

Note

Head-bobbing in the Ring-billed Gull (*Larus delawarensis*)

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Many birds bob their head as they walk or run on the ground. The functional significance of this behaviour is unclear, but there is strong evidence that it plays a significant role in enhancing visual perception. If head-bobbing is advantageous, however, then it is a puzzle that some birds do not head-bob. As a group, gulls (Laridae) are among the birds that reportedly do not head-bob, yet here we report head-bobbing among Ring-billed Gulls (*Larus delawarensis*), observed and filmed in Ontario, when walking relatively slowly while foraging on the ground. This suggests that head-bobbing plays a key role in the visual detection of food items in this species. We suggest that head-bobbing may be a relatively common behaviour in foraging Ring-billed Gulls and speculate that other gulls (and indeed other birds) previously thought not to head-bob may in fact do so under certain circumstances.

Key Words: Ring-billed Gull; *Larus delawarensis*; head-bobbing; behaviour; foraging; head movement; head stabilization; motion parallax; visual perception

Introduction

Many birds display characteristic head movements as they walk and run on the ground. Called head-bobbing, this behaviour involves repeated backward and forward movements of the head (termed the “hold” and “thrust” phases, respectively; Frost 1978) with respect to the moving body, but not the surrounding environment. During the hold phase, when the head appears to be moving backward, it is actually held stationary while the body continues to move forward (Dunlop and Mowrer 1930; Frost 1978). During the thrust phase, the head is rapidly moved forward, catching up with the constantly moving body. Head-bobbing has been reported in a wide range of birds (Dunlop and Mowrer 1930; Whiteside 1967; Friedman 1975; Dagg 1977; Frost 1978; Cronin *et al.* 2005; Necker 2007; Hancock *et al.* 2014) and is most commonly associated with walking and running, although some water birds (such as grebes, loons, moorhens, and mergansers) also head-bob during swimming and/or when diving under water (Lindroth and Bergström 1959; Dagg 1977; Necker 2007; Gunji *et al.* 2013).

Although head-bobbing may play a role in gait stabilization and the maintenance of balance (Daanje 1951; Dagg 1977; Fujita 2002, 2003), there is strong evidence that it enhances visual perception significantly in 2 important ways (Dunlop and Mowrer 1930; Walls 1942; Lindroth and Bergström 1959; Friedman 1975; Frost 1978; Davies and Green 1988; Troje and Frost 2000; Cronin *et al.* 2005; Necker 2007). First, during the hold phase when the head and the eyes are stabilized, the image on the retina is also stabilized, which will improve both object recognition and the ability to distin-

guish between self-motion and object motion. Second, the rapid forward movement of the head during the thrust phase might allow a bird to perceive depth cues through motion parallax. Motion parallax is a phenomenon in which objects at different distances from an observer moving through space appear to move across the visual field at different rates, with close objects moving more quickly than objects further away.

Although head-bobbing has been observed in a number of avian taxa, a range of birds reportedly do not head-bob (Whiteside 1967; Dagg 1977; Fujita 2004; Necker 2007). Head-bobbing is presumed to be beneficial because it requires energy and because this behaviour is present in a wide variety of avian species (Dagg 1977). If head-bobbing is advantageous in terms of visual perception or in some other way, then it remains a puzzle why some species of bird head-bob while others apparently do not (Dagg 1977; Fujita and Kawakami 2003; Necker 2007). To identify ecological and behavioural correlates of head-bobbing across species, which in turn may help us understand the functional significance of this behaviour, it is important to determine which bird species head-bob and which do not, and also under what circumstances head-bobbing occurs (Fujita and Kawakami 2003; Fujita 2006; Necker 2007).

Gulls (Laridae) are among the birds that have been consistently reported as non-head-bobbers (Whiteside 1967; Dagg 1977; Fujita 2004; Necker 2007). However, Fujita (2006) reported that Black-headed Gulls (*Chroicocephalus ridibundus*) do occasionally head-bob under specific conditions when foraging on the ground. This led us to predict that other gulls may also head-bob. We tested this prediction by observing and filming Ring-billed Gulls (*Larus delawarensis*) foraging on the

ground in a riverside park in Brockville, Ontario, in August 2014.

The Ring-billed Gull is a medium-sized gull that is very common along the St. Lawrence River and throughout the Great Lakes region of eastern Canada, where its numbers have increased dramatically since the 1940s (Ludwig 1974; Lévesque *et al.* 2000). This species is a highly opportunistic feeder and has adapted extremely well to human activity (del Hoyo *et al.* 1996; Olsen and Larsson 2003). In Brockville, these gulls are commonly found in parks along the St. Lawrence River during summer months, where they forage in short grass, chase insects, and beg for food from picnickers.

