

The use of distal rhynchokinesis by birds feeding in water

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Summary

The use of distal rhynchokinesis, which consists of the movement of the distal part of the upper jaw with respect to the cranium, is well documented in long-billed shorebirds (Scolopacidae), commonly being associated with the deep probing feeding method. However, the functional and evolutionary significance of distal rhynchokinesis and other cranial kinesis is unclear. We report for the first time the use and occurrence of distal rhynchokinesis in wild long-billed shorebirds feeding on small prey items suspended in water. We tested whether prey size in captive dunlins *Calidris alpina* influences the occurrence of distal rhynchokinesis during feeding and also whether its use affects foraging efficiency. We found that wild dunlin, curlew sandpiper *Calidris ferruginea*, sanderling *Calidris alba* and little stint *Calidris minuta* commonly use distal rhynchokinesis to strike, capture and transport small prey items. Prey size influenced the occurrence of distal

rhynchokinesis during the transport phase, with this type of cranial kinesis being more frequently used with larger prey. The rhynchokinesis protraction angle (a measure of bill tip elevation) during prey strike and transport was affected by prey size, and bill gape was modulated through the use of distal rhynchokinesis in relation to prey size. Finally, the use of distal rhynchokinesis throughout intra-oral prey transport was related to shorter transport times, which improved foraging efficiency. We conclude that distal rhynchokinesis is a mechanism that could contribute to the flexible feeding behaviour of long-distance migratory shorebirds, enhancing small prey profitability and so improving foraging efficiency, and may have played a role in the evolutionary radiation of Scolopacidae (Charadrii).

Key words: distal rhynchokinesis, shorebirds, water, foraging, feeding behaviour.

Introduction

The mechanical sophistication of the jaw apparatus in birds is highly developed (Bühler, 1981). All modern birds can move the upper jaw, or a part of it, with respect to the cranium, i.e. they present cranial kinesis (Zusi, 1984), which is an important characteristic in the feeding behaviour of birds (Bock, 1964; Gussekloo and Bout, 2005a). Cranial kinesis is achieved in part through the bending zones (thin bone) distributed in the bird's jaw apparatus [see description of the mechanics in Gussekloo et al. (Gussekloo et al., 2001) and Gussekloo and Bout (Gussekloo and Bout, 2005a)]. Three general kinds of cranial kinesis have been described in birds: prokinesis, amphikinesis and rhynchokinesis [see Bock (Bock, 1964) and Zusi (Zusi, 1984) for detailed descriptions]. Rhynchokinesis is known to exist in Charadriiformes, Gruiformes, Columbiformes, Struthioformes, Trochilidae, Threskiornithidae, and in some Passeriformes (for reviews, see Bühler, 1981; Zusi, 1984).

In rhynchokinetic birds, the dorsal flexion zone of the upper jaw is displaced more or less rostrally along the dorsal bar of the upper jaw [see Fig. 1 (Zusi, 1984)]. Five types of rhynchokinesis can be distinguished according to the position of the bending zone in the dorsal bar of the upper jaw: (i) proximal rhynchokinesis (the bending zone is in the base of the

dorsal bar); (ii) central rhynchokinesis (there is a large bending zone in the central area of the upper jaw); (iii) extensive or elongated rhynchokinesis (an extended bending zone is located along the dorsal bar); (iv) double rhynchokinesis (for which there are two hinges on the dorsal bar); and (v) distal rhynchokinesis (the bending area is in the distal part of the dorsal bar) (Bühler, 1981; Gussekloo and Bout, 2005a; Gussekloo and Bout, 2005b; Zusi, 1984).

Hypotheses regarding rhynchokinesis vary, some stating that it increases bill gape when birds are feeding on large prey (Zusi, 1984), while others state that it is used in order to reduce the force required to spread their jaws (Bout and Zweers, 2001; Nuijens and Bout, 1998) or that it allows simultaneous movement of the upper and lower jaw, thereby increasing the speed of jaw (bill) movement (Bout and Zweers, 2001). However, the functional and evolutionary significance of rhynchokinesis and other types of cranial kinesis is unclear (Bout and Zweers, 2001; Gussekloo and Bout, 2005b).

Many long-billed shorebirds (Scolopacidae) are known to feed by probing in the mud or sand to capture benthic macroinvertebrates. Distal rhynchokinesis in these species has commonly been associated with the deep probing feeding method, where it has been hypothesised to reduce the force

needed to open the bill (Zweers and Gerritsen, 1997), as well as improving the grip on food items within the substratum (Burton, 1974; Zusi, 1984; Zweers and Gerritsen, 1997).

