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SURFACE-TENSION FEEDING IN PHALAROPES: DISCOVERY OF A NOVEL FEEDING MECHANISM

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ABSTRACT.—We report the discovery of a previously undescribed feeding mechanism in an avian planktivore, the Red-necked Phalarope (*Phalaropus lobatus*). We employed high-speed video to elucidate the kinematics of prey transport, and to test hypotheses generated by a model describing prey transport as a function of surface tension. Prey items are transported individually from the tip of the beak to the mouth by forces resulting from the surface tension of water surrounding prey. Experiments conducted with the beak of a dead bird demonstrate that surface tension is sufficient to explain prey transport in Red-necked Phalaropes without the use of suction or tongue motions. This feeding mechanism may be widespread among the shorebirds and represents a potential intermediate step in the evolution of filter feeding in birds. *Received 12 November 1991, accepted 22 June 1992.*

THE MECHANICAL basis of feeding in aquatic birds, despite illuminating work by a few investigators (Zweers et al. 1977, Kooloos et al. 1989), remains largely unexplored. The literature describing the feeding mechanics of aquatic birds is based mostly on dissections alone (e.g. Burton 1974), with notably few experimental exceptions (e.g. Crome 1985).

The feeding systems of all aquatic predators incorporate solutions to problems unique to the aquatic environment. Water exhibits properties that contribute to the difficulties a predator faces when trying to extract prey from a fluid medium. In its liquid state, water is 900 times denser than air, relatively adhesive, and incompressible (for discussion of the assumption of incompressibility in fluids, see Vogel 1981). Aquatic predators, unless they are physiologically prepared to process large volumes of water, must mechanically separate their prey from the water before swallowing it.

Because water is incompressible the movement of feeding structures through the water will displace water. Aquatic conditions present greater difficulties to planktivores (eaters of tiny, drifting invertebrate prey) than to other aquatic predators. If the prey item has a mass (and hence inertia) lower than or equivalent to that of the volume of water being displaced by the feeding apparatus, then the prey will be displaced along with the water, making capture difficult. This phenomenon is similar to the problem one faces when trying to fish a small particle out of a cup of coffee; success is far more likely with a pair of needle-nosed forceps than with a pair of blunt fingers.

Prey must also be transported to the pharynx to be swallowed. Planktivores might be expected to experience considerable difficulty at

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this stage of feeding, because the very low inertia of small planktonic prey precludes employment of inertial feeding or "head throwing" (Gans 1961, 1969) as a means of food transport.

Most planktivores address these mechanical barriers to successful prey capture and transport with some form of filter feeding. Because birds are secondarily adapted to aquatic life, filter feeding must be viewed as a derived method of prey capture. Well-documented avian examples include flamingos (Jenkin 1957) and ducks (Zweers et al. 1977). These filter feeders use their bills and tongue movements to pump a volume of water containing prey through structures (such as mandibular lamellae or lingual papillae) that catch and retain prey, rather than displace water in an attempt to seize prey individually.

Red-necked Phalaropes (*Phalaropus lobatus*) are among the smallest avian planktivores. Although they are known to take a variety of prey during the breeding season (Wetmore 1925, Höhn 1968, Baker 1977), their diet during the eight months of the year that they spend at sea consists almost entirely of copepods (Briggs et al. 1982, Mercier and Gaskin 1985, Brown and Gaskin 1986). In contrast to the solutions to planktivory outlined above, descriptions of the feeding behavior of Red-necked Phalaropes in the field (Höhn 1968, Mercier and Gaskin 1985) indicate that they "peck" their food out of the water (i.e. capture prey items individually), rather than taking mouthfuls of water as might be expected if they were filter feeding. Red-necked Phalaropes have needlelike bills; "tweezering" prey items out of the water by seizing them in the beak tips would be consistent with the idea that decreasing resistance to the passage of the feeding structure through the water is an important consideration. Once prey are captured they must be transported along the length of the bill. Studies of Red-necked Phalaropes in the Bay of Fundy (Mercier and Gaskin 1985, Brown and Gaskin 1986) and Red Phalaropes (*P. fulicarus*) in the Arctic (Dodson and Egger 1980) indicate that these birds are size-selective predators, and that they consistently choose prey of 6 mm length or less, rather than the largest prey available. Small prey sizes (Dodson and Egger 1980, Briggs et al. 1982) and exceedingly high pecking rates of feeding birds ($\bar{x}$ = 95 pecks/min; Mercier and Gaskin 1985, Rubega unpubl. data) make inertial food transport unlikely.