Methods

Ring-billed Gulls were both observed and filmed in Hardy Park, Brockville (44°35'N, 75°41'W). For filming, we used either a Rebel T1i or a Rebel SL1 digital SLR camera (Canon Inc., Tokyo, Japan), supported on a tripod; the resolution was 1280 × 720 pixels and the progressive frame rate was 30 (Rebel T1i) or 60 (Rebel SL1) frames/s. Films were downloaded to a computer and edited so that only sequences showing birds walking in an approximately horizontal direction perpendicular to the optical axis of the camera were used for analysis (Fujita 2006). Using ImageJ (Wayne Rasband, Research Services Branch, National Institute of Mental Health, Bethesda, Maryland, USA), landmark positions on the head (the eye) and body (e.g., the anterior or posterior tip of the wing, the tip of the tail feathers, or a prominent wing colour patch) were digitized for each frame (Fujita 2003, 2006; Fujita and Kawakami 2003). In addition to the head and body landmarks, the position of a static environmental landmark, such as a rock or piece of vegetation, in approximately the same plane as the bird was also digitized (Fujita 2006), allowing us to correct for displacements in the positions of the head and body landmarks resulting from panning movements of the camera. The head length of each bird was also measured, from the tip of the beak to the back of the head, allowing walking speed to be expressed in head lengths/s.

Results and Discussion

Approximately 30 individual gulls were observed. Both immature and mature gulls were present (as determined by plumage differences), but adults made up the majority of the group. Over several hours of observation, all of the gulls displayed head-bobbing repeatedly while foraging in short grass (Figure 1A, B, D; Video S1). However, in contrast to some birds, such as pigeons, the gulls did not head-bob all of the time when walking (Figure 1C, E). Rather, head-bobbing occurred only when gulls were walking slowly and foraging. When the same gulls were walking quickly or running, they did not head-bob. These observations were confirmed by analysis of head and body position in immature and mature

gulls, based on 22 videos, half of which showed head-bobbing (Table 1). A comparison of walking speeds (calculated by dividing the total distance travelled by the body marker by the time of the film sequence and expressed in head lengths/s) revealed that walking speeds during head-bobbing were slower (2.56 ± 0.66 head lengths/s, $n = 11$) than during non-head-bobbing (3.98 ± 1.48 head lengths/s, $n = 11$). Our finding that head-bobbing only occurs at slow walking speeds in Ring-billed Gulls is consistent with previous results for Black-headed Gulls (Fujita 2006), Bar-tailed Godwits (*Limosa lapponica*; Dagg 1977), and Japanese Night-herons (*Gorsachius goisagi*; Fujita and Kawakami 2003). Moreover, Little Grebes (*Tachybaptus ruficollis*), a species that head-bobs when diving under water, tend to head-bob only when swimming slowly (Gunji *et al.* 2013). This suggests that across many species, head-bobbing is particularly advantageous to birds looking for food while moving at relatively slow speeds, perhaps because the visual functions of head-bobbing are most beneficial at these speeds.

This is the first account of head-bobbing in Ring-billed Gulls, and only the second report of such behaviour in any species of gull. In a previous study, Fujita (2006) found that Black-headed Gulls head-bob, but only occasionally under specific conditions, namely when foraging while wading slowly on a submerged mud substrate. Fujita (2006) suggested that one possible reason for this is that it is difficult to see a submerged substrate and, thus, under these conditions, Black-headed Gulls may head-bob to better visually assess the condition of the substrate they are walking on. In contrast, head-bobbing in Ring-billed Gulls appears to be a relatively common behaviour when these birds are foraging on grass. As flat grass is not as difficult to see or move on as submerged mud, we believe that Ring-billed Gulls use head-bobbing primarily for the detection of food items, as opposed to visualizing the substrate.

Indeed, we were surprised to find how common head-bobbing is in Ring-billed Gulls, given that these birds are among those that supposedly do not head-bob. Because ground foraging is the most common foraging method in gulls (Burger 1988), we speculate that many other species may also use head-bobbing when feeding on the ground. There are other examples of birds originally thought to be non-head-bobbers, but reclassified as more evidence became available. For example, herons and stilts, initially classified as non-head-bobbers by Dagg (1977), have since been shown to head-bob commonly as they walk (Fujita 2003; Fujita and Kawakami 2003). Therefore, we recommend that the walking behaviour of other gulls (and indeed other birds currently considered to be non-bobbers) be subjected to greater scrutiny to determine whether they truly are non-head-bobbing species. Given how abundant and easy-to-observe many species of gull are, there are opportunities for both amateur and professional ornithologists to collect useful information on the head-bobbing behav-

A

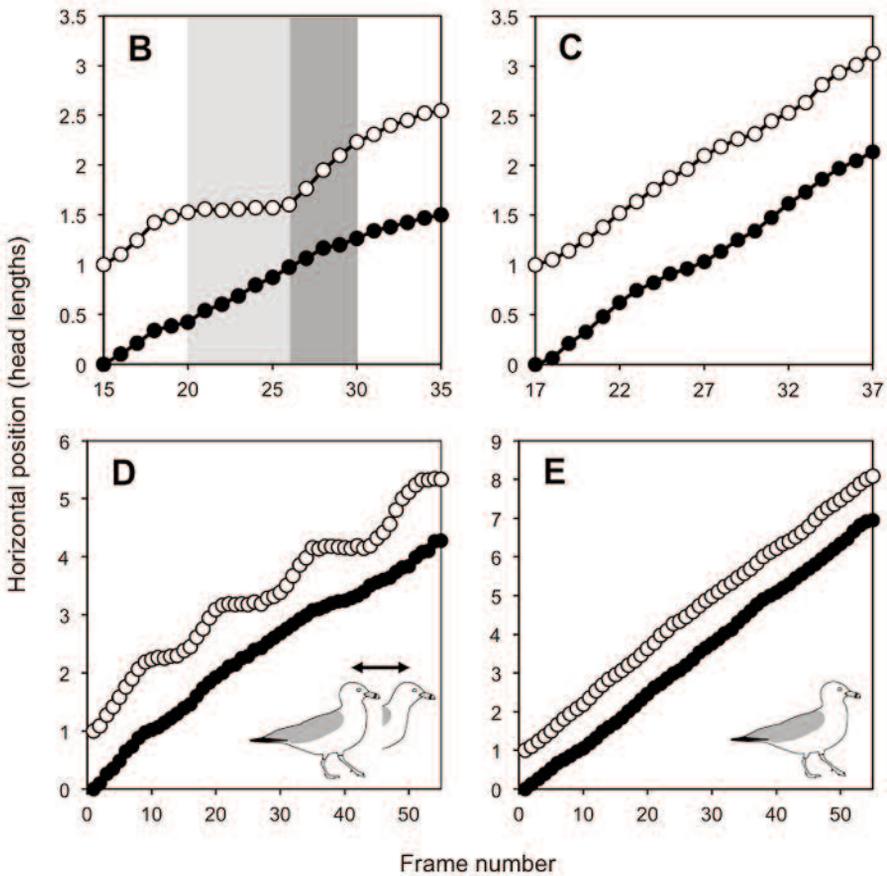
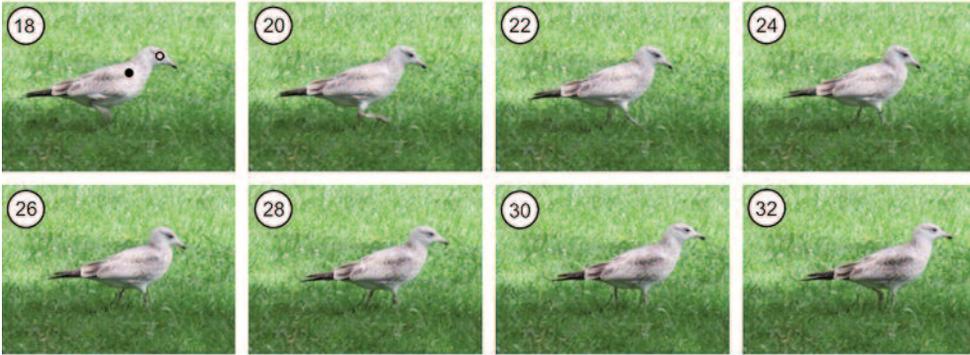


FIGURE 1. A. Series of 8 frames from a video (2 frames apart) showing 1 complete head-bob by a juvenile Ring-billed Gull (*Larus delawarensis*). In frame 18, the landmark positions on the head (eye, white circle) and body (white patch on shoulder, black circle) are shown. B. Plot of the horizontal position of the head (white) and body (black) against time (frame number) for the same series of frames shown in A. During the hold phase (light grey) the head is held stationary while the body continues to move forward; during the thrust phase (darker grey) the head is rapidly thrust forward at a speed greater than that of the forward-moving body. C. In a plot of the horizontal positions of the head and body in a gull walking without head-bobbing across the same number of frames, both the head and the body move forward together at a constant speed. D and E. Plots of horizontal head and body position over longer periods (55 frames) illustrate walking with (D) and without (E) head-bobbing. In D, 4 head-bob cycles with distinct hold and thrust phases can be seen. Photos: Tom Lisney.

TABLE 1. Number of immature and mature Ring-billed Gulls (*Larus delawarensis*) filmed head-bobbing and non-head-bobbing and included in the analysis.

Category	No. gulls filmed		
	Head-bobbing	Non-head-bobbing	Total
Immature gulls	3	4	7
Mature gulls	8	7	12*

*3 adult gulls were filmed displaying both behaviours.

four of these birds. Such information is essential if we are to determine the functional significance of head-bobbing in birds and solve the puzzle of why some birds head-bob while others do not.

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SUPPLEMENTARY MATERIAL:

VIDEO S1. Footage of an adult Ring-billed Gull head-bobbing while walking and foraging (Quicktime movie).

<https://youtu.be/6DCj2z06hRc>