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Lee W. Casperson
Portland State University

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Head Movement and Vision in Underwater-Feeding Birds of Stream, Lake, and Seashore

LEE W. CASPERSON

The Rochester Theory Center for Optical Science and Engineering and The Institute of Optics, University of Rochester, Rochester, NY 14627-0186

Water-associated birds face special challenges in dealing with their two worlds of air and water. This study considers as a class those birds that seem to plan their underwater foraging from a wading or above-water perched position. A vertical bobbing motion of the head is particularly common among these birds, and the somewhat diffuse literature on this subject is reviewed and correlated. The vertical head movement may aid a bird in acquiring visual information through the interference and distortion caused by reflection and refraction at the air/water boundary.

Vision *Head movement* *Underwater feeding* *Bobbing*

There are wide variations in the physiological and behavioral aspects of vision among the members of the animal kingdom. The number of eyes that an animal has, the placement of those eyes on the animal's body, their physical mechanism of operation, their movement during use, and the processing of the visual information that they provide all vary widely. However, no matter how peculiar the aspects of an animal's visual system might seem from a casual human perspective, further investigation usually reveals some reasonably appropriate functionality with respect to the visual environment that the animal might experience (Martin, 1994).

Many animals move their heads up and down or from side to side, apparently to gain spatial information (Lee, 1994, p. 279). Examples include at least certain cats, squirrels, gerbils, reptiles, birds, and insects. The general relationships between head and eye movements in birds and their visual perceptions of position and motion have come under increasingly detailed investigation in recent years (Wallman & Letelier, 1993), and several head movement patterns in birds have already been connected with their vision abilities. For example, birds that lack substantial eye mobility rotate their heads to obtain a wide view of their surroundings. Also, in birds where the position of the eyes is relatively lateral (as opposed to frontal) there is only limited overlap in the visual fields of the two eyes (McFadden, 1994, p. 63). Thus, in a stationary bird an up-and-down or horizontal movement of the head might be understood to enhance the bird's otherwise more limited depth perception. However, depth perception is generally difficult to measure and may be dependent on both monocular and binocular cues. Head movement could also serve to scan visual information across the retinal regions of greatest acuity.

Some birds move their heads in a step-wise or hitching fashion while they walk, and the stationary or slowly moving periods in this process may allow more time for clear image formation and processing than the otherwise blurred images that would be obtained with steady and continuous head motion. On the other hand, certain kestrels are able to hover with their heads almost motionless in spite of wing flapping and changing wind conditions, and this behavior may aid them in detecting the movement of the small animals on the ground that constitute their main diet (Videler, Weihs, & Daan, 1983). A remarkable degree of head stabilization is also shown by some kingfishers as they hover above their prey (Frost, Wylie, & Wang, 1994, p. 260). In all of these cases it is assumed that the movement or lack of movement of the bird's head plays a key role in optimizing its visual ability and for some birds may be essential for survival.

The various possible head and body movements in birds do not always occur independently. In particular, head movement may serve a primarily mechanical rather than visual function as a bird is engaged in, for example, walking, swimming, or launching itself into flight. Thus, head movements may, with other movements such as tail wagging, leg flexing, or waddling, serve to improve a bird's balance or overall locomotor efficiency (Daanje, 1951; Dagg, 1977). The head movements themselves are also sometimes not simply one-dimensional. In the great titmouse and blue titmouse, for example, the head may execute a U-shaped trajectory transverse to the direction that the bird is facing, and in ducks vertical and forward motions are sometimes combined (Daanje, 1951, pp. 60, 64). In spite of such complications, it is generally acknowledged that, as suggested above, head movements often play a key role in enhancing the visual capabilities of birds. Also, in the birds emphasized here the vertical head movements of interest do not seem to be involved with other types of head motion.

The subject of this investigation concerns the head movement of certain water-associated birds and its possible connection to their vision. It may be noted at the outset that one of the most important activities of all birds is the finding of food while delaying becoming food. In this effort there are many birds that prefer to pluck their prey from an underwater location, and such birds face special challenges. Thus, birds that find and acquire their food while underwater need eyes that can adjust to the higher index of refraction that water presents at their eye surfaces, and in addition they require some appropriate system of buoyancy and underwater propulsion. On the other hand, birds that locate their underwater food from above water must be able to deal with the formidable obstacle to vision presented by the air/water interface (Lythgoe, 1979, pp. 134–135). Among the most important consequences of this interface for seeing down into the water are interference from unwanted reflected and scattered light and distortion caused by refraction of the useful transmitted light (Horvath & Varju, 1990). If the water surface is not calm, the appearance of an underwater object may be subject to substantial movement and distortion, while the level of illumination of that object is also strongly varying in time (Loew & McFarland, 1990, pp. 18–32). These complications may have important consequences for a bird's behavior.

The behavior being emphasized here has been recognized previously in a general sort of way, but its significance seems not to have been fully appreciated, and the related literature hasn't been reviewed. Thus, as noted above, some have suggested that head displacement might provide a way for birds to more accurately estimate distance. "Presumably to enhance this distance-measuring method, shorebirds and waterfowl often bob their heads up and down" (Ehrlich, Dobkin, & Wheye, 1988, p. 229). Equivalently, "the bobbing up and down of the head characteristic of many shorebirds may be an effort to gauge distances" (Pasquier, 1987, p. 81). My first purpose here is simply to emphasize that these birds form a habitat/behavior class, and a survey of some of the birds that commonly bob their heads in the vertical direction is included in the following section. These examples include representatives of several different bird orders that all have in common a lifestyle that is closely tied to the watery environment of a stream, lake, or seashore. A second purpose is to briefly inquire why vertical head movement is so common in water-associated birds. Many bird species seem to plan their underwater foraging from wading or above-water perched positions, and it is striking how many of these particular birds also exhibit some type of up-and-down bobbing of their heads. It is possible that in some cases this behavior enhances the birds' ability to locate food through the interposed refracting and reflecting boundary of the water surface.

Birds That Bob

As mentioned above, the category of birds that I shall be emphasizing includes those that seem to spend much of their time viewing their underwater prey from an above-water observation point. This class contains many examples, and I shall focus on those that bob their heads while they seemingly are doing their viewing. While this behavior occurs widely among birds that are identified with a water environment, it is not so common among non-water-based birds. Furthermore, this behavior generally occurs among individual birds near the water, whereas in other cases bobbing would seem to be more of a social activity as the birds interact with other members of their own or other species. The following subsections will include a brief identification of the birds under consideration, an indication of their food-hunting environment, and a short description of their bobbing behavior.

