Stationary underwater prey missed by reef herons, *Egretta gularis*: head position and light refraction at the moment of strike

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Summary. This paper attempts to verify the importance of spatial positioning of the eyes of reef herons *Egretta gularis schistacea*, when coping with light refraction at the air-water interface. The herons' striking of prey, while their approach angle was restricted, was observed. (a) The herons' capture success in the restricted situation was markedly lower than in the unrestricted situation. (b) The points of strike (STR) in unsuccessful strikes differed from those of successful strikes, and from those of the unrestricted situation. (c) The larger the difference between the observed and the predicted ratio of prey depth to apparent prey depth, the higher the probability of missing a prey. These results support predictions of a model presented elsewhere (Katzir and Intrator 1987) that a heron will attempt to reach spatial positions at which prey's real depth and apparent depth are linearly correlated.

Introduction

Light rays are refracted at the air/water interface, in accordance with Snell's law. This causes an underwater object to appear to an aerial observer somewhere along the line of refraction, i.e. higher than it actually is (Bergmann and Schaeffer 1956; Jenkins and White 1976; Lythgoe 1979; Fig. 1). Fish eating (piscivorous) birds, which locate underwater prey, and commence their capturing movements towards it while their eyes are above the water, may thus be faced with the problem of light refraction (Dill 1977; Katzir and Intrator 1987). To accurately strike at an underwater prey, such birds may need to perform certain corrections.

The ability to correct for light refraction in birds has been demonstrated to date only in the western reef heron *Egretta gularis schistacea* (Katzir and Intrator 1987). In the movement of the heron's head as it approaches and strikes submerged prey, there is a unique point characterized by a change of velocity and path angle. This point was termed 'point of strike' (STR). Although this point was spatially variable, a highly significant correlation was observed between prey depth (Y_p), and apparent prey depth (Y_{app}), measured for the heron's eye position at that instant. A typical correlation was $Y_p = 1.4 * Y_{app} - 1.7$. A model presented by these authors suggested that the heron will attempt to achieve this correlation, by choosing appropriately the point of strike, STR, and
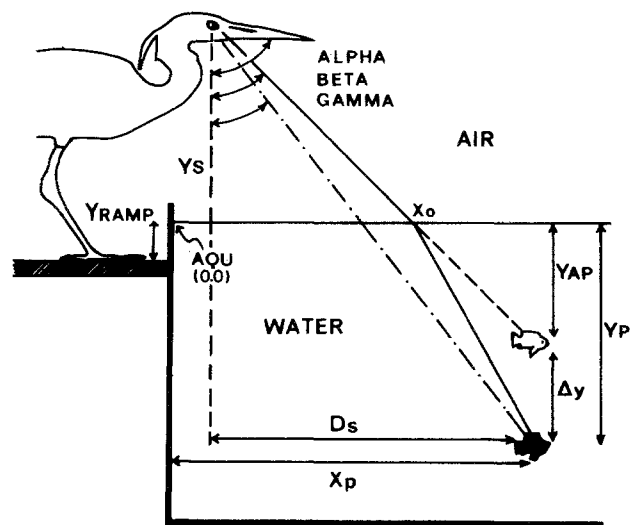

Fig. 1. Light refraction causes real prey (black fish) to appear in an imaginary (apparent) position along the refracted light ray (white fish). Parameters obtained from films: Y_p, real prey depth; Y_{app}, calculated apparent prey depth; X_p, prey distance from edge; D_s, horizontal distance between eye and prey at the moment of strike. *Alpha*, angle of eye-bill line; *Beta*, angle of sighting of apparent prey; *Gamma*, angle of eye to real prey

using this correlation it is able to correct for the air/water light refraction.

Two predictions of the model are: (a) Because the heron performs within a set of parameters, then forcing it to act outside its range (e.g. at very acute angles) should increase the frequency of misses. (b) The frequency of misses should be related to the difference between the expected and the observed ratio of Y_p to Y_{app}. To test these predictions, an experiment was conducted in which the heron could approach and view its prey at acute angles only.

Methods

The experiment was conducted with captive hand-reared western reef herons, *E. gularis schistacea* (Cramp 1978; Hancock and Kushlan 1984; Katzir and Intrator 1987). Birds were tested individually after they had become familiar with the experimental setup.

