

## Prey detection by great cormorant (*Phalacrocorax carbo sinensis*) in clear and in turbid water

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### SUMMARY

The scattering and absorption of light by water molecules and by suspended and dissolved matter (turbidity) degrade image transmission and, thus, underwater perception. We tested the effects on visual detection of prey size and distance (affecting apparent prey size) and of low-level water turbidity in hand-reared great cormorants (*Phalacrocorax carbo sinensis*) diving for natural prey (fish) in a forced-choice situation. The cormorants' detection of underwater prey relied on vision. The minimal tested subtending visual angle of the prey at detection ranged between ~34.2' (prey size constant; distance varied) and 9.5' (distance constant; prey size varied). For all tested distances (0.8–3.1 m) the mean detection success was significantly higher than the chance level. The probability of a correct choice declined significantly with increased distance, with Detection success =  $-0.034D + 1.021$  (where  $D$  is distance,  $r^2 = 0.5$ ,  $N = 70$ ,  $P < 0.001$ ). The combined effect of turbidity and distance on the probability of detection success was significant, with both variables having a negative effect: Detection success =  $-0.286D - 0.224Tu + 1.691$  (where  $Tu$  is turbidity,  $r^2 = 0.68$ ,  $N = 144$ ,  $P < 0.001$ ). At prey detection threshold, the relationship between distance and turbidity was:  $D = 3.79e^{-4.55Tu}$ . It is concluded that (i) the subtending angle of natural prey at detection was lower than that of resolution of square-wave, high-contrast grating and (ii) turbidity, at levels significantly lower than commonly used in behavioural experiments, had a pronounced effect on visually mediated behaviour patterns.

Key words: cormorant, aquatic vision, underwater visual resolution, water turbidity, underwater prey detection.

### INTRODUCTION

The underwater photic environment is markedly different from that of air and visual functions may differ greatly between these media (Baddeley, 1968; Aksnes and Giske, 1993; Aksnes and Utne, 1997; Sandstrom, 1999; Utne-Palm, 2002; Gislen et al., 2003; Gislen and Gislen, 2004). This holds true for visually mediated interactions between species such as predation (Radke and Gaupisch, 2005; Van de Meutter et al., 2005) and within species such as courtship (Endler, 1987; Endler, 1991; Seehausen et al., 1997). At the air–water interface light is refracted and reflected with light intensity underwater declining and its chromatic composition shifting (Lythgoe, 1979; Loew and McFarland, 1990; Loew, 1999). Light interacting with water molecules is scattered and absorbed, leading to a marked degradation in image transmission (Lythgoe, 1979). Consequently, even in clear water, the range at which targets can be visually detected is reduced by 3 orders of magnitude compared with that in air and a target will be viewed as relatively light against a darker background space light (Duntley, 1974; Loew, 1999).

Natural water bodies contain suspended and dissolved matter, both organic and inorganic, which further scatters and absorbs light, alters its chromatic characteristics and results in apparent turbidity. In the light path between an object and an observer in turbid water, scatter results in a decrease in the light intensity reaching the eye while ambient light intensity is increased. Consequently, turbidity adds to the deterioration in the quality of an observed image through the reduction in the intensity of light reflected off objects and the consequent loss of contrast and spatial information (Gazey, 1970;

Duntley, 1974; Vogel and Beauchamp, 1999). With increased concentration of suspended matter the light intensity reflected off an object will equal that from the water itself, thus reducing contrast to the point of the object being indiscernible (Gazey, 1970; Duntley, 1974; Muntz and Lythgoe, 1974).

Visual range, i.e. the maximal distance at which an animal is capable of detecting a target, is commonly used as a measure of the animal's visual capacity under given photic conditions. Visual range is determined by target features such as size and motion, by the animal's optical and visual systems, by the physical properties of a particular stimulus situation such as the medium's absorption and scatter, and by the behaviour of the observer such as its direction of gaze. An indicator frequently used for an animal's visual range is its reactive distance – the distance at which the animal performs a specified behaviour pattern indicative of its detecting a given target (Aksnes and Giske, 1997; Utne-Palm, 1999; Vogel and Beauchamp, 1999; Mazur and Beauchamp, 2003). The biological implications of visual range are broad, including females' capacity to detect a courting male or the capacity of predators and prey to detect each other.

Studies of underwater vision in vertebrates have mostly focused on predation by fishes on invertebrate prey (e.g. Utne-Palm, 1999; Van de Meutter et al., 2005) while relatively few studies have tested the reactive distance of piscivorous fishes to fish prey (e.g. Abrahams and Kattenfeld, 1997; Radke and Gaupisch, 2005) or to other visual stimuli. Moreover, the effects of turbidity, an all-important determinant of underwater vision (Gazey, 1970; Lythgoe, 1979;

Aksnes and Giske, 1993; Vogel and Beauchamp, 1999; Radke and Gaupisch, 2005), have been surprisingly little studied within this general framework.

In the two-spotted goby, *Gobioculus flavescens*, both decreased illumination and increased turbidity have a negative effect on reactive distance to copepod prey, with the longest reaction distances observed at intermediate turbidity levels (Utne, 1997). Prey contrast and mobility result in an increase in reactive distance, with both being independent of turbidity levels. For high-contrast, mobile prey the longest reactive distance was also observed at intermediate turbidity levels (Utne-Palm, 1999). In comparison, the reactive distance of the piscivorous lake trout (*Salvelinus namaycush*) to salmonid prey increased rapidly with increased light levels and then levelled off and declined as a decaying power function of turbidity. For the range of prey size tested, reactive distance was not affected by prey size (Vogel and Beauchamp, 1999).

Birds depend heavily on vision for their activities (Pough et al., 1995; Davies and Green, 1994; Hodos, 1994; Lee, 1993; Frost et al., 1994; Ghim and Hodos, 2006) and it is expected that species that pursue their fish prey underwater will also rely on vision underwater. This is supported by the observations that pursuit divers (e.g. penguins, *Spheniscus* sp.; mergansers, *Mergus* sp.; cormorants, *Phalacrocorax* sp.) perform rