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Capture of submerged prey by little egrets, *Egretta garzetta garzetta*: strike depth, strike angle and the problem of light refraction

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Abstract. How little egrets catch submerged prey was observed in the field. The proportion of successful strikes was measured relative to the angle and depth of the strike and the water level in the pond. Prey capture success was significantly related to strike angle, being highest at the most acute angles. Strike depth had no effect on capture success. Strikes were more successful in shallow streams than in full or partly drained ponds. Adult breeding birds were as successful as non-breeders and juveniles, but performed deeper strikes more often. There was also significant variation between individuals in capture success. Light refraction had no apparent effect on the egrets' capture success.

A predator is frequently faced with the task of estimating the position of a prey item accurately. This is especially apparent for predators such as praying mantids (Mittelstaedt 1957), chameleons (Harkness 1977), toads (Ewert 1980) or egrets and herons (Hancock & Kushlan 1984) which perform a single rapid strike or lunge at the prey. During the final movement there is no evidence for further motor corrections. Such animals must therefore estimate the prey's position, its movement and so forth, prior to the final strike. Owing to their nature, these predatory situations are valuable for the experimental testing of parameters used by the predator in estimating the prey's position and subsequent motor behaviour (e.g. Dill 1977; Harkness 1977).

Egrets and herons, as well as other fish-eating birds such as kingfishers and terns, have to detect prey and estimate its position across two optical media, namely air and water. Here, light reflection (Krebs & Partridge 1973), surface movement (Dunn 1973; Grubb 1977) and light refraction must be coped with. Refraction (Dill 1977; Katzir & Intrator 1987) results in a disparity between real and apparent (observed) prey position (Snell's law, cf. Jenkins & White 1976). The magnitude of the disparity is determined by the egret's eye position relative to the prey at the moment of strike. Reef herons, *Egretta garzetta schistacea*, presented with stationary prey, are capable of correcting for light refraction within a range of disparities (Katzir & Intrator 1987; Katzir et al. 1989). However, the majority of studies on the prey-catching and foraging behaviour of egrets and herons (cf. Kushlan 1976; Hafner et al. 1982; Hancock & Kushlan 1984; Draulans 1987) do not provide information about the optical problems. For example: is prey capture success related to the angle of sighting or striking at the prey? What are the effects of different light/surface conditions on the birds' hunting behaviour?

Our aim in this study was to examine the effect of strike angle and strike depth on the probability of prey capture of little egrets.

METHODS

We carried out the study during August and September 1986 at the Maagan Michael Nature Reserve, 60 km north of Tel Aviv. The reserve consists of fish ponds (average size: $70 \times 500 \times 1{\cdot}5$ m; width × length × depth, respectively) containing mainly carp, *Cyprinus carpio*, and tilapia, *Tilapia* spp. We observed little egrets between 0600–1100 and 1500–2000 hours, using 9×25 binoculars, at distances of 10–60 m. All observations were conducted by A.L. The choice of pond depended on the presence of active egrets. A focal bird (Altmann 1974) was chosen if its body axis was approximately perpendicular to the observer's line of sight. Information was recorded onto a portable tape recorder. An observation session for a focal bird