Most hypotheses regarding the function and benefits of rhynchokinesis are scarcely substantiated by direct observations (for reviews, see Bout and Zweers, 2001; Gussekloo and Bout, 2005a; Gussekloo and Bout, 2005b), and field and experimental analyses of distal rhynchokinesis with respect to feeding behaviour are lacking. For example, although many long-billed shorebirds commonly also feed in the water column (Cramp and Simmons, 1983; Piersma et al., 1996), to the best of our knowledge, no published data on the use of distal rhynchokinesis in shorebirds feeding on prey items suspended in water exist.

In this study we report for the first time the use and occurrence of distal rhynchokinesis in wild long-billed shorebirds feeding on small prey items suspended in water. We experimentally tested in the laboratory whether the occurrence of distal rhynchokinesis during feeding was affected by prey size, and whether these birds varied the protraction or upward angle in relation to prey size. In accordance with Zusi (Zusi, 1984), we predicted that the protraction of the bill tip during the strike and transport phases would be greater with larger sized prey. Finally, we tested whether the use of distal rhynchokinesis affected the intra-oral prey transport times in captive dunlins, which would in turn affect their foraging efficiency.

Materials and methods

Field data collection

During spring and summer periods from 2002 to 2004, random long-distance migratory shorebirds of the species curlew sandpiper (*Calidris ferruginea* L., $N=22$), dunlin (*Calidris alpina* L., $N=19$), sanderling (*Calidris alba* L., $N=16$) and little stint (*Calidris minuta* L., $N=13$) were filmed during daylight (between 09:00 and 12:00 h GMT) feeding actively at high rates (38–102 prey items min^{-1}) in the water column of hypersaline pans in south western Spain [see Masero (Masero, 2003) for details regarding the study area], from a vehicle and at a distance of less than 30 m. Each individual was recorded for periods ranging from 30 to 60 s at 25 frames s^{-1} using a JVC digital video camera (JVC GR-DVL145EG optical zoom $\times 16$, Victory Company of Japan, Ltd, Yokohama, Kanagawa, Japan).

Field film analysis

The video camera was capable of de-interlacing each frame in two, resulting in 50 images s^{-1} . Viewing the sequences frame by frame allowed us to describe the use and examine the occurrence of distal rhynchokinesis in wild birds feeding on small prey items (mainly the crustacean brine shrimp *Artemia* spp.) suspended in the water column. We considered that distal rhynchokinesis was being employed during the feeding process (prey strike, capture and transport) when the distal part (tip) of the upper jaw was elevated or depressed independently of the rest of the upper jaw.

Laboratory experiment

Four dunlins were captured in Cádiz Bay Natural Park in November 2003, and maintained in captivity in a 1.80 m \times 0.92 m \times 0.92 m indoor aviary. Fresh and saline water,

brine shrimps and living fly larvae were offered *ad libitum* for bathing, drinking and feeding. Dunlins were weighed regularly, and no significant weight loss was found in any bird throughout the experiment.

The experimental prey was brine shrimp, a naturally occurring and common aquatic prey of shorebirds (Masero, 2003; Sánchez et al., 2006; Verkuil et al., 2003). We placed a large amount of live brine shrimps into a plastic tray with hypersaline water, and many of them were sorted visually by hand into four size classes. Randomly, individuals from each size class were set aside in order to accurately determine the mean body length (\pm s.d.) of brine shrimps under a binocular microscope equipped with an ocular micrometer. Mean values were: size class 1, 4.10 \pm 0.52 mm (range: 3.50–4.99 mm; $N=12$); size class 2, 5.34 \pm 0.04 mm (range: 5.32–5.40 mm; $N=14$), size class 3, 6.85 \pm 0.35 mm (range: 6.00–7.00 mm; $N=8$); and size class 4, 8.89 \pm 0.46 mm (range: 7.98–9.50 mm; $N=10$).

Trials were carried out in a 0.90 m \times 0.30 m \times 0.40 m cage, which was completely closed off so as to avoid birds being disturbed by researchers in the vicinity of the cage. A light source simulating natural light was situated in the ceiling of the cage. All the trials were carried out in the afternoon, from 16:00 h. In order to encourage the birds to feed during the trials, food was removed around 11:00 h [see van Gils et al. (van Gils et al., 2003) for similar procedure]. Before birds were placed in the experimental cage, they were held in dark boxes for an hour to recover from capture stress [see similar procedure in Piersma et al. (Piersma et al., 2003)]. Between 15 and 20 live brine shrimps of each class size were offered randomly to the experimental individuals in a 71.6 cm^2 Petri dish (0.5 cm deep water) placed in the cage. Water salinity and temperature were kept as near as possible to constant (salinity: 36‰; mean temperature: 18.7 \pm 0.93°C).