It may be useful at the outset to indicate more explicitly what is meant by head bobbing, as there is now some ambiguity in terminology. Formerly there had been a clearer distinction between the two principal classes of avian head movement, with the quick vertical movement of a typically stationary bird usually referred to as bobbing (or sometimes as nodding, bowing, dipping, etc.) and the step-wise or saltatory horizontal head movements of a typically walking or swimming bird referred to as hitching or described in some other way. The principal dictionary definitions of these intransitive verbs include the following (Merriam-Webster's Collegiate Dictionary, tenth edition, 1997):

> bob: "to move up and down briefly or repeatedly"
> hitch: "to move with halts and jerks"

The usage of the word bob in the present discussion corresponds to this dictionary definition, and thus bobbing will be taken to mean a behavior including sharp vertical changes in head position. It should be noted though that in other recent bird-related literature the word bob has sometimes been employed in place of hitch or other terms in describing the relative forward and backward horizontal head movements of some walking or swimming birds. Thus, one may also now "refer to this (horizontal) movement as a bob, for want of a better word" (Dagg, 1977, p. 537). The backward movement in this case is only apparent as the bird's head stops (or slows) during the more steady forward motion of the bird's body.

It will be shown that the form of bobbing varies from one species to another. In fact, there seem to be three essentially different mechanical functions that a bird might employ to bob its head up and down. In their purest form these would include leg bending with the head and body otherwise rigid, teetering or see-sawing with the head and tail alternately rising and falling, and neck extension and retraction with the body stationary. The birds discussed below employ various combinations of these three mechanisms as they move their heads up and down. I haven't had an opportunity to observe all of these birds first hand, and the relevant literature isn't always clear and consistent on this topic. Nevertheless, as a starting point for what would seem to be an interesting area for more detailed investigation, I have attempted to comment tentatively with several brief supporting quotations on what might be the dominant head-bobbing mechanisms for these bird categories. By using such quotations, the difficulty of interpretation and the subjectivity of the various previous reports on this topic will also be evident.

A second interest concerns the possible relationship of bobbing to viewing through a water surface, and for that purpose the detailed mechanisms of bobbing are in principle not essential. One might expect, however, that the mechanisms employed by a particular species would have some relationship to its morphology. Thus, for example, the length and strength of legs and neck together with other size and weight considerations might have some determining influence on the particular form of head-bobbing that a species would employ. Also, some kinds of movement may be more open than others to detection by underwater prey. This could be undesirable if the prey response allows it to avoid capture, or desirable if the response is to be flushed out of hiding. Yet again, it might be important to employ a bobbing strategy that minimizes the bird's visibility or appeal to its own predators. Considerations such as these would be significant to a comprehensive understanding of the development of head-bobbing behavior.

Dippers

Probably the best known stream-bank birds of the type being emphasized here are the dippers (order Passeriformes, suborder Oscines, family Cinclidae). These birds resemble stocky wrens (about 17 cm long). There are four or five species of dipper worldwide, depending on taxonomy, including the American dipper (*Cinclus mexicanus*) (Leahy, 1982, p.

173). Water crow and water ouzel are respectively traditional Scottish and English names for *Cinclus aquaticus* (Newton & Gadow, 1896, p. 1024), and the common names in some European countries mean water blackbird and water starling (Thomson, 1964, p. 195). John Muir's rapturous account of the American dipper is considered to be his best known writing about an American bird (Muir, 1894/1987, pp. 174–184).

The bobbing of the dipper is one of its most conspicuous behavioral characteristics. While perched on a rock, apparently studying a stream, the dipper may bob up and down rapidly, reportedly as often as several times per second (Lyttle, 1983, p. 54), and over an extended period as often as 40–60 times per minute (Bent, 1948, p. 107). In fact, the name dipper now in general use is said to have been invented in 1804 by the author of Bewick's *British Birds*, because "it may be seen perched on the top of a stone in the midst of the torrent, in a continual dipping motion, or short courtesy often repeated" (Newton & Gadow, 1896, p. 151). Thus, the name does not, as is sometimes supposed, refer to its habit of entering the water in search of food.

Dippers are common around mountain streams of western North America, and I have observed them many times in the Pacific Northwest. Related dipper species are well recognized in other areas of the world. Although they have sometimes been accused of excessive consumption of the eggs and young of game fish, their principal diet consists of insect larvae and small aquatic molluscs, crustaceans, and worms.

It has been noted that the bobbing of the dipper "is not really a teetering like that of the spotted sandpiper, nor is it really nodding, for there is no downward nod of the head or up and down movement of the tail. It is a strictly vertical movement of the whole body, accomplished by bending the long legs to a crouching position and then raising them to a high standing position" (Bent, 1948, p. 107). More briefly it has been stated that dippers "characteristically bob their whole bodies up and down" (Perrins, 1990, p. 261). The overall vertical motion amounts to a distance of 2–3 cm. The spotted sandpiper, with which the dipper's bobbing has been contrasted, will be considered further below.

There are various theories regarding the function of dipping. I have felt that the need for accurate vision through the water surface is a likely reason for bobbing in several types of birds. In the particular case of dippers, a brief mention of a connection to vision has recently been given as one of several possible interpretations (Kingery, 1996, pp. 9–10). A discussion of the implications of head movement for vision in dippers and other bird species will be included below.

Waterthrushes

This is the standard English name for certain members of the wood warbler genus *Seiurus* (order Passeriformes, suborder Oscines, family Parulidae). The waterthrushes favor watery habitats, especially including forest streams. The northern waterthrush (*Seiurus noveboracensis*, 14 cm) and the Louisiana waterthrush (*Seiurus motacilla*, 14 cm) of North America are noted for their behavior of teetering almost constantly, alternately raising or lowering their head or tail. The waterthrushes' "life in the flooded bottom lands and wooded swamps has made them ridiculously like little Sandpipers; when not running along some half-submerged log, they are constantly teetering up and down in much the manner of the 'spotties' of the shore" (Peterson, 1934, p. 126).

Some further brief quotations may provide additional insight into the bobbing behavior of these birds. The northern waterthrush is sometimes observed "wading even up to his knees in the shallow miniature lakes, like a Sandpiper by the seashore, all intent in quest of the aquatic insects, worms, and tiny molluscs and crustaceans that form his varied food. But as he rambles on in this gliding course, the mincing steps are constantly arrested, and the dainty stroller poises in a curious way to see-saw on his legs, quite like a Titlark or Spotted Sandpiper" (Bent, 1953, p. 481). From such a description it is easy to imagine that the teetering interludes give the waterthrush an opportunity to look for its next morsel of food and also that the teetering motion itself somehow sharpens its visual ability to find and identify such food. Concerning the actual mechanics of the bobbing, another observer has remarked that this teetering action "is accompanied by a springy motion of the legs" (Bent, 1953, p. 481).