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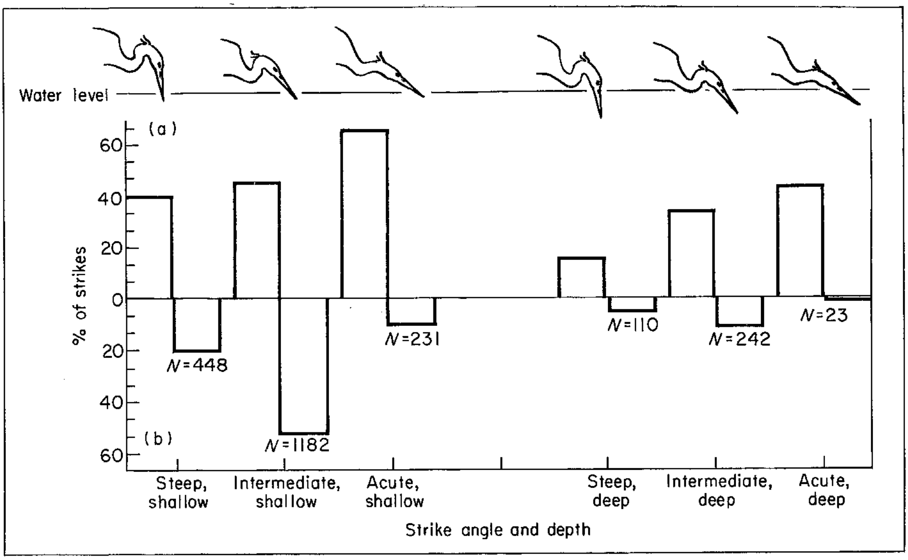

Figure 1. (a) Capture success (% of the number of strikes of the given combination of angle and depth); (b) frequency of use of the different strikes (% of the total observed). N = the number of strikes observed.

terminated when it moved out of sight, and ranged between 30 and 810 s. Observations were mostly conducted when the ponds contained many tens of egrets, and after an observation session on one focal bird, a different part of the flock was watched. For each bill strike by an egret at an underwater prey item we recorded strike angle, strike depth and outcome (success/failure). 'Strike angle' was the angle between the water surface and the eye–bill axis, as the bill entered the water. Angles were classified into three groups: steep, 70–90°; intermediate, 45–69°; and acute, less than 45° (Fig. 1). 'Strike depth' was the depth of penetration of the bill into the water: shallow, not more than half the bill was submerged; deep, at least half the bill but not deeper than the eye level was submerged. There were only eight deeper strikes, in which the head was submerged above the eye level, and these were excluded from the analysis. Bill length was taken as 82 mm (mean for both sexes combined; Cramp et al. 1977). 'Capture success' was the proportion of successful strikes, regardless of duration of foraging (see Draulans 1987 for a different definition). A successful strike was recorded when we saw a prey item in the egret's bill. After several hours of focal bird observations we were confident enough to estimate prey size. Thus in 237 of the 965 successful captures, estimated prey size (shorter or longer than half the bill length) is given.

Water turbidity in each pond was measured using a secchi disk at the pond's edge. Ponds were assigned to three categories ('conditions'): 'full', 'partly drained' and 'shallow streamlets'. The ponds are constructed so that the bottom slopes gradually from the sides to a central deep area. When full, the central area was ca 1·50 m deep, and the entire pond surface was covered with water. When partly drained, the central area was ca 0·5–1·0 m deep, and 50–75% of the bottom was exposed. Subsequently fish densities under these conditions were much higher. Shallow streamlets were less than 10 cm deep. Birds were classified as 'adult breeders' and 'others' based on morphology (Cramp et al. 1977). As non-breeding adults resemble juveniles, 'others' most probably included both classes. The statistical analysis is described below.

RESULTS AND DISCUSSION

We observed 131 focal birds during 9 h. We cannot be certain, but it is likely that any one bird was observed only once (see Methods), and we assume that the birds are distinguishable for the statistical analysis. Each bird was assigned an 'ID' number (1–131). We recorded 2244 prey capture attempts, of which 964 (43·0%) were successful. Secchi

Table I. Capture success at different strike combinations

Depth:	Shallow			Deep			
Angle:	Steep	Intermediate	Acute	Steep	Intermediate	Acute	Total
Adult breeders							
Number of strikes	196	498	98	93	202	19	1106
Successful strikes	81	236	63	16	63	8	467
% Success	41	47	64	17	31	42	42
Others							
Number of strikes	252	684	133	17	40	4	1130
Successful strikes	94	296	88	1	17	2	498
% Success	37	43	66	6	42	50	44
Total							
Number of strikes	448	1182	231	110	242	23	2236
Successful strikes	175	532	151	17	80	10	965
% Success	39	45	65	15	33	43	43

