negative effect because it has to be compensated by muscle force or quicker walking. Actually, there is no forward component in the sweeping bill as the bill is moved over a part of a wide arc with a lateral side in front. A step is made when the bill is about at the end of the curve. Thereafter, the bill moves over a new arc in another direction till a step is made with the other leg. Thus each sweep is associated with a step. Fig. 3 shows the resulting path made by foot and bill.

(6) The other benefit suggested by Weihs and Katzir (1994) is that the suction force would be profitable for minimising the risk of damage to the bill tip. This indeed would be a profit when (a) a spoonbill would feed on benthos instead of nekton, and (b) would select water bottoms of rock or stones as feeding habitats instead of bottoms of fine sediments (Matheu and del Hoyo 1992, Yu and Swennen 2004).

(7) The test with a bill mounted on a wheel showed that the small empty shells were swirled up and displaced over distances of up to about 6 cm after the bill had passed their

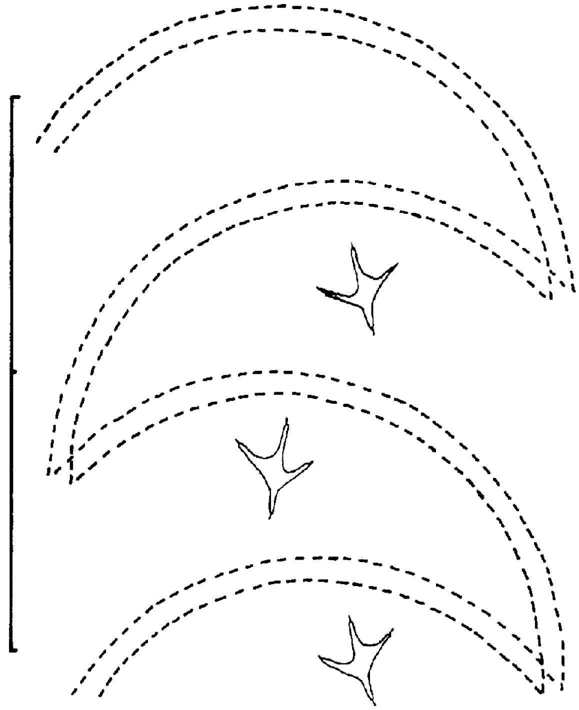

Fig. 3. Reconstruction of the route described by the bill tips and feet during searching for prey in areas without obstructions such as submersed aquatic plants. Shorter curves are made when submerged plants are present. Length of the ruler is 100 cm. The gape of the bill tips is set at 4 cm.

initial position. It was supposed that such items would be caught by the next sweep (Weihs and Katzir 1994). However, these results are irrelevant because: (a) The size of the chosen test prey (0.8–1.2 cm) is at the lowest end of the range of the sizes taken as food, thus larger live food objects will not be displaced. Food size of black-faced spoonbills varies between 2 and 21 cm (Swennen and Yu 2005) and of Eurasian spoonbills up to a length of 15 cm (Cramp and Simmons 1977); the larger ones are most profitable (Kemper 1995). (b) The moved objects did not come between the mandibles, but moved in an unfavourable direction because the next sweep runs three or more times further than the empty objects did (Fig. 3). (c) When a larger potential prey such as a fish or a shrimp resting in or on the bottom will be disturbed by a suction force that operates after the bill has passed, it will hurry off in an unpredictable course and be difficult to locate by touch. A food searching spoonbill moves its feet carefully and keep its bill far from its feet in the water for catching a prey by surprise (Swennen and Yu 2005). It closes the bill at once as soon a prey has been contacted between the mandibles. Measurements of the bill-snap reflex are lacking for spoonbills, but the American wood stork, another ciconiiform bird that sweeps its bill in turbid water for catching fish, reacts in about 25 ms (Kahl and Peacock 1963).

Conclusion

The hypothesis of Weihs and Katzir (1994) that during feeding the bill of a spoonbill induces a hydrodynamic suction force on the bottom that can be used for capturing prey is based on incorrect assumptions concerning the food and the shape of the bill. The outcomes of their test about the immersion depth of the bill in relation to the water depth apparently supporting the hypothesis do not hold for spoonbills in the field. The supposed benefits are also dubious such as the reduction in effort required for moving the submerged bill forward, and for minimizing the risk of damage to the tip. Therefore the hypothesis has to be rejected. The hydrodynamic properties of the laterally flattened legs and the dorso-ventrally flattened bill together with the movements during searching prey seem just adapted for minimizing resistance and turbulence aiming at not alarming potential prey before it is touched and caught between the mandibles (Swennen and Yu 2004, 2005).

The fundamental mistake in the discussed paper is that assumptions about a strange feeding structure and a rare feeding behaviour have directly been related to a supposed function. This function seemed strongly supported by a series of hydrodynamic formulae, but the preconditions for the use of the formulae were wrong. Before using the hydrodynamic formulae, it had been necessary firstly to obtain a better knowledge of the anatomy of the bill as well as of the food and feeding behaviour in the wild. The tests supporting the hypothesis were conducted with a live bird under wrong circumstances, since: (1) the behaviour was influenced by training such as eating immobile food from the bottom instead of food moving in the water column, and (2) the offered feeding opportunity was too small for conducting the normal feeding behaviour of the test bird. Actually, the suggestive paper only shows a negligible vortex for an imaginary function for catching imaginary food.

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