During the making of an educational film (University of California 1985) on Red-necked Phalaropes, we noted an apparently novel mechanism of prey transport involving the rapid spreading of the birds' jaws. As a result, we analyzed the mechanics of prey capture and transport in this species. We tested the hypotheses that: (1) prey transport is accomplished using the surface tension of water; and (2) surface-tension forces are enough to account for prey transport in the absence of other feeding mechanisms, such as suction or tongue manipulation. To familiarize the reader with the basis and aim of our experimental procedures we outline below the model upon which our hypotheses are based.

THE MODEL

Surface tension as a means of prey transport.—The surface tension of water is a product of the physical property of cohesion, or the attraction of water molecules to each other (Streeter and Wylie 1979). Because of cohesive forces, in any body of water molecules at the surface are experiencing a force directed toward the center of the body. These forces create a tendency for a water mass to assume a shape with the smallest possible surface area per volume (hence, the spherical nature of free-falling water drops). Surface tension is the energy or work required to draw enough molecules to the surface of the mass to form one new unit of surface area. Any increase in the surface area will create a concomitant increase in the potential energy stored in that surface.

Also, water molecules are attracted in varying degrees to other substances, a property known as adhesion. The concave meniscus observed at the top of a test tube is caused by the adhesion of water to glass. The degree of adhesion of water to any particular substance can be measured using the contact angle between the two (Prandtl and Tietjens 1957). An acute angle indicates a high degree of adhesion or "wetting," whereas an obtuse angle indicates little to no adhesion, or "nonwetting." The more acute the angle, the greater the degree of attraction. In cases of extreme attraction, water simply will form a film over the substance it is in contact with and, in cases of extreme repulsion (as with water on wax), water will bead up and display a very obtuse contact angle (Fig. 1).

It follows, therefore, that a phalarope with wettable beak rami would be able to transport a single prey item in a drop of water if the degree of adhesion between bill surface and water were high enough to allow the bird to stretch the surface of the drop by spreading its mandibles. If the proper balance were struck between cohesion of the drop and its adhesion to the bird's beak, progressive mandibular spreading would increase the amount of potential energy stored in the surface of the drop by increasing the free surface area of the drop. Because physical systems move to reduce potential energy (unless this tendency is opposed), the drop would move in the direction that was most likely to reduce free surface area. As long as drop positions more proximal to the gape result in smaller free surface areas and, hence, lower energy states, than those at the distal end of the bill, the drop should move toward the buccal cavity.

Expectations generated by model.—If phalaropes are transporting prey by using the surface tension of water, we predicted that: (1) prey are contained in a drop of water; (2) the drop will display acute contact angles at all points of contact with the bird's bill, thus indicating that the bill has the wettable surface necessary to increase the surface area of the drop by mandibular spreading; (3) progress of the drop from the distal to the proximal end of the bill will be associated with increased mandibular spread (i.e. with increased gape); (4) the free surface area of the drop will decrease progressively with posteriorly directed movement of the drop; and (5) if surface-tension transport alone is responsible for prey transport, drop movement will occur in the absence of suction or tongue-based manipulations by the bird.

In this study we present results supporting all of the predictions stated above with the exception of number 4. Because of the complexity of the three-dimensional analysis of bill morphology required, we will elaborate on the fourth prediction in another paper (Rubega in prep.).

MATERIALS AND METHODS

Adult Red-necked Phalaropes were captured in 1989 at Mono Lake, California using mist nets set over water. The birds were maintained in captivity at the University of California, Irvine, where experiments were conducted. We report here a description of the mechanism, and a test of the model using one individual; two other captive individuals (one male and one female) exhibited the phenomenon as well. Subsequent observations of free-living Red-necked Phalaropes revealed that mandibular spreading, characteristic of the transport mechanism, is commonly employed during feeding.

High-speed video of feeding and prey/drop transport was obtained on standard VHS video tape using an NAC HSV-400 high-speed video camera with synchronized stroboscopic lights. Filming was conducted in color at 200 fields/s.