The quotations just given refer specifically to the northern waterthrush. However, the bobbing behavior of the Louisiana waterthrush does not seem to be different in any essential way, and most authors do not make any distinction. It has been observed though that there is also a slight but noticeable difference in actions and foraging posture between the two species: "on Northern, the tail flicking is restricted to the tail," whereas "on Louisiana, the whole rear end of the bird is 'bobbed' (with the motion appearing to run through the whole body)" (Curson, Quinn, & Beadle, 1994, p. 167).

It has often been noted that similar head-bobbing behavior occurs in more than a single bird species. In a quotation above it was observed that the seesawing behavior of the waterthrushes is like that of the titlark or spotted sandpiper, and both of these birds will be discussed below. It has also been remarked that the waterthrushes "have a tail-bobbing motion much like that of a Wagtail *Motacilla* sp. or a Common Sandpiper (*Actitis hypoleucos*)" (Thomson, 1964, p. 876). In commenting on the bobbing of the Louisiana waterthrush it has been said, "Both the movement and the bird itself suggest the Dipper (*Cinclus*) but the Dipper is more of a bobber, the whole body moving from the knee, while the Water-Thrush is a tilter or teeterer, its longer tail accentuating this type of motion" (Chapman, 1907, p. 228). Thus, in these few quotations the bobbing behavior of waterthrushes has been compared to that of spotted sandpipers, common sandpipers, dippers, and pipits. In an earlier quotation the bobbing of dippers was compared to the teetering of spotted sandpipers. As will be emphasized below, these bird species share much more than just their habit of bobbing or teetering. Most of them also prefer to nest near water, and water-based insects and other animals constitute much of their diets.

River Warblers

The migrating waterthrushes of North America are not the only members of the wood warbler family (Parulidae) to exhibit the bobbing/teetering behavior that is of interest here. Their sedentary cousins of the genus *Basileuterus*, subgenus *Phaeothlypis* (or genus *Phaeothlypis*) dwelling in Central and South America are very similar in both habitat and behavior. The river warbler (*Basileuterus rivularis*, 13.5 cm) lives in eastern South America, favoring swampy areas and along rivers and streams. It is largely terrestrial, and its diet consists mostly of insects and other invertebrates that it finds while hopping by the water's edge. Significantly here, it "constantly swings its tail from side to side and pumps it up and down in the distinctive manner of this subgenus" (Curson et al., 1994, p. 229).

Closely related to the river warbler is the buff-rumped warbler (*Basileuterus fulvicauda*, 13.5 cm), which is also found in Central and South America. These two species, buff-rumped and river, are sometimes considered to form a superspecies within the *Phaeothlypis* subgenus. The buff-rumped warbler is also found along rivers and streams and in swamps. It prefers running water and also hops along finding insects and other invertebrates (Curson et al., 1994, p. 228). These birds are considered "to fill the same ecological niche as the Louisiana waterthrush of the eastern United States," and they both are found "wagging their tails in exactly the same way" (Aldrich, 1964, p. 258). As we have noted, vertical tail-wagging is apparently often to be associated with a more general teetering body movement, and the author just quoted speaks elsewhere of the "body teetering" of the Louisiana waterthrush (Aldrich, 1964, p. 283).

Water Pipits

The water pipit (or American pipit or titlark) is a small songbird of the wagtail and pipit family (family Motacillidae, order Passeriformes). The wagtails are so called because of their habit of wagging their tails, and it is notable in the present context that many of these birds nest near water. In North America the water pipit (*Anthus spinoletta*, 16 cm) is now sometimes referred to as the American pipit (*Anthus rubescens*) (Verbeek & Hendricks, 1994, p. 1). We employ the name water pipit in this context to emphasize the frequent association of this bird with a water habitat. In particular, these birds often feed along shore flats, where their diet consists largely of insects, small molluscs, and crustaceans (Bent, 1950, p. 29); and they sometimes forage "while walking in very shallow water" (Kaufman, 1996, p. 493).

There isn't full agreement in descriptions of the tail-wagging behavior of the water pipit (or of the other wagtails and pipits), and in fact this behavior is reported to vary somewhat from bird to bird and from time to time (Bent, 1950, pp. 31–32). In general, these birds walk rather than hop, and a sideways wagging of the tail seems to accompany the swaying of their bodies when they are walking slowly. The water pipits sometimes also move their tails up and down, and this behavior is most noticeable and distinguishable when they are not walking. As with other water-associated birds, this vertical tail movement is the most conspicuous aspect of the more general see-sawing of a bird's body (Bent, 1953, p. 481). As such, it is also accompanied by vertical head movement, and sometimes the tendency of these birds to nod their heads is also noted explicitly (Wetmore, 1964, p. 231).

Kingfishers

The azure kingfisher (*Ceyx azureus*, 16 cm) of New Guinea is noted for bobbing up and down while perched close to the water's edge at forest margins (Beehler, Pratt, & Zimmerman, 1986, p. 143). This small kingfisher feeds primarily on fish that it locates from its nearby perch or while hovering above the water of a stream or pool. The azure's smaller cousin, the dwarf kingfisher (*Ceyx lepidus*, 12 cm), is very similar in appearance and behavior. Both are found only near water, and both are noted for their bobbing behavior. The diet of the dwarf is perhaps more diverse than the azure, including various insects in place of fish (Rand & Gilliard, 1968, p. 283).

Bobbing behavior also occurs in the green kingfisher of the Americas (*Chloroceryle americana*, 19 cm). "Generally solitary, the Green Kingfisher would easily go unnoticed as it watches for prey were it not for its characteristic habit of frequently raising its head and bobbing its tail" (Perrins, 1990, p. 201). While information on the bobbing behavior of kingfishers is somewhat limited, this movement would certainly seem to include neck extension.