Captive birds were recorded with the digital video camera mentioned previously. The Petri dish was situated in front of the video camera lens positioned in an opening made in the cage. The area where the Petri dish was located had a white background in order to make the bill more easily visible. We only analysed the sequences where a lateral view of the bird was clear and the bill was perpendicular to the camera.

Captivity film analysis

During the prey strike and transport phases, the maximum rhynchokinesis protraction angle was measured, taking the dorsal line of the upper jaw as the reference line (Fig. 1A). The protraction angle was calculated as the obtuse angle made between the distal part of the upper jaw and the dorsal part of the rest of the upper jaw structure (Fig. 1B). Therefore, the smaller the angle, the greater the protraction of the bill tip. The angle vertex was situated in the torsion area (Fig. 1B). Maximum bill gape was defined as the maximum distance between bill tips (Fig. 1A).

The extraction of digital images from videotape to PC was made with the program Pinnacle Studio 8.12 (Pinnacle Systems Inc., Mountain View, CA, USA 1998–2003). Rhynchokinesis protraction angle and bill gape measurements were determined with the program Corel Draw 10 (Corel Corporation, Ottawa, Ontario, Canada, 2000). The calibration of bill gape was carried

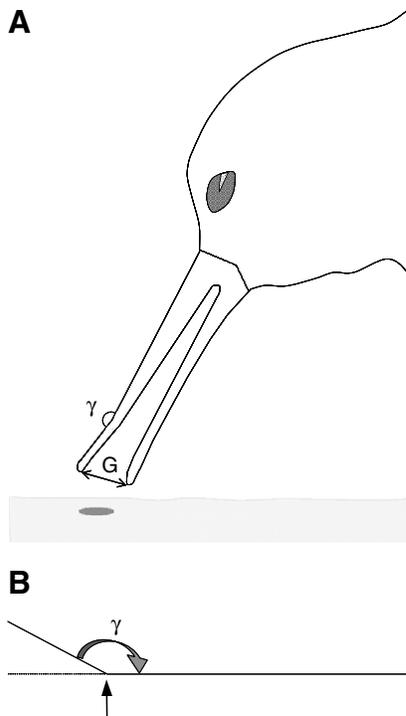


Fig. 1. (A) Schematic drawing of the rhynchokinesis protraction angle (γ) and bill gap (G). (B) Schematic drawing describing the measurement method for the rhynchokinesis protraction angle. The angle vertex (torsion area) is indicated by an arrow.

out using the bill length (culmen) of each individual (Podos et al., 2004).

The effect of the use of distal rhynchokinesis in the prey transport phase was evaluated through the kinematic variable 'time of transport' for the trial size class 3. This size class (0.30–0.40 mg ash-free dry mass) is within the size range for brine shrimps commonly captured by wild shorebirds (Masero and Pérez-Hurtado, 2001; Verkuil et al., 2003). Video films were analysed frame by frame and the use ('yes' or 'no') of distal rhynchokinesis during prey transport and the duration of transport were noted. The intra-oral prey transport began when the prey was held in the tips of the bill out of the water and was completed when the prey was swallowed with the bill closed. All dunlins used a feeding mechanism termed surface tension transport (STT), which relies on the use of the surface tension of a drop of water to convey a single prey contained in it from bill tip to mouth (Estrella et al., 2007; Rubega and Obst, 1993; Rubega, 1997). Although the prey transport time using STT is very small, by making use of the time elapsed between images (0.02 s), calculation of the duration of prey transport from bill tip to mouth is possible (Estrella et al., 2007).