The kinematics of prey capture and transport were quantified by analysis of high-speed video of a captive phalarope feeding in a 115-L tank in the laboratory. The bird was deprived of food for 12 h before filming to ensure motivation. Feeding events were filmed using brine shrimp (*Artemia salina*) as an appropriately sized, readily available model for the bird's planktonic prey. The bird was filmed feeding in front of a 1-cm^2 grid to facilitate measurement of kinematic variables from the video. The unit of analysis for this study was a drop transport sequence. Because a complete transport event (defined as the movement of prey from bill tip to mouth) may involve several cycles of mandibular spreading, a drop transport sequence was defined as the drop movement associated with a single mandibular spread, with the starting position of the drop at the bill tips. Only those sequences for which the long axis of the bird's bill was parallel or nearly parallel to the film plane were scored in order to insure accurate measurement of variables. The phalarope was swimming freely in the feeding tank, so these criteria excluded all but a small portion of the filmed prey capture/transport sequences.

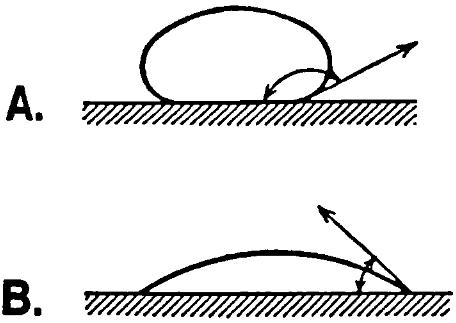

Fig. 1. Contact angle, θ, is measure of degree of adhesion of water to a substrate type. Angle at point of contact measured through drop: (A) an obtuse angle indicates nonwettable substrate; (B) an acute angle indicates wettable substrate. Surface-tension transport requires a wettable beak surface, and we expect to see acute contact angles between beak and drop any time a bird employs the mechanism to transport prey (drawing adapted from Prandtl and Tietjens 1957).

To test the hypothesis that drop transport is accomplished in the absence of suction or tongue motions on the part of the bird, the bird was sacrificed after the completion of filming. High-speed video was then used to record the movement of drops of water loaded one at a time with a 1-cc syringe fitted with a 26-gauge needle onto the beak of the dead bird. Drop loads were approximately 0.01 mL. The bird's head was held in a fixed position, and the beak tips spread slightly. Mandibular position was held constant during a drop transport sequence. No attempt was made to hold gape size at a constant value between sequences, because gape size was, of necessity, randomized in live bird sequences. Sequences using the dead bird were filmed in front of the same 1-cm^2 grid used for the sequences of the feeding live bird, filmed at the same film speed, and analyzed for the same kinematic values.

Head, beak and drop movements were analyzed frame by frame on a microcomputer using custom motion-analysis software. Variables measured were