In part I of the experiment, two birds (RW/R & YR) were tested. Prey (a small dead *Tilapia* sp. <1.5 cm in length, or the caudal peduncle of a small *Tilapia* sp. 0.5–1.0 cm in length),

a

b

Fig. 2. a Setup of part I: 1 to 3 denote locations at which prey was presented; Hatched, plastic mesh. **b** Setup of part II of the experiment. 1, aquarium; 2, feeding rod; 3, prey; 4, mesh; 5, ramp; 6, hide and filming apparatus

impaled at the tip of a thin rod, was presented in a tank (200 × 50 × 50 cm) in an outdoors aviary. A concave plastic mesh was fitted above the tank. Prey was presented at any one of 3 positions (Fig. 2a), which differed in the angles at which they could be viewed. Prey was presented submerged (tank with water) or unsubmerged (tank without water). When presentation was with water, the mesh bottom was 3 cm under the surface. On each experimental day, up to 50 prey were given, and a record taken of success/failure and of latency to strike.

In part II of the experiment, one of the above birds was tested (YR). Prey was presented in an aquarium (75 × 50 × 30 cm), at predetermined positions under a concave plastic mesh (Fig. 2b). Prey was presented submerged or unsubmerged. When prey was presented submerged the mesh bottom was 2–3 cm above the water surface. After the heron had caught the prey, another was presented at a different position. In each test up to 26 prey were given. The heron's capturing movements were filmed and the films analysed (see Katzir and Intrator 1987). Experiments were conducted at noon, after the heron had been deprived for 24 h. That the heron could see the prey was verified in both parts of the experiment, by gentle swaying of the rod sideways occasionally and observing the movements of the heron's head. Statistical tests are based on Sokal and Rholf (1981) and Zar (1984).

Results and Discussion

The results of part I indicated that (a) Misses of submerged prey (34 out of 263) were significantly more frequent than of unsubmerged prey (0 out of 167; $\chi^2 = 21.9$; $P < 0.0001$; df = 1). Also, the proportion of misses increased from position 1 to 3 (Fig. 3). (b) Latencies to strike submerged prey were longer than for unsubmerged prey. Latencies increased from position 1 to position 3 (Fig. 4). No such trend was found for unsubmerged prey. Misses were thus related to the angle of sighting: the more acute the angle, the higher the probability of missing. The fact that unsubmerged prey was not missed indicated that the herons' difficulties stemmed from air/water light refraction at acute angles, more than merely a physical inability to reach the prey.