A repeated measurement analysis of variance (RM-ANOVA) in a general linear model (GLM) procedure was used to test the influence of prey size on the occurrence of rhynchokinesis during the feeding process and on the maximum protraction angle. For the latter, we analysed protraction angle as a function of class prey size and phase (strike or transport), including the interaction term 'class prey size \times phase'. Student's *t*-test for dependent samples was conducted to investigate the influence

of the use of distal rhynchokinesis on the time of prey transport. Before conducting statistical analyses, occurrence frequencies were arcsine transformed to acquire normality. A mixed linear model was performed to examine the relationship between rhynchokinesis protraction angle and bill gap during prey strike and intra-oral prey transport. In this model, individual identification was entered as a random factor, protraction angle as a covariate and phase (strike or transport) as a fixed factor. To test whether the slopes of the regression lines differed between the two phases, we included the interaction term 'protraction angle \times phase' in the model. We considered between two and ten prey captures for each of the four birds filmed foraging on four different classes of prey size. Measurements of maximum protraction angle and bill gap in the transport phase from two individuals of the trial prey size classes 1 and 2, and in the strike phase from one individual of trial prey size class 3 were not obtained because the images were not of high enough quality to measure the protraction angle of distal rhynchokinesis. *P* values ≤ 0.05 were considered statistically significant. All statistical analyses were performed using Statistica 7.0 (StatSoft, Inc., Tulsa, OK, USA 2004).

Results

Use and occurrence of distal rhynchokinesis in shorebirds feeding in water

All wild shorebird species filmed used distal rhynchokinesis during the feeding process (Fig. 2). When shorebirds attacked prey located in the upper layers of the water, it was possible to observe that only the distal part of the upper jaw was elevated (Fig. 3A). If the prey was captured using distal rhynchokinesis, the distal part of the upper jaw was depressed, and the prey was gripped in the bill tip (Fig. 3B). During the prey transport event,

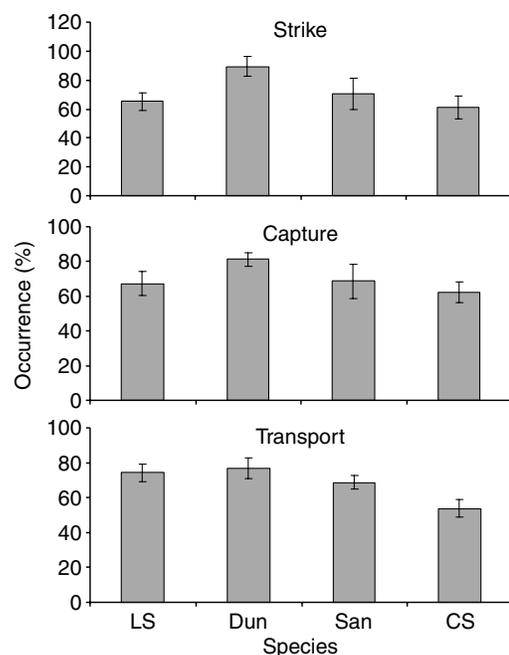


Fig. 2. Observed occurrence (mean \pm s.e.m.) of the use of distal rhynchokinesis in curlew sandpiper (CS), dunlin (Dun), sanderling (San) and little stint (LS) feeding on small prey suspended in the water column in the field during prey strike, capture and transport.

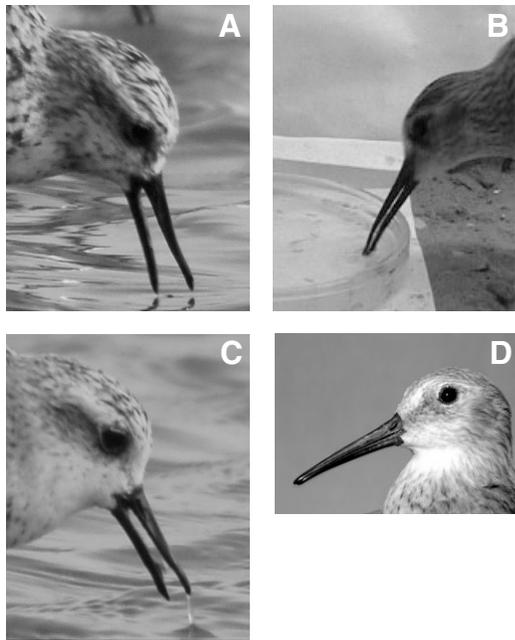


Fig. 3. Digital images showing the use of distal rhynchokinesis during the strike of a prey suspended in the water column (A) and in the transport of a small prey by a Sanderling in the field (C). (B) Use of distal rhynchokinesis to grip a prey in the water column by a dunlin in the laboratory (B). A digital image of a captive dunlin with its bill in the resting position is shown for comparison (D).

the use of distal rhynchokinesis was indicated by the elevation of the upper jaw tip (Fig. 3C).