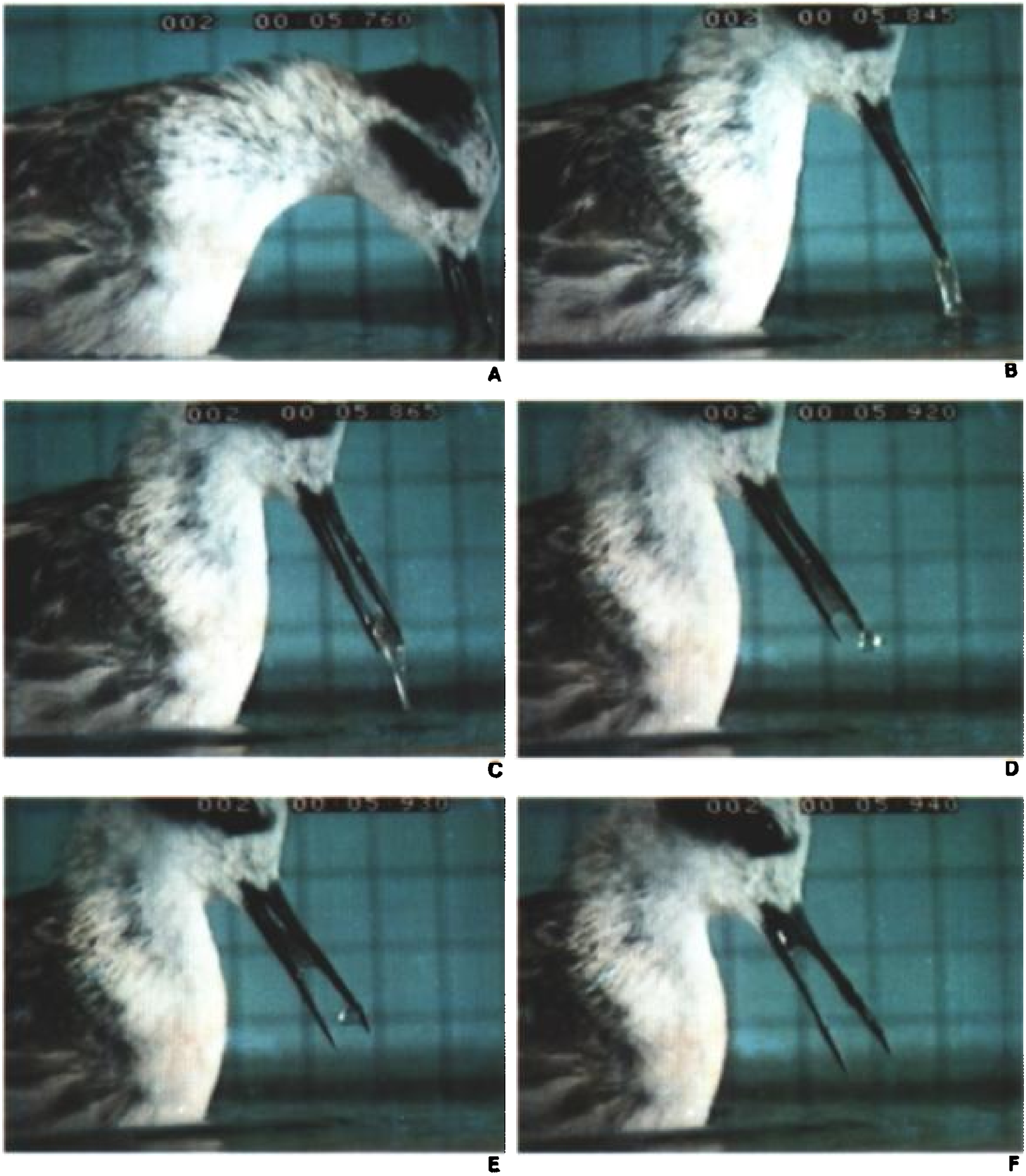

Fig. 2. Surface-tension prey transport by Red-necked Phalarope. Numbers across top of frames indicate time in 0.001-s increments. This previously unknown feeding mechanism uses surface tension of water to rapidly transport prey from bill tip to mouth without use of suction or tongue movements by bird. After bird seizes prey with bill tips (frames A–B), transport of prey along bill is accomplished by rapid mandibular spreading (frames C–F). This motion, by increasing free surface area of drop that surrounds prey and adheres to bird's bill, drives drop up bill and into the bird's mouth. Note presence of prey in drop, as evidenced by brine shrimp eyes visible in frame C.