Shorebirds

It has often been remarked that many shorebirds exhibit a distinctive head-bobbing behavior. The term shorebird is considered generally to correspond to the suborder Charadrii (order Charadriiformes) (Leahy, 1982, p. 634), and available reports suggest that the behaviors of interest here are widespread within this suborder. The most widely noted example is perhaps the spotted sandpiper (*Actitis macularia*, subfamily Tringinae, family Scolopacidae, 20 cm). Thus, it has been said that "some shorebirds such as spotted sandpipers characteristically bob their heads up and down" (Burtt, 1967, p. 27). The accompanying teetering motion of these birds has been described as follows: "the fore parts are lowered a little, the head is drawn in, the legs are slightly bent, while the tail bobs up with a jerk." This process is then repeated "with the regularity of clock work" (Coues, 1903, p. 835). This behavior has also been called "teeter-tottering" (Connor, 1988, p. 182), and it is common to the *Actitis* genus. Both spotted sandpipers and common sandpipers (*Actitis hypoleucos*) frequent the banks of rivers and lakes "and have a marked 'bobbing' or 'teetering' action" (Thomson, 1964, p. 714). The common sandpiper "is the Eurasian counterpart to our own Spotted Sandpiper, and it walks with a similar teetering action along the edges of streams and ponds" (Kaufman, 1996, p. 197).

Unlike the spotted and common sandpipers, the birds of the *Tringa* genus dip there heads more conspicuously than their tails when bobbing. Thus, the solitary sandpiper (*Tringa solitaria*, 21 cm) is said to have "rather sedate manners, except the curious bobbing up and down of the head, which is as habitual with this species as the teetering of the tail of the Tip-up" (a common name of the spotted sandpiper) (Coues, 1903, p. 834). The solitary sandpiper "when foraging, walks about actively in shallow water, constantly nodding head" (Moskoff, 1995, p. 6). The yellowlegs, another *Tringa* species, has been compared to the spotted sandpiper: "The Spotted Sandpiper teeters up and down nervously as if too delicately balanced on its matchstick legs, while its relative the Yellowlegs (*Tringa flavipes* or *Tringa melanoleuca*) merely makes a sedate bob or curtsy" (Peterson, 1964, p. 380). The following observation has been made on the related wandering tattler (*Heteroscelus incanus*, 26 cm): "Since it bobs frequently and has a gray back, the tattler most resembles a giant winter-plumaged spotted sandpiper" (Connor, 1988, p. 179).

The behavior of these and many other shorebirds can also be gleaned from Bent's *Life Histories of North American Shore Birds*, and several examples from that source relating to head bobbing are grouped together here:

"The bobbing motion characteristic of several of the plovers is a common habit of the piping plover (*Charadrius melodus*, subfamily Charadriinae, family Charadriidae, 17 cm). This is a single hitching motion by which the body is tilted up and down on the legs as a fulcrum. It is apparently identical with the bob of the semipalmated plover (*Charadrius semipalmatus*, 17 cm) and is made frequently as the birds stand about on the beach" (Bent, 1929, p. 244). Concerning the bobbing motion of the snowy plover (*Charadrius alexandrinus*, 16 cm), "there is an abrupt upward tilt of the body at intervals. . . . Their habit of bobbing the head is doubtless useful at times, but the motion often catches the eye when without it they would not be separated from the sand" (Bent, 1929, p. 250).

Concerning again the spotted sandpiper, "its habit of teetering makes identification certain. The only bird which resembles the spotted sandpiper at all closely is its larger relative the solitary sandpiper, but the characteristic motion of this bird is a ploverlike hitching movement or bob, as if hiccoughing, very different from the spotted sandpiper's rapid swaying up and down of the hinder part of the body" (Bent, 1929, p. 91).

The solitary sandpiper "frequently indulges in a peculiar tilting and nodding habit, similar to that of the spotted sandpiper, but it is more deliberate and not so pronounced; it seems to be more of a bow than a tip-up more like the bobbing of the yellowlegs" (Bent, 1929, p. 6).

The wandering tattler is also known "to bob and teeter, somewhat like our familiar spotted and solitary sandpipers. It is generally solitary and seems to be satisfied with its own society" (Bent, 1929, p. 41). "The movements of wandering tattlers are often suggestive of spotted sandpipers with which they are sometimes associated; they indulge in the same 'tip-up' motion of the body, though less frequently" (Bent, 1929, p. 45).

Regarding the greenshank (*Tringa nebularia*, 30 cm), "when searching for food it often wades out into the water until it reaches nearly to the torsal joint and moves 'with rapidity, running rather than walking and almost constantly vibrating its body' " (Bent, 1927, p. 313). It also sometimes "stands and vibrates." It is not clear how to interpret "vibrating," but I am inclined to equate it with the teetering seen in other *Tringa* species.

The "well-known bobbing habit" of the lesser yellowlegs (*Tringa flavipes*, 25 cm) has been described in more detail: "Method of bobbing was to raise the head by stretching the neck and at the same time lower the tail, the whole body being held rigid, then lower the head with the bill pointing somewhat downward and raise the tail to normal. The body seems to turn on a pivot, but the lengthening of the neck is an independent movement" (Bent, 1927, p. 341). The greater yellowlegs (*Tringa melanoleuca*, 35 cm) has "the same habit of tilting its body and alternately lengthening and shortening its neck with a bobbing motion" (Bent, 1927, p. 340).

The eastern willet (*Catoptrophorus semipalmatus*, subfamily Tringinae, 38 cm) is said to "indulge in the bobbing or nodding motions less frequently and more moderately than the yellowlegs do." It has been noted that "in bobbing, the head is drawn back and the tail lowered at the same time, the whole body turning as on a pivot, then the head is brought forward and the tail raised to its natural level" (Bent, 1929, p. 33).

The black oystercatcher (*Haematopus bachmani*, family Haematopodidae, 45 cm) is said to be "one of the most peculiar birds of the region, in its motions, having a grave, solemn and stilted gait, and bobbing its head up and down with every step." Also, when standing on slippery rocks they are said to nod "with grotesque dignity" (Bent, 1929, pp. 320, 323). Concerning the behavior of European oystercatchers (*Haematopus ostralegus*, 42 cm), it is said that "sometimes, but not always, the whole body is bobbed up and down at intervals in the way common to so many wading birds, but not very markedly" (Bent, 1929, p. 307).

The preceding accounts show that distinctive vertical head movement occurs in a wide variety of birds that are closely associated with a watery habitat. Most of these birds locate a substantial part of their food by observations made through a water surface, and the head movement may help with these observations. A summary of several of these birds and their head-bobbing behavior is included in Table 1. It should be emphasized that this is only a preliminary table to try to collect the rather scattered, subjective, and sometimes ambiguous data on this subject that have been considered here. Hopefully, more detailed observations using video technology will lead to more rigorous and complete information.