In captive dunlins, distal rhynchokinesis was used in $91.6 \pm 13.3\%$ ($N=110$), $42.1 \pm 32.1\%$ ($N=105$) and $76.1 \pm 24.4\%$ ($N=109$) of prey strike, transport and capture events, respectively, following a similar pattern to that in wild birds. The occurrence of distal rhynchokinesis during the strike and capture phases was not affected by prey size (RM-ANOVA, strike: $F_{3,9}=1.35$, $P=0.31$; capture: $F_{3,9}=2.74$, $P=0.10$). However, prey size affected the occurrence of distal rhynchokinesis during the transport phase (RM-ANOVA, $F_{3,9}=18.31$, $P<0.001$; Fig. 4), rhynchokinesis being used more often when prey were larger.

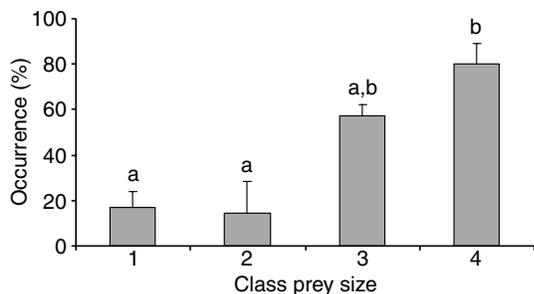


Fig. 4. Observed occurrence (mean \pm s.e.m.) of the use of distal rhynchokinesis in prey transport by dunlins in the laboratory. Values with different letters are significantly different (Tukey's test).

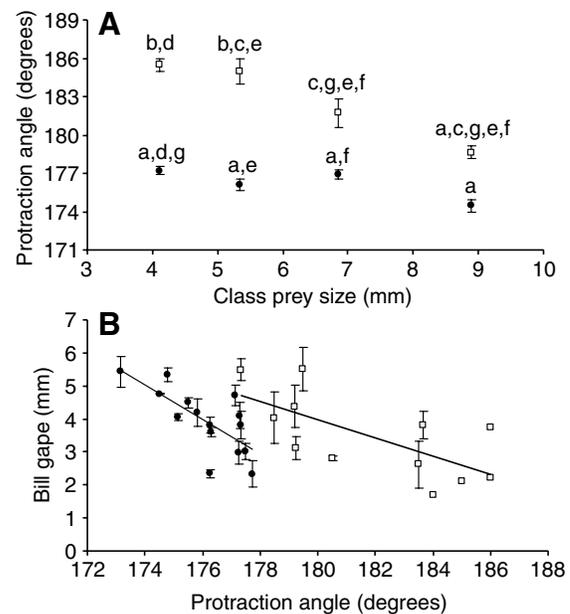


Fig. 5. (A) Effect of prey size and phase (strike or transport) on the rhynchokinesis protraction angle (mean \pm s.e.m.). Values with different letters are significantly different (Tukey's test). (B) Relationship between bill gape (mean \pm s.e.m.) and rhynchokinesis protraction angle. Filled circles represent prey strike and open squares represent prey transport.

Rhynchokinesis protraction angle, prey size and bill gape

The rhynchokinesis protraction angle was affected by prey size and phase (RM-ANOVA, prey size: $F_{3,6}=16.4$, $P<0.01$; phase: $F_{1,2}=232.5$, $P<0.01$; prey size \times phase: $F_{3,6}=9.3$, $P<0.05$; Fig. 5A), the tip of the upper jaw being more elevated for larger prey. We also found that strike and transport bill gape were negatively correlated with the rhynchokinesis protraction angle (mixed linear model, protraction angle: $F_{1,23}=17.84$, $P<0.001$; Fig. 5B), bill gape and the slopes of the regression lines being similar in the two phases (mixed linear model, phase: $F_{1,23}=1.58$, $P=0.22$; phase \times protraction angle: $F_{1,23}=1.68$, $P=0.21$; Fig. 5B).

Use of distal rhynchokinesis and duration of prey transport

The use of distal rhynchokinesis during prey transport affected the duration of transport, this being significantly shorter when birds used distal rhynchokinesis (t -test, $t_{1,3}=3.48$, $P<0.05$; Fig. 6).