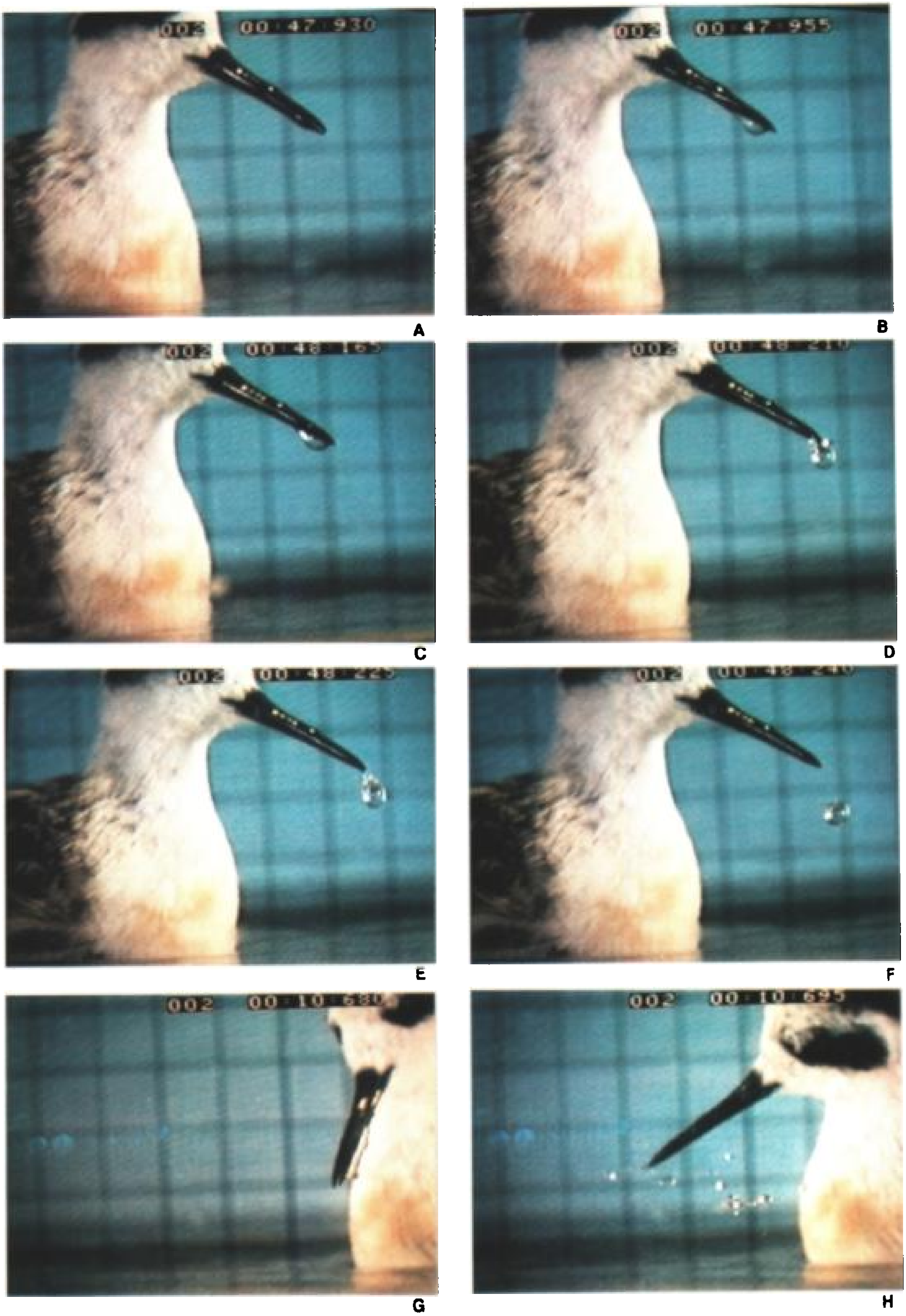

Fig. 3. Disposal of transport water at end of a feeding sequence. Disposal is either passive (E–F) or active (G–H). Frames G and H are from a different feeding sequence than that depicted in frames A through F, but the same individual bird.

TABLE 1. Drop movement data for surface-tension transport in a live and a dead individual. See text for explanation of how measures were defined and taken.

Sequence	Transport time (s)	Drop distance (cm)	Gape increase (cm)	Speed (cm/s)
		Live bird		
1	0.015	0.838	0.200	55.867
2	0.020	0.566	0.191	28.300[a]
3	0.010	0.513	0.131	51.300
4	0.010	0.677	0.167	67.700
5	0.010	0.780	0.084	78.000
6	0.020	1.561	0.373	78.050
7	0.010	0.995	0.190	99.500
$\bar{x}$	0.014	0.847	0.191	65.531
SD	0.005	0.355	0.090	22.923
		Dead bird		
1	0.090	1.715	0.147	19.060[b]
2	0.070	0.532	0.049	7.600
3	0.120	0.774	0.013	6.445
4	0.110	0.602	0.004	5.470
5	0.035	0.287	0.004	8.194
6	0.020	0.189	−0.004	9.470
7	0.495	1.048	−0.011	2.117
$\bar{x}$	0.134	0.735	0.029	8.337
SD	0.163	0.519	0.055	5.281

[a] Minimum drop speed for transport event with living bird.

[b] Maximum drop speed for transport event with dead bird.

gape size (distance between bill tips of upper and lower jaws), and drop distance (distance along a line connecting center of the distal meniscus of the water drop to a vertical line connecting bill tips). Calculated variables are time of transport (time elapsed from beginning of the sequence, calculated using an on-screen clock timing to 0.001 s), transport distance (change in drop distance over a single cycle of mandibular spreading), drop speed (calculated using drop distance and time of transport) and gape increase (change in gape size between beginning and end of a sequence). Videotape was inspected for confirmation of, or deviation from, the expectations generated by our model.