It is suggested by Table 1 that head movement behavior of water birds, when it occurs, tends to be quite uniform across a genus. For example, the *Actitis* species of Scolopacidae seem to have common bobbing characteristics that are distinguishable from the bobbing characteristics of the *Tringa* species of the same family. There are, of course, other birds not represented in the table that also feed underwater but for which significant head-bobbing has not been

Table 1. Dominant Head Movement Mechanisms of Some Vertical Bobbing Birds

	Bend Legs	Tilt Body	Extend Neck
Dippers (Cinclidae)			
Cinclus			
American dipper	yes	no	no
European dipper	yes	no	no
Waterthrushes (Parulidae)			
Seiurus			
Louisiana waterthrush	some	yes	no
Northern waterthrush	some	yes	no
River warblers (Parulidae)			
Basileuterus or *Phaeothlypis*			
River warbler	maybe	yes	no
Buff-rumped warbler	maybe	yes	no
Water pipits (Motacillidae)			
Anthus			
American Pipit	no	yes	no
Kingfishers (Alcedinidae)			
Ceyx			
Azure kingfisher	no	maybe	probably
Dwarf kingfisher	no	maybe	probably
Chloroceryle			
Green kingfisher	no	maybe	yes
Shorebirds (Scolopacidae)			
Actitis			
Common sandpiper	no	yes	no
Spotted sandpiper	no	yes	no
Heteroscelus			
Wandering tattler	no	yes	no
Catoptrophorus			
Eastern willet	no	yes	yes
Tringa			
Common greenshank	no	probably	maybe
Greater yellowlegs	no	yes	yes
Lesser yellowlegs	no	yes	yes
Solitary sandpiper	no	yes	yes
Shorebirds (Charadriidae)			
Charadrius			
Piping plover	no	yes	no
Semipalmated plover	no	yes	no
Snowy plover	no	yes	no
Shorebirds (Haematopodidae)			
Haematopus			
Black oystercatcher	no	probably	probably
European oystercatcher	no	probably	probably

reported. Thus, while head bobbing may be of value in recognizing underwater prey, it is clearly not a requirement for all underwater feeding species. On the other hand, there are also birds that are known to exhibit vertical head bobbing for which this movement has nothing to do with vision through a water surface. As noted above, bobbing in some of these cases has been suggested to be an aid to above-water depth perception or enhancement of visual acuity. Usually this bobbing is interpreted as intention

movements (Daanje, 1951), or it is considered to be a social behavior as the birds seek to communicate with members of their own or other species. Examples of such social head movements are found among woodpeckers, swallows, crows, sparrows, killdeer, mourning doves, nuthatches, orioles, owls, falcons, and probably others (Stokes, 1979, 1983, 1989).

In summary, most cases of vertical head-bobbing that have not been clearly identified as social occurrences or intention movements seem to occur in water-associated birds. On the other hand, it has been noted that "Most of the non-bobbing birds live near water" (where bobbing in this quote refers to hitching as defined above) (Dagg, 1977, p. 538). However, there are at least a small number of birds exhibiting a hitching head movement that also live near water. Examples include the swamp hen (*Porphyrio porphyrio*) and the crested grebe (*Podiceps cristatus*), which show this behavior while swimming (Dagg, 1977, 538). I have observed this behavior in swimming American coots (*Fulica americana*). Feeding Wilson phalaropes (*Phalaropus steganopus tricolor*) are also reported to sometimes show "a hitching motion of the head" (Bent, 1927, p. 33). These should not be considered counterexamples to the general trends noted here, because the birds in these cases are moving rather than stationary. In short, the hitching behavior seems to be most common in birds that locate food or otherwise view their environment while moving (usually but not always away from water), while vertical bobbing seems most closely identifiable with otherwise stationary perched or wading birds that find their food through a water interface.

Seeing Beneath the Surface

There are several factors that can influence a bird's ability in seeing objects located beneath the surface of a stream or other body of water. These can be regarded as primarily physical phenomena that affect the amount of useful light that reaches the bird's eyes and also the amount of extraneous light that might detract from the bird's ability to recognize fainter items. In addition, there are food and safety considerations that are related to the bird's motivation for looking down through the surface in the first place. In this section several of these factors are briefly summarized, and schematic representations of some of them are included in Figure 1. This figure represents a dipper or other bird standing near the water's surface and examining an underwater morsel. This bird also needs to be aware of underwater predators, as represented by the fish. The bird's view of underwater food and predators is limited by such factors as refraction-related distortion and displacement, obscuration by objects floating on the water surface and elsewhere, scattering of light by small particles in the water, and unwanted reflections and glare from the water surface. Refraction and reflection effects are sometimes made still more complex by motion of the water surface (Loew & McFarland, 1990, pp. 18–32).

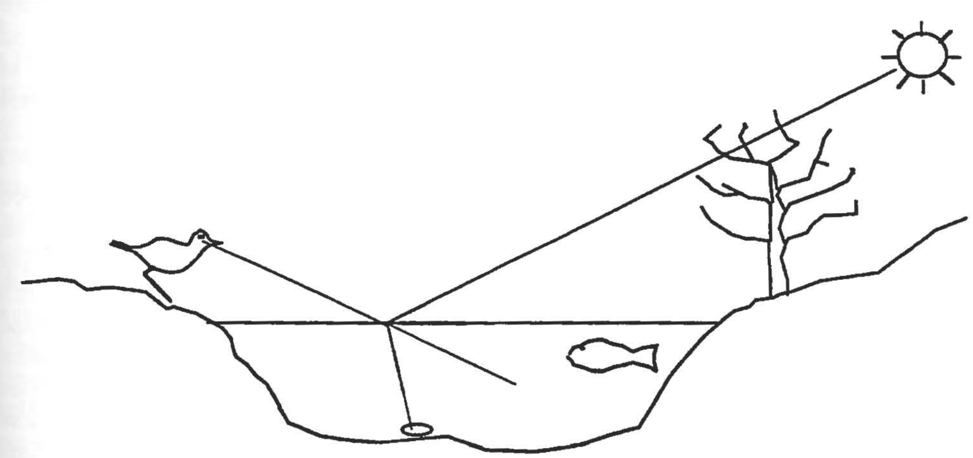

Figure 1. Schematic representation of a bird viewing underwater food. The appearance of this food is obscured by reflections and scattering of undesired light and by refraction of the desired image.

Functional Considerations

All of the birds of interest here find a significant portion of their food by looking down through the water surface. Thus, dominant prey include small molluscs, crustaceans, worms, and insects. More specific details on the diets of the various members of this bird group were included in the previous sections. Typically, the animals that constitute these diets are either camouflaged or at least not brightly colored. Therefore, if these birds are to be adequately fed, it is important for them to obtain the clearest possible view of their underwater domain.