Table II. Frequency of strike combinations at different pond conditions

Depth:	Shallow			Deep					
Angle:	Steep	Intermediate	Acute	Steep	Intermediate	Acute	Total	Number of strikes	% Successful strikes
Full pond	178	331	38	10	44	3	604	262	43
Partly drained	225	632	115	100	198	20	1290	514	40
Shallow stream	45	219	78	—	—	—	342	189	55
Total	448	1182	231	110	242	23	2236	965	43

depths in the ponds where the egrets foraged ranged from 16 to 20 cm (mean = 18·6 cm). This may explain the scarcity ($N = 8$) of strikes deeper than 14 cm (i.e. deeper than eye level). We analysed 2236 strikes.

The distribution of strike combinations by angle and by depth, and the percentage of successful strikes are given in Fig. 1 and Table I: 83% of the strikes were shallow, and 17% deep; 25% of the strike angles were steep, 63·7% were intermediate and 11·3% were acute. The frequencies of strike combinations at different pond conditions are given in Table II.

We employed an ANOVA model with interactions. In the model, each combination of depth and angle, for which at least one attempt was made, was considered as an observation. Thus some birds contributed several observations (if they attempted several combinations of depth/angle) while others contributed only a single observation. There were 347 observations. Our model, with the proportion of success as the dependent variable, included five main effects and one interaction: strike angle, strike depth, class (i.e. adult breeders versus others), pond condition (i.e. water level) and the bird ID (i.e. bird identification) which is nested within pond condition*class. The interaction term was between depth and angle.

Not all the proportions of success were estimated based on the same sample size. We therefore used weighted ANOVA, where the weights were taken to be the sample sizes (i.e. the number of attempts on which the estimated proportions of success were based; SAS 1985). Thus, a proportion of success of 0·5 based on 40 attempts was given more weight than a proportion of 0·5 based on four attempts. The ANOVA model based on $N = 347$ yielded an $R^2 = 0·61$ (SAS 1985, Table III). As some of the sample sizes were small, we checked the normality of the data. Analysis of residuals showed their distribution to be symmetric, and the normal probability plot showed no extreme violation of the

Table III. ANOVA ($N=347$) of factors potentially affecting capture success

Source	*df*	SS	MS	*F*	PR>*F*	R^2
Model	131	79·170	0·60	2·52	0·0001	0·61
Error	215	51·550	0·24			
Corrected total	346	130·720				
Depth	1	0·274		1·14	0·2860	
Angle†	2	3·616		7·54	0·0007	
Depth*angle†	2	1·657		3·46	0·0330	
Class	1	0·024		0·10	0·7504	
Pond conditions†	2	1·816		3·79	0·0242	
Bird ID†	123	53·972		1·83	0·0001	

†$P<0·05$.

Table IV. Results of Tukey's Studentized range test for the probability of success (type I experiment $\alpha=0·05$)

Shallow*			Deep†		
Mean	*N*	Angle	Mean	*N*	Angle
0·5813	57	Acute[a]	0·4268	58	Intermediate[a]
0·4267	79	Steep[ab]	0·4077	13	Acute[a]
0·3658	106	Intermediate[bb]	0·2022	34	Steep[a]

Means with the same letter are not significantly different.
*Minimum significant difference = 0·1915.
†Minimum significant difference = 0·3352.

Table V. Number of fish larger or smaller than 4 cm, captured at different strike combinations

Depth:	Shallow			Deep		
Angle:	Steep	Intermediate	Acute	Steep	Intermediate	Acute
Fish <4 cm	19	63	32	5	29	1
Fish >4 cm	10	6	17	11	36	8

assumptions. We therefore felt that our analysis was statistically valid.

There was a significant angle effect, but no depth effect on capture success (Table III). Adult breeders and all other birds had similar capture success. There was a significant difference between individuals and pond condition also had an effect. A significant interaction was found between angle and depth.