RESULTS

Live-bird sequences.—High-speed videos of the phalarope feeding reveal that prey are drawn up into the bill inside a drop of water (Fig. 2, frame C). Once the drop is contained within the rami of the beak, it assumes acute contact angles at all points of contact with the beak (Fig. 2, frame D). Progress of the drop from the distal to the proximal portion of the bill is associated with increased mandibular spreading (Fig. 2, frames D–F). The same frames also show a substantial air space behind the drop. Even with a very large increase in volume in the buccal cavity, it is extremely unlikely that the bird could have generated enough negative pressure to apply suction across an open-sided space of this size. No movement in the throat region typical of the hyoid pumping used to produce suction in birds (for review of mechanism and literature, see Zweers 1982) was observed either just before or during the time the drop was in motion. Video footage of this individual drinking revealed vigorous and easily detectable hyoid pumping.

Drop transport was very rapid (Table 1). Some complete transports were accomplished in as little as 0.01 s. Drop speeds were highly variable, although transport distance, gape increase, and transport time were not. Much of this variation is probably attributable to variation in prey size (and, hence, mass being transported), which was uncontrolled in this experimental series.

A complete transport event culminated in abrupt closure of the bird's spread jaws. Water immediately appeared on the outside of the bill at the level of the rictus (Fig. 3A) after which the water ran distally along the beak to collect in a drop at the tip (Figs. 3B–D). The water then either dropped off (Figs. 3E–F) or was vigorously shaken off (Figs. 3G–H).

The use of this mode of prey transport was invariant. If the bird captured a prey item, mandibular spreading was always used to transport it. Conversely, mandibular spreading was never seen after a failed capture attempt.

Dead-bird sequences.—Drops of water loaded to the bill of a dead bird moved up the bill in exactly the same manner as drops containing prey in the live bird (Fig. 4). Drop speeds (Table 1) generally were slower than those seen in the live-bird sequences. We did not modulate gape size or head angle during any transport sequence and, because the bird's bill was held below level (and, hence, transport was occurring in spite of gravitational forces), it is not surprising that drop speeds lagged behind those observed when the bird was alive and actively modulating bill movements and head position. However, we did attain drop speeds with the dead specimen that were similar to the slowest drop speeds seen in the live bird (Table 1; maximum dead-bird drop speed vs. minimum live-bird drop speed).