In part II of the experiment, the pattern of head and neck movements observed was similar to the 'pre-strike' and 'strike' of the unrestricted situation (Katzir and Intrator 1987). The point of sudden acceleration was therefore considered here also as a 'point of strike' (STR). The frequency of misses was significantly higher in the restricted situation (17 out of the 51) compared with the unrestricted situation (no misses in $n > 180$ tests; $\chi^2 = 59.9$; df = 1; $P < 0.0001$). Bill tips during misses slid just above or just below the prey. As no misses were observed when prey was presented unsubmerged, it is safe to assume that they were not caused by difficulty in reaching prey with the bill. Rather they were caused by difficulty in estimating the prey's real position at acute angles.
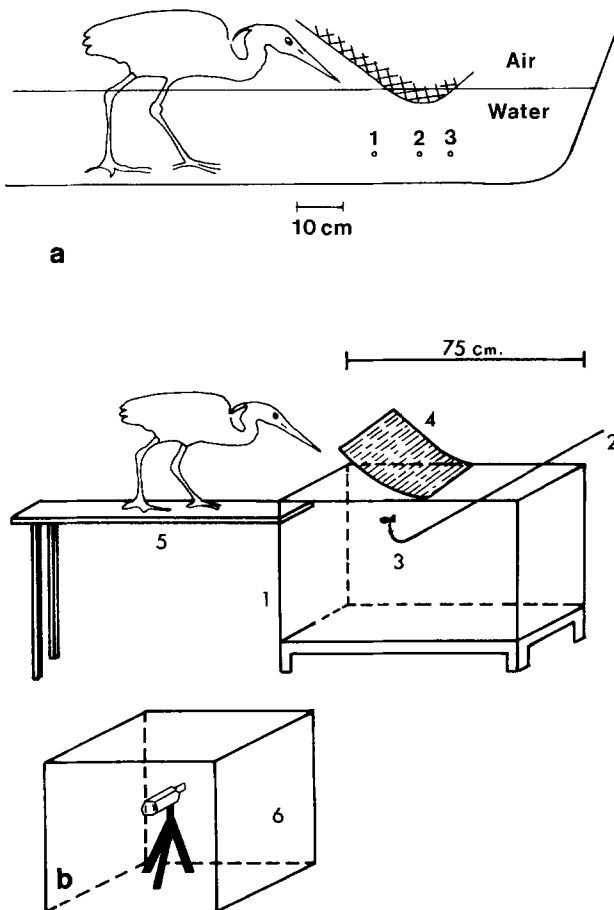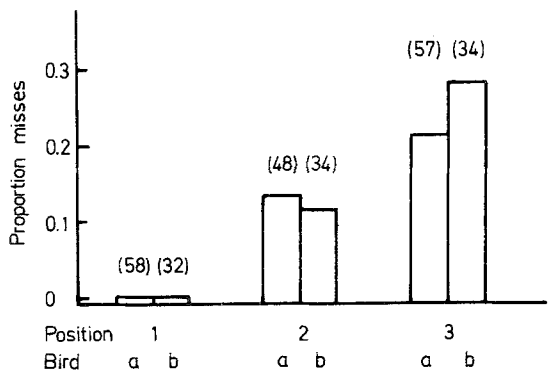
Fig. 3. Proportion of misses of submerged prey by two reef herons at 3 prey positions (see Fig. 2a). In brackets, total number of attempts
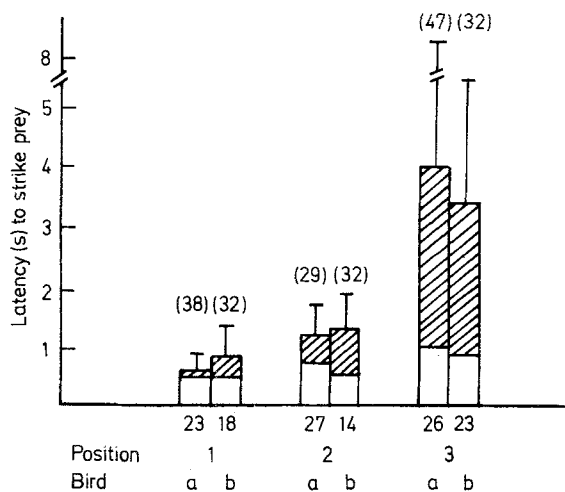

Fig. 4. Latency to strike ($\bar{X}\pm$s.d.) submerged prey (hatched) and unsubmerged prey (clear). In brackets – total number of attempts for submerged prey. Without brackets – total number of attempts for unsubmerged prey

Fig. 5. Relationship of prey depth (Y_p, cm) to apparent prey depth (Y_{ap}, cm) at the point of strike (STR), in a restricted situation. '\$', successful attempts (hits); solid squares, unsuccessful attempts (misses)

Fig. 6. Relationship of prey depth (Y_p, cm) to apparent prey depth (Y_{ap}, cm) at the point of strike (STR), in an unrestricted situation (from Katzir and Intrator 1987)