Strike angles were further investigated using Tukey's Studentized range test (Kendall et al. 1983; SAS 1985). The test was performed for each depth separately, as the interaction between depth and angle was significant. For deep strikes there was no significant difference between strike angles. For shallow strikes, strike angles could be divided into two homogeneous groups: steep plus acute and intermediate plus steep (Table IV).

That strike depth had no significant effect on capture success may seem contrary to the data presented in Fig. 1. This may be the result of the difference between individual birds (bird ID in our

ANOVA model). When a simple two-way ANOVA model was used, with angle and depth as main effects, but ignoring the differences between individuals, depth did have a significant effect ($P = 0{\cdot}0022$). However, the proportion of variation explained by the model was low ($R^2 = 0{\cdot}17$). Adding possible differences between individual birds to our model increased the proportion of variation explained to $R^2 = 0{\cdot}6$, and may have obscured any depth effect.

Since pond condition had a significant effect, multiple comparisons (Tukey's multiple range test; SAS 1985) were conducted. The probability of success in shallow streamlets was higher (0·57) than in full ponds (0·40) or partly drained ponds (0·38), which were similar. Shallow streamlets probably provided better visibility for the egrets, as well as higher densities of smaller fish.

Adult breeders were as successful as all other birds (Tables I and III) but struck deeper significantly more often (28·4% versus 5·4%, respectively: $\chi^2 = 211{\cdot}7$, $df = 1$, $P < 0{\cdot}0001$). Deep strikes yielded in general relatively larger prey: 61% of 4 cm or more, versus 22% ($\chi^2 = 35{\cdot}7$, $df = 1$, $P < 0{\cdot}0001$; Table V). In contrast, different strike angles did not yield prey of different sizes ($\chi^2 = 4{\cdot}6$, $df = 2$, $P = 0{\cdot}1$; Table V). Prey size was not included as a main effect in our ANOVA model since it would have led to approximately 100 observations being treated as missing (owing to no information on prey size).

Numerous studies of fish-eating birds strongly suggest that adults and juveniles differ in their prey capture success (cf. Quinney & Smith 1980; Brandt 1984; Draulans 1987; Carl 1989). The difference between age groups in our present study may have been obscured as the class 'others' probably included non-breeding adults as well as juveniles. Adult breeders, however, did perform more of the deeper strikes which yielded on average larger fish. They were thus gaining more energy, for their own and their offspring's consumption.

It seems pertinent to compare our observations on little egrets with results obtained by film analysis for the related sub-species, reef herons, *E. garzetta gularis* (Hancock & Kushlan 1984) in captivity (Katzir & Intrator 1987; Katzir et al. 1989). Little egrets struck at fish at depths varying from 0 to 15 cm, and at angles varying from 30 to 90°. This is within the range of strike depths and angles of reef herons. Reef herons keep the line of sight to the prey at the beginning of a strike at a rather constant angle below the eye–bill line (Katzir & Intrator 1987). Strike paths then tend to curve downwards to the line of sight. If little herons behave in a similar manner, they must be confronted with problems of light refraction on the majority of their strikes. If refraction is not corrected for, we would expect a lower capture success at larger disparities, i.e. at acute angles and at deeper strikes. Our data suggest that the opposite may be the case: capture success increased with increased acuteness of strike angles, while strike depth had no apparent effect on success. Light refraction therefore appears to have little effect on little herons' capture success. The herons are probably able to correct for the disparity between real and apparent prey positions. This is in accordance with the finding that reef herons correct for light refraction over a wide range of sighting angles (Katzir & Intrator 1987; Katzir et al. 1989).

One reason why capture success is higher at more acute strike angles may lie in the prey's ability to detect the approaching predator. Fish are known to respond rapidly to avian predators detected above the surface (cf. Whoriskey & FitzGerald 1984; FitzGerald & van Havre 1985). For a fish, an aerial object close to the horizon will appear dimmer and smaller relative to a similar object overhead (Protasov 1968; Walls 1967). It may be that an egret approaching a fish at an acute angle is more difficult to detect.