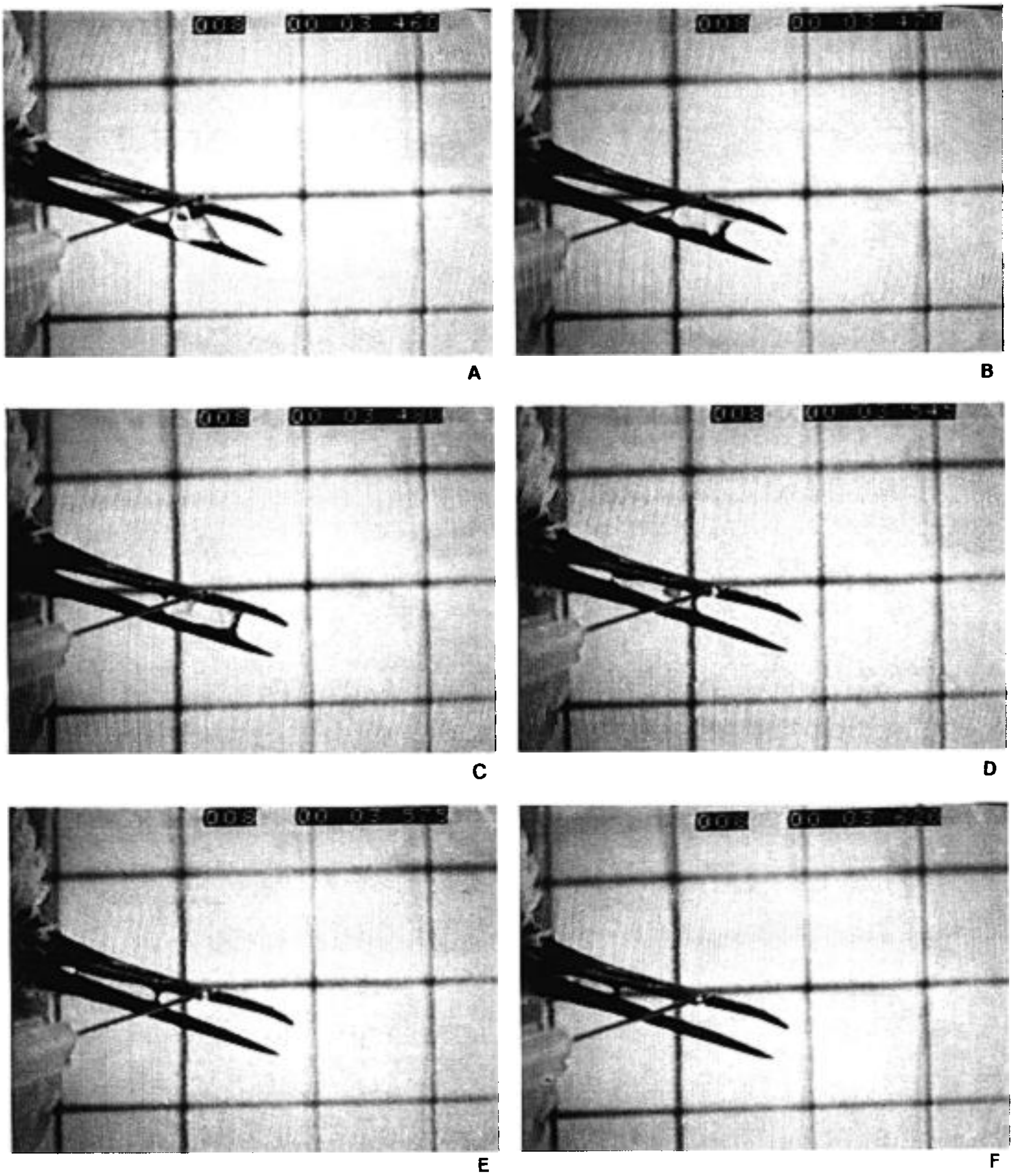

Fig. 4. Surface-tension transport can occur in absence of suction or tongue movements. Object in lower left and center of pictures is a syringe used to deposit a drop of water in bill of a dead bird. Syringe is not in contact with drop in frames B through F. Transport happened so rapidly there was not enough time to move syringe out of picture.

DISCUSSION

Our results support the hypotheses that Red-necked Phalaropes use the surface tension of water to transport prey and that surface-tension effects are sufficient to explain this phenomenon without invoking suction or tongue movements on the part of the bird. The discovery of this novel feeding mechanism has a variety of implications for the study of shorebird feeding systems, and for the study of avian feeding mechanisms in general. The most important aspect of the phenomenon stems not from its novelty, but from its potential generality.

Potential for surface-tension transport in other birds.—Although one may be tempted to view the phenomenon of surface-tension transport as a derived feature of a shorebird pecularily specialized for a pelagic life style, note that the morphological requirements generated by our model are relatively simple. A wettable bill surface (if we assume that adhesivity of water to keratin varies little) is very likely commonplace among birds, as is the ability to modulate gape size. What cannot be assumed to be commonplace are bill morphologies that ensure a progressive decrease in free-surface area of the transport drop as water moves from more distal to more proximal positions. Indeed, the test of that expectation for even the single species examined here is sufficiently complex to be outside the scope of this paper. Nevertheless, using the bill morphology of the Red-necked Phalarope as a model for bill shapes that will support this phenomenon, it is likely that any bird with a needle-shaped bill will be capable of some degree of surface-tension transport.

Our model of surface-tension transport hypothesizes that the phenomenon is the result of a balance of the forces generated by the cohesion of water versus those generated by its adhesion to the beak rami. If correct, we predict an upper limit to internal bill volume and surface area (and, hence, an associated increase in drop adhesion relative to cohesion) at which functional drop movement can be expected. (Doubt about the intuitive basis for this statement can be allayed by imitating the action of the bird's bill as described here with a pair of needle-nosed forceps and a pair of butter knives, respectively, as models for the bird's jaws. Drops of equal size will run rapidly and for some distance up the forceps, and will split before moving an equivalent distance on the butter knives.) Furthermore, the surface tension of pure water at 20°C is only 74 dyne/cm; this value declines with increases in solutes. The forces that birds employing this technique in brackish or salt water can generate by mandibular spreading will decline accordingly. This means that there must be an upper limit, probably fairly low, on the combined mass of prey and water that can be transported by this mechanism.