A second important reason for having a good view is that the underwater region is not without hazards. Thus, there must be at least some risk to a bird like a dipper of being caught and drowned in underwater currents, vegetation, or submerged objects. More dramatically, there is also a possibility of a bird being eaten outright by some full-time inhabitant of the water. In this regard there are reports of dippers being swallowed by trout (Elliott & Peck, 1980, p. 524; Johnson, 1953, p. 158). Birds that only wade in the water are also subject to hazards. A misstep by one of these birds can lead to it having its foot caught by an inconspicuously lurking crayfish or mussel (Bent, 1929, p. 92). Thus, for both diet and safety, always having the clearest possible view may be regarded as essential. It is possible that these birds would adjust their position, timing, and behavior during foraging to optimize their vision and hence to obtain the most preferred food with the least effort and risk.

Reflections

Among the most important obstacles to vision that are presented by the water surface are reflections of light from the sun and sky and possibly also from above-water objects. These reflections are superimposed on the useful light that is coming up toward a bird from its underwater prey. In the worst case the surface reflections can be in the form of a glare that entirely obscures any light from below the water surface.

A significant aspect of the light reflected from the water surface is its angle dependence. In general, the shallower the angle between the reflected light from the sky or other object and the surface of the water, the higher the fraction of the light that will be reflected and interfere with the light from below the surface. In other words, if one looks out almost horizontally over a smooth water surface, that surface will appear much like the surface of a mirror. In this case, any information about underwater fish or other objects would tend to be swamped by the much brighter reflected light. On the other hand, if one looks more vertically downward on the water surface the reflection coefficient (fraction of light reflected) is only about 2%. The detailed angle-dependence and polarization-dependence of the reflection coefficient are governed by well-known but complicated mathematical formulas (Stratton, 1941, pp. 490–511), and a quantitative discussion of such effects is not appropriate for this review. Suffice it to say that the smaller the reflection coefficient, the less visual interference caused by light reflection. It would seem though that in terms of minimizing the interference from glare it is advantageous for the bird to be as directly above its prey as possible.

The fraction of the light arising from the underwater prey that actually reaches the bird's eyes also depends on the angle at which that light hits the water's surface from below. At shallower angles with respect to the water surface, that surface appears from below to be increasingly mirrored, and for angles greater than 48.75° from the normal to the surface (in fresh water) the scattered light is totally reflected back down into the water. Thus, even under the best conditions only a somewhat vertical view of an underwater object is available from an above-water perch. An underwater animal, on the other hand, can view the above-water world, but that view is distorted and compressed into "Snell's window," a circular region above the animal having a half-angular aperture of 48.75°. The calculation of this angle is indicated below. In terms of overall light level, image size, and freedom from distortion, it would seem that a steeper angle of view would be advantageous to a predator. The reality, though, might not be so simple.

In addition to considering the reflection coefficient at the water surface, it might be necessary to consider the brightness of the light being reflected. In the worst case the reflected light will include the direct glare of the sun. On the other hand, it is possible that in a narrow stream environment a shallower angle, while yielding a higher reflectivity, will actually produce the reflection of a dark stream bank or wooded environment that is much darker than the sun or sky, as suggested in Figure 1. In this case a shallower angle would be more effective than a more vertical view. The brightness of a particular region of the sky also depends, of course, on the nature of any cloud cover. Thus, it isn't possible to reach a single general conclusion about the best direction for a bird to look in order to minimize interference from surface-reflected light.

Besides its choice of standing location and viewing direction, a bird might adopt other strategies for reducing glare. Thus, a long-winged bird might stretch out its wing over the region being viewed, so that the viewing is done through the darker wing shadow. This behavior has been documented in the Louisiana heron (*Hydranassa tricolor*) and others (Meyerriecks, 1962, p. 52). In a similar way a long-necked bird might extend its neck sideways toward the sun to move the region of surface glare farther from the region in which it wishes to hunt. This behavior is seen in great blue herons (*Ardea herodias*) and others (Krebs & Partridge, 1973, pp. 533–535). Thus, there may be several methods that a water-feeding bird could employ to reduce glare from the water surface.

Refraction

Another major obstacle to vision through a water surface is the refraction or bending of light from an object under the water. This refraction occurs right at the surface and changes the apparent position of an object. Refraction also leads to a substantial magnification of the object and a corresponding reduction in its apparent brightness (Austin, 1974, pp. 320). It is not always straightforward even in principle to look at an underwater object and determine its true size and location. For example, if the water surface is perfectly calm and flat, then that surface itself is invisible. All that can be seen are reflected or refracted views of light sources that are located above or below the surface. Due to refraction, a lack of information about the location of the surface translates into a lack of information about objects seen through the surface.

This ambiguity just mentioned is lessened if there are floating objects or other light-scattering structures at the water surface due to bubbles or splashing. If the location and orientation of the surface with respect to an observer (i.e., a bird) can be determined by any means, then it becomes possible to more accurately estimate the size and location of objects seen through the water surface. While the corresponding calculations seem complex from a human perspective, they may occur in an intuitive or instinctive way in the water-associated birds of interest here.

Benefits of Bobbing

The previous paragraphs have emphasized some of the difficulties faced by a bird perched near a water surface trying to locate underwater food. Due to interference from glare and other unwanted light and inefficient transmission of useful light, it is sometimes difficult to see potential food at all. Furthermore, once any prey has been found, the intervening air/water interface makes it difficult to estimate the size and location of that prey. There are several ways in which an organized bobbing of the head might make the task of underwater predation somewhat easier. I begin this discussion by including a basic model for refraction and reflection at the water surface.

Model

Some aspects of vision through a water interface can be given a formal mathematical description, and basic elements of such a description are included here. The coordinate system to be used in this calculation is shown in Figure 2. The subscript e refers to the eye of the bird and thus x_e and y_e are the x and y coordinates of the eye. Similarly, the subscript o refers to the object being observed, and the x axis corresponds to the surface of the water. The index of refraction of the air and water are n_1 and n_2, respectively. A light ray from the object to the eye is refracted at the surface, which it crosses at the coordinate x_s. The angle between the light ray in air and a line perpendicular to the surface is θ_1, and the corresponding angle in water is θ_2.