Discussion

Long-billed shorebirds feeding on small prey items suspended in water commonly use distal rhynchokinesis while feeding. These results show that the use of distal rhynchokinesis in long-billed migratory shorebirds is not exclusively related to the terrestrial probing feeding technique, as may have been deduced from previous studies (Gussekkloo et al., 2001; Zusi, 1984; Zweers and Gerritsen, 1997). Many long-distance migratory shorebirds show flexible and opportunistic feeding habits (Elner and Seaman, 2003; Mathot and Elner, 2004;

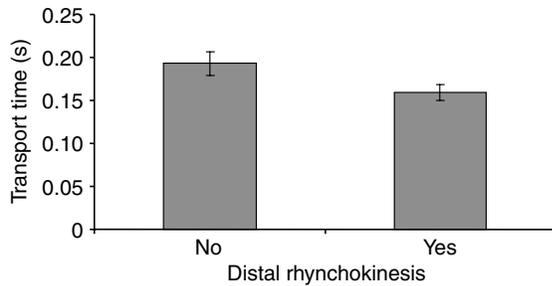


Fig. 6. Effect of the use of distal rhynchokinesis on the intra-oral transport time (mean \pm s.e.m.) when small prey items are transported using surface tension transport (STT).

Skagen and Oman, 1996), which allow them to take advantage of different habitats and/or prey types and, therefore, successfully face their migrations. The avian jaw apparatus forms part of the feeding system, and the fact that shorebirds use distal rhynchokinesis to strike, capture and handle small prey items in water suggests that this type of cranial kinesis contributes to flexible and opportunistic feeding.

Viscosity and drag forces in the aquatic medium are distinct from those encountered in the terrestrial medium (Vogel, 1994). The use of distal rhynchokinesis by long-billed shorebirds feeding on small prey items suspended in water may be related to economy of movement, as Bout and Zweers (Bout and Zweers, 2001) suggest in reference to upper jaw kinesis in birds. To feed profitably on small prey items, shorebirds must capture and handle them at high rates (e.g. Verkuil et al., 2003; Zwarts and Wanink, 1993), so mechanisms that reduce capture and handling time of small prey items enhance small prey profitability. When a shorebird's bill penetrates the water with the entire jaw open, the resistance must be greater than that encountered when only the distal part of the upper jaw is elevated. Therefore, long-billed shorebird species that use distal rhynchokinesis are theoretically able to take advantage of this reduced resistance and strike a prey item suspended in water faster. In the same way, distal rhynchokinesis may minimise the volume of water required to displace the small prey items suspended in water. Accordingly, distal rhynchokinesis is thought to contribute to enhancing small prey profitability.

Small-sized Sandpipers feeding on small prey items suspended in the water column use the STT mechanism (Estrella et al., 2007; Masero, 2002; Rubega, 1997), which allows them to feed profitably on small prey (Estrella et al., 2007). A characteristic of STT is the presence of jaw spreading to produce an increase in the free surface area of the drop of water (Rubega and Obst, 1993). The increased occurrence of distal rhynchokinesis during the transport of large prey suggests that this type of cranial kinesis contributes to achieving the greater bill gapes required to transport them using STT (J.A.M. and S.M.E., unpublished observations), this being shown by the fact that bill tip elevation increased with prey size.

In shorebirds feeding on small prey items, prey transport time approximates total handling time, since killing or cleaning prey is not necessary (Zwarts and Wanink, 1993). Also, at high prey

densities, search time approaches zero, so the handling time can be considered as the inverse of pecking rate (see Zwarts and Wanink, 1993). Since the use of distal rhynchokinesis in birds using STT was related to a diminution of the transport time, the use of distal rhynchokinesis may enhance feeding efficiency in shorebirds using STT.

As indicated, distal rhynchokinesis has commonly been related to the probing technique used by long-billed shorebirds when feeding on prey buried in the substratum. It is probably also used by long-billed shorebirds as they peck prey from the substratum surface. In these situations the use of distal rhynchokinesis may save time in capturing through the adjustment of bill gape to prey size, as has been hypothesised in Clark's nutcrackers *Nucifraga columbiana* (Möller et al., 2001). Moreover, if during pecking or probing the conditions for using STT are met (small prey and substratum with a layer of water or with enough interstitial water to generate a drop of water to transport the prey), the simultaneous use of distal rhynchokinesis and STT may reduce the prey transport time of birds combining the two foraging mechanisms. Therefore, the use of distal rhynchokinesis may also enhance feeding efficiency in terrestrial conditions.

Rubega (Rubega, 1997) postulated that STT may have played a role in the evolutionary radiation of Scolopacidae (a shorebird family with many species equipped with long and needle-shaped bills), allowing them to exploit different types of habitat dominated by small prey items suspended in water, which are unprofitable to other groups of shorebirds. If this hypothesis is true, distal rhynchokinesis may also have contributed to this radiation, enabling shorebirds to exploit small prey items buried in the substratum or suspended in the water column.

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