Most species of shorebirds possess a needle-shaped bill. The calidrine sandpipers possess some of the smallest beaks (in absolute, rather than relative terms) and seem likely candidates for the ability to perform surface-tension transport. In support of this prediction, drops of water have been observed running on the beak rami of Sanderlings (*Calidris alba;* Gerritsen [1988], as cited in Zweers [in press]) in much the same way as in the dead-bird drop transport we have described. However, note that no prey transport was observed in conjunction with this apparently undirected movement of water along Sanderling bills (Zweers pers. comm.).

Bill morphology, surface-tension transport and the evolution of filter feeding.—Zweers (1991) postulated that the movement of water drops along the bills of Sanderlings (and by association, surface-tension transport) is an epiphenomenon of bill morphology "maximizing for probing requirements" in the sandpipers. He viewed the evolution of bill morphology that supports this means of transporting water as a step along the "deductive pathway" from pecking (primitive) to filter-feeding (derived) mechanisms. Although his scheme is intuitively attractive in a mechanistic sense, its utility in an evolutionary sense is probably limited. Taxonomic relationships of the major avian filter-feeding groups (the Anatidae and the Phoenocopteridae) to the shorebirds are by no means a matter of consensus (see Olson and Feduccia 1980a, b, Cracraft 1988) and a common ancestor joining these three groups seems highly unlikely. Leaving aside these taxonomic issues, we can examine the idea that avian filter-feeding mechanisms may arise by degrees from shorebirdlike bill morphologies.

Zweers (pers. comm.) views the derived "fetch and carry" mechanism as it appears today (equivalent to surface-tension transport) as distinct from "filter feeding" as a feeding mechanism. However, he defines filter feeding as the "transport of food by water into the mouth, where food particles are retained and water is expelled, with some ability or limit of the system to discriminate (or retain) food particles of a particular size" (Zweers in press). If we use this definition, it would seem reasonable to view surface-tension transport as a simple form of filter feeding, rather than as a mechanism distinct from filter feeding. Mahoney and Jehl (1985) have already inferred filter feeding in Wilson's Phalaropes (*Phalaropus tricolor*) from tongue and beak morphology, despite the fact that these birds lack the large internal beak volumes and extensive lamellae of "typical" filter feeders.

Surface-tension transport and phalarope systematics.—Wilson's Phalaropes differ sufficiently from the other two species of phalarope to have sometimes been placed in the monotypic genus *Steganopus*. Although currently all three species are joined in the genus *Phalaropus*, the monophyly of the group has been questioned. Dittmann et al. (1989) could not corroborate the monophyly of the phalaropes using allozyme data. Subsequent analysis of mitochondrial-DNA (mtDNA) variation in phalaropes and other shorebirds (Dittmann and Zink 1991) showed that no mtDNA fragment (out of 393) unambiguously united the phalaropes as a monophyletic group. They noted that phalarope monophyly is supported by only one apparent invariant morphological character (Strauch 1978). However, Dittmann and Zink (1991) concluded that monophyly of the group seemed more likely than convergence in Wilson's Phalarope, especially in light of many shared general traits that seem to be synapomorphies. Dittmann and Zink (1991) acknowledged the possibility that those traits might be correlates of the aquatic lifestyle so apparently uncommon in the shorebird lineage. For reasons outlined above, the capacity to use surface-tension transport is unlikely to prove a phalarope synapomorphy. If it were widely distributed among shorebirds and were combined with intermediate stages of the other characters that seem to unite the phalaropes (toe lobing, flattened tarsi, waterproof plumage) in clades that are clearly distantly related to phalaropes, convergence of the phalaropes as a consequence of aquatic lifestyle would be more plausible.

Because the feeding mechanism we describe here has been unknown, and yet seems likely to be widely distributed among the shorebirds, we suggest two areas of future investigation. First, we believe it would be of considerable interest to determine the ways in which bill morphology both supports and limits the phenomenon of surface-tension transport. A deeper understanding of the mechanistic basis of surface-tension feeding would contribute to a clearer picture of how bill morphology influences the likelihood that terrestrial birds may give rise to aquatic ones. Second, because of the potential usefulness of the phenomenon as a taxonomic character, it would be profitable to determine how widespread surface-tension transport is among the shorebirds.

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COLOR PLATES

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