The most basic relationship governing the bending of a light ray at an interface between two refracting media is Snell's law:

$$\frac{n_1}{n_2} = \frac{\sin\theta_2}{\sin\theta_1} \qquad (1)$$

From Figure 2 it also follows that the angles θ_1 and θ_2 are related to the eye, surface, and object coordinates by the relations

$$\tan\theta_1 = \frac{x_s - x_e}{y_e} \qquad (2)$$

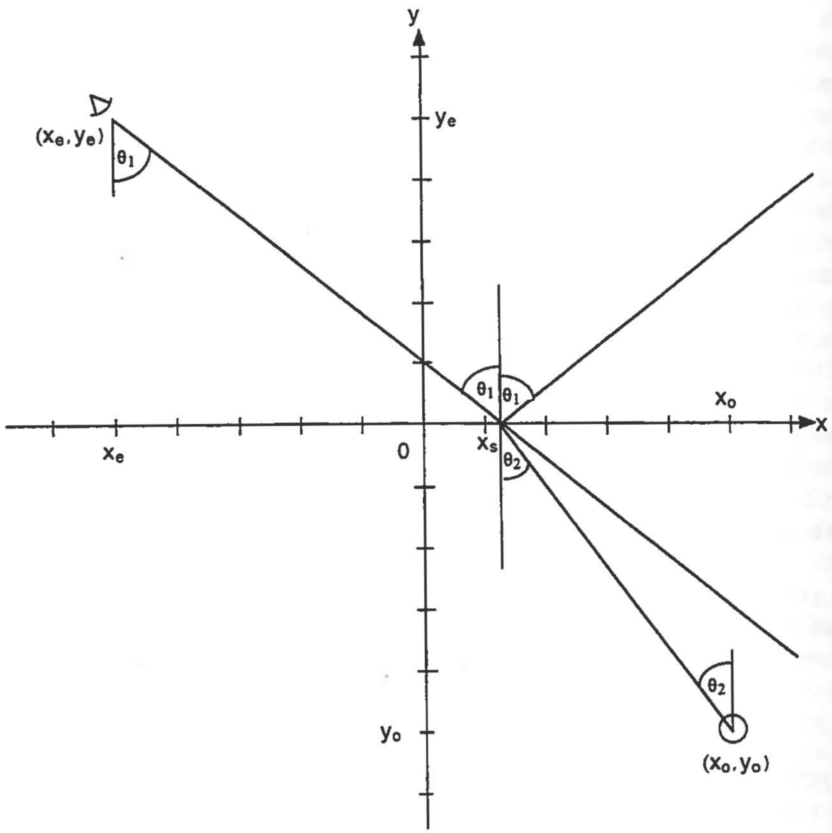

Figure 2. Coordinate system for calculation of the trajectory of a light ray propagating from the underwater object to the eye of the predator. The coordinates of the eye are x_e and y_e, and the coordinates of the underwater object are x_o and y_o. The apparent direction of the object and the direction of the reflected source are also shown.

$$\tan\theta_2 = -\frac{x_o - x_s}{y_o} \qquad (3)$$

The sine functions in Snell's law can be replaced by tangent functions using an identity which for this configuration takes the form

$$\sin\theta = \frac{\tan\theta}{\left(1+\tan^2\theta\right)^{1/2}} \qquad (4)$$

Combining eqs. (1)–(4) one obtains

$$\frac{n_1}{n_2} = \frac{x_o - x_s}{x_s - x_e}\left[\frac{y_e^{\,2} + (x_s - x_e)^2}{y_o^{\,2} + (x_o - x_s)^2}\right]^{1/2} \qquad (5)$$

Equation (5) and its predecessors can be viewed in different ways. For purposes of constructing the ray trajectory corresponding to known eye and object locations, this result is simply a single implicit relationship for the unknown quantity x_s, the point at which the light ray crosses the water surface. This result shows clearly that the ray path and hence the apparent position of the object depend in a nonlinear way on the coordinates of both the eye and the object with respect to the water surface. From the standpoint of a bird, the change in the apparent direction of an underwater object (perhaps with respect to above-water references) as a function of eye height can be used with these equations to determine the true object location and if necessary also the height of the bird above the transparent water surface. If the location of the components of an extended target can be determined, the size of the object is also known.

A further specific solution to eq. (5) is plotted in Figure 3. In this example it is assumed that the bird's eye is initially at a height of 10 cm above the water surface, while the food object is at a depth of 10 cm and at 20 cm horizontal distance from the bird. The index of refraction of the air is taken to be $n_1 = 1$, while the index for fresh water is about $n_2 = 1.33$ (Forsythe, 1969, p. 530). [With these numbers the half-angle of Snell's window mentioned above is $\sin^{-1}(n_1/n_2) = 48.75°$.] The bird is then assumed to lower its head to a height of 5 cm, leading to both a change of the apparent direction to the food object and a change of the direction from which interfering rays arrive. It will be noted that only the apparent direction to the food object is suggested in the figure, and no attempt is made to actually suggest an apparent location. The water surface introduces astigmatism, so the image would not be sharply focusable unless the bird's eyes also had some compensating and adjustable astigmatism.