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REFERENCES

Altmann, J. 1974. Observational study of behaviour. *Behaviour*, **49,** 227–264.

Brandt, C. A. 1984. Age and hunting success in the brown pelican: influence of skill and patch choice on foraging efficiency. *Oecologia (Berl.)*, **62,** 132–137.

Carl, R. A. 1989. Age-class variation in foraging techniques by brown pelicans. *Condor*, **89,** 525–533.

Cramp, S. T. (Ed.). 1977. *Handbook of the Birds of Europe, the Middle East and North Africa. Vol. 1.* Oxford: Oxford University Press.

Dill, L. M. 1977. Refraction and the spitting behaviour of the archerfish (*Toxotes chatareus*). *Behav. Ecol. Sociobiol.*, **2,** 169–184.

Draulans, D. 1987. The effect of prey density on foraging behaviour and success of adult and first year grey herons (*Ardea cinerea*). *J. Anim. Ecol.*, **56,** 479–493.

Dunn, E. 1973. Changes in fishing abilities of terns associated with wind speed and sea surface conditions. *Nature, Lond.*, **244,** 520–521.

Ewert, J. P. 1980. *Neuroethology*. Berlin: Springer Verlag.

FitzGerald, G. J. & van Havre, N. 1985. Flight, fright and shoaling in sticklebacks (Gasterosetidae). *Biol. Behav.*, **10,** 321–331.

Grubb, T. H. 1977. Weather dependent foraging in ospreys. *Auk*, **94,** 146–149.

Hafner, H., Boy, V. & Gory, G. 1982. Feeding methods, flock size and feeding success in little egrets, *Egretta garzetta* and squacco heron *Ardeola ralloides* in Camargue, southern France. *Ardea*, **70,** 45–54.

Harkness, L. 1977. Chameleons use accommodation to judge distance. *Nature, Lond.*, **267,** 346–349.

Hancock, J. & Kushlan, J. 1984. *The Herons Handbook*. London: Croom Helm.

Jenkins, F. A. & White, H. E. 1976. *Fundamentals of Optics*. 2nd edn. New York: McGraw Hill.

Katzir, G. & Intrator, N. 1987. Striking of underwater prey by reef herons, *Egretta gularis schistacea*. *J. comp. Physiol. A*, **160,** 517–523.

Katzir, G., Lotem, A. & Intrator, N. 1989. Stationary underwater prey missed by reef herons, *Egretta gularis*: head position and light refraction at the moment of strike. *J. comp. Physiol. A*, **165,** 573–576.

Kendall, M., Stuart, A. & Ord, J. K. 1983. *The Advanced Theory of Statistics. Vol. 3.* New York: Macmillan.

Krebs, J. R. & Partridge, B. 1973. The significance of head tilting in the great blue heron. *Nature, Lond.*, **245,** 533–535.

Kushlan, J. A. 1976. Feeding behavior of North American herons. *Auk*, **93,** 86–94.

Mittelstaedt, H. 1957. Prey capture in mantids. In: *Recent Advances in Invertebrate Physiology* (Ed. by B. T. Scheer), pp. 51–71. Oregon: University of Oregon Publications.

Protasov, V. R. 1968. *Vision and Near Orientation of Fish.* Jerusalem: Israel Program for Scientific Translations.

Quinney, T. E. & Smith, P. C. 1980. Comparative foraging behavior and efficiency of adult and juvenile blue herons. *Can. J. Zool.*, **58,** 1168–1173.

SAS. 1985. *User's Guide: Statistics.* Version 5. North Carolina: SAS Institute.

Walls, G. L. 1967. *The Vertebrate Eye and its Adaptive Radiation* (Facsimile of 1942 edition). New York: Hafner Publishing Company.

Whoriskey, F. G. & FitzGerald, G. J. 1984. The effects of bird predation on an estuarine stickleback (Pisces; Gasterosteidae) community. *Can. J. Zool.*, **63,** 301–307.