At the point of stike (STR) prey depth (Y_p) and apparent prey depth (Y_{app}) were significantly correlated within successful strikes and within unsuccessful strikes ($r=0.899$; $P<0.05$; $r=0.969$; $P<0.01$, respectively; Fig. 5). The lines' equations were $Y_p = 1.35*Y_{app}-3.77$ for successful and $Y_p = 1.13*Y_{app}-7.5$ for unsuccessful strikes. Comparably, in the unrestricted situation Y_p and Y_{app} were significantly correlated, with the line's equation $Y_p = 1.4*Y_{app}-1.7$ (Katzir and Intrator 1987; Fig. 6). Regression lines of successful strikes in the two situations not differ in their slopes ($t=0.92$, df$=165$; $P>0.05$, one tailed), but differed significantly in their elevation ($t=5.17$; df$=167$; $P<0.0001$; one tailed). The points of strike in unsuccessful strikes, when the heron was restricted, were above those of the successful strikes (Fig. 5). The difference was not significant ($t=1.56$ for slopes,
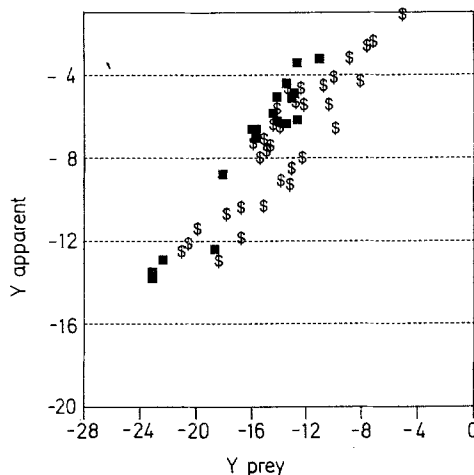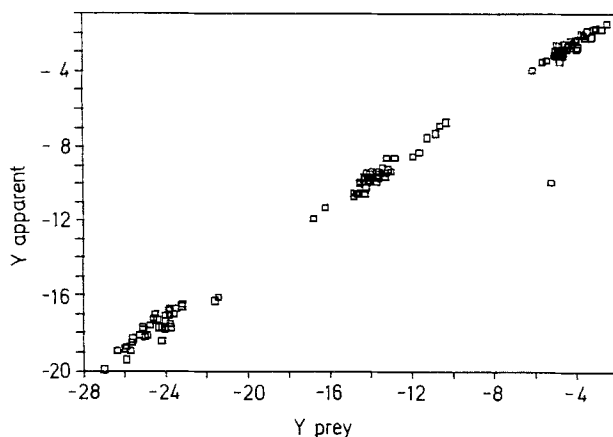
$t=1.09$ for elevations, df$=48$, $P>0.05$). However, for any given Y_p, the larger the difference between the observed Y_{app} and the predicted Y_{app}, the higher the probability of missing a prey (Fig. 7).

The marked increase in the frequency of misses, as the heron was forced away from the strike positions predicted for the unrestricted situation, supports the first prediction of the model. The increase in the probability of misses as the difference between the observed and the expected ratio of Y_p to Y_{app} increased, supports the second prediction of the experiments. The observation that a linear relationship was retained between Y_p and Y_{app}, when the heron struck at very acute angles, may indicate that it attempted to attain new constants.
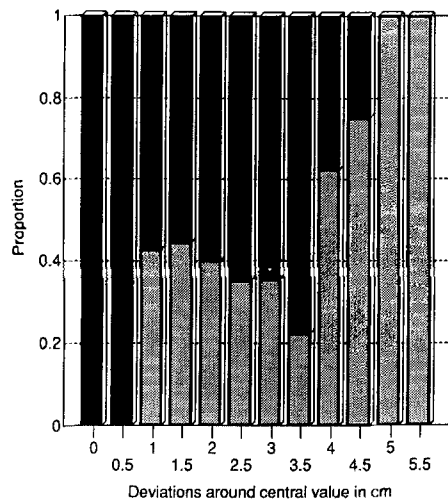
Fig. 7. Proportion of hits/misses of submerged prey, as a function of the deviation from the ratio of Y_p to Y_{app}, predicted by the model. □ Misses; ■ hits

In other words, it was learning to perform within the new limitations. This may explain the greater dispersion in the points of strike here, compared with the unrestricted situation.

There are no reports on the success rate of reef herons in the field. In the closely related (and probably congeneric) little egret, *E. garzetta*, frequency of successful strikes vary between 40% and 90% (Hafner et al. 1982; Ashkenazi 1983; Lotem and Katzir, unpublished). Misses in the field and in the experiments here probably stem from different causes. In the field factors such as water turbidity, prey species, prey movement and availability of shelter must be important. Here these factors were eliminated and we therefore conclude that misses

were caused by the herons' difficulties to correct for refraction at very acute angles.

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