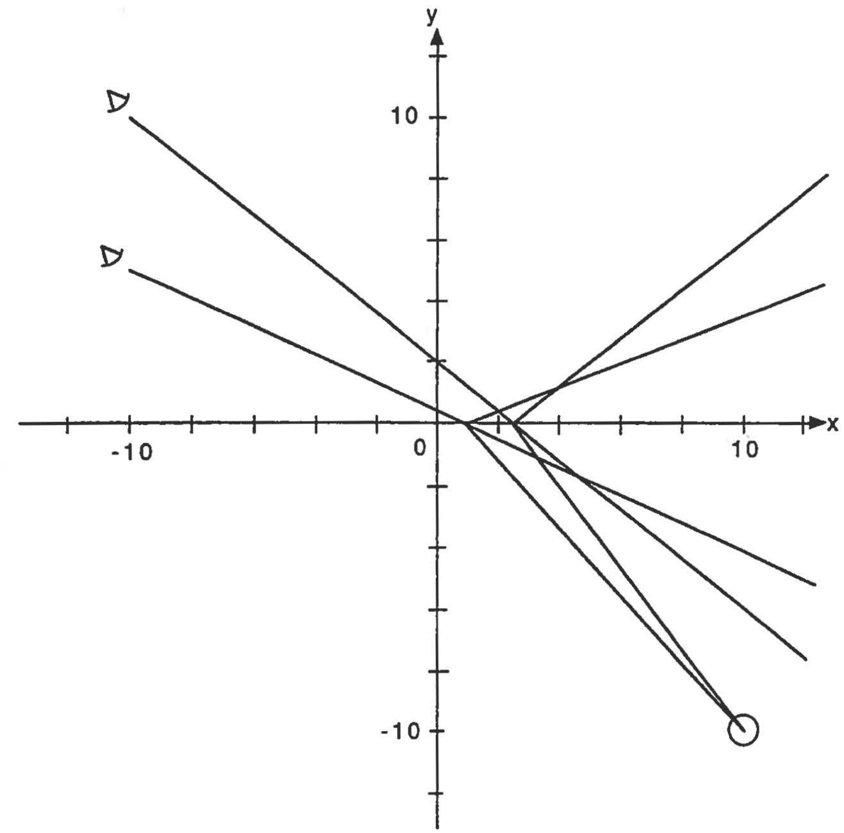

Figure 3. Solutions for the ray trajectories from an underwater object to the eye of the predator for two different values of the eye height. Significant changes in the directions of the rays from the object and the above-water interfering source occur with changes in eye height.

A further complication arises if the water surface is not smooth, and in that case significant variations in the apparent prey location might occur between successive observations. For a relatively turbulent mountain stream, it would probably be necessary to make these calculations quickly and repeatedly in order to obtain a meaningful estimate of prey location and size. It may not be coincidental that the bird that is reported to bob most quickly—the water dipper—also is routinely found foraging in the most turbulent mountain streams.

Reflections

I shall consider further the possible effects that head-bobbing might have on interference from undesirable reflections. Bobbing while watching a point under the surface of the water changes the direction of the light sources causing the interfering light. If this interference is due mainly to glare from rather uniform reflected sky light, then the small angle changes resulting from bobbing will have little effect on the level of the glare. On the other hand, if the reflected light arises from the much darker and more structured objects that might occur across the surface of the water, then bobbing could have a more dramatic effect. As a specific example, we might imagine a dipper sitting on a rock and looking down into a stream in such a way that the dominant surface reflections come from brush on the opposite stream bank, as suggested in Figure 1. In this case bobbing might bring its head into a position in which reflections would be dimmer.

Alternatively, bobbing could create motion parallax between the underwater target and the reflected image of overhead foliage. The relative motion of a viewed object and the superimposed reflected image that results from bobbing is also evident in Figure 3. Motion parallax has been understood to aid in target detection in typical above-water viewing (Davies & Green, 1988; Frost, Wylie, & Wang, 1990), and it could also help a bird to distinguish between underwater objects of interest and the superimposed reflections.

From the point of view of minimizing reflection effects, advantages of vertical head bobbing over possible head movements in the lateral or front and back horizontal directions may exist for certain geometries, but these possible advantages would not seem to be either universal or dramatic. From a mechanical standpoint, however, the horizontal hitching movements of a walking or swimming bird may sometimes, as noted before, serve to improve the bird's locomotory efficiency. Also, the stationary or slower portions of the hitching behavior probably enhance the bird's visual capabilities. But these advantages do not exist in the same way for a bird that is doing its observing from a fixed location, and such birds do not generally exhibit front and back head movements. It is possible that for these birds vertical head movements are easier to implement, and they might also be less conspicuous to potential predators of the birds.

Refraction

One obstacle to vision for which the vertical motion is particularly useful is the distortion mentioned previously. Because a water surface is essentially horizontal, refraction at the water surface always bends light rays and distorts scale primarily in the vertical direction. A lateral movement of a bird's head would, to a first approximation, cause no change in the refraction angles of the light rays from the object being viewed; and, for shallow viewing angles, front and back movement would also not be useful. Thus, such movements would yield little information that could be used to refine any estimate of the size, shape, or location of an object being viewed. On the other hand, a vertical head movement, as shown above, would change all of the ray angles in a manner that would be characteristic of the prey and water boundary positions. It would be possible, at least in principle, for a bird to interpret this refraction information in such a way as to identify the original undistorted object.

That birds are in fact able to compensate for refraction has been demonstrated in studies of certain piscivorous (fish-eating) birds that locate prey and commence capturing movements with their eyes above the water surface. These birds generally need to cope with light refraction at the air/water interface. If the birds' eyes are not directly above the prey, there will be a disparity between the prey's apparent and real positions, and for the western reef heron (*Egretta gularis schistacea*), for example, this disparity may exceed 10 cm (Katzir & Intrator, 1987, pp. 517–523). The capture success rate of these birds confirms their ability to deal with such distortions. Detailed experiments with herons suggest that these birds gain the necessary information for determining prey size and position during an initial slower and somewhat horizontal prestrike head movement. At some point in the prestrike when required corrections have been determined, the movement changes to a more rapid downward directed thrust, which is intended to capture the prey.

Similar movement patterns are observed when pied kingfishers (*Ceryle rudis*) dive for fish. These birds initially hover several meters above the water surface with their heads stable. Then for fish deeper than about 15 cm they commence a slow curved dive during which they may be acquiring the information needed to calculate prey position and size. This initial motion is followed by a straight and more rapid descent (Katzir, 1993, p. 311). Kingfisher retinae have been studied, and the visual capabilities of these birds can now be estimated (Moroney & Pettigrew, 1987). Their capture success rate shows that these kingfishers are able to make the necessary distortion corrections.

With the known success of birds like herons and kingfishers at correcting for distortion, it should not be surprising if other birds that observe their prey through the water surface have corresponding abilities. It is possible that vertical head-bobbing yields the same visual information as the optical transformations produced by the slow prestrike of herons or the slow curved dives of kingfishers. An important difference, though, comes from the fact that herons and kingfishers feed largely on highly mobile fish, while the various birds emphasized in this study are more interested in stationary or slow-moving prey. A heron or flying kingfisher must make its final refraction calculations during its actual strike approach in order to delay detection and limit evasion tactics by prey. On the other hand, with slow or nonmoving targets, the gathering and processing of refraction data can be carried out over a more extended period of time, and it would seem that the vertical head-bobbing of perched kingfishers and other birds discussed here might play a central role in acquiring the necessary refraction data. Thus, the refraction angles change as a bird moves its head vertically, and with suitable interpretation these angular variations can yield unambiguous information about water-surface and prey locations. It is notable that whatever roles this head-bobbing behavior may play, it is a common feature of the foraging periods.

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Correspondence concerning this article should be sent to Lee W. Casperson, Department of Electrical and Computer Engineering, Portland State University, P.O. Box 751, Portland, OR 97207-0751. Electronic mail may be sent via Internet to lcaspers@ee.pdx.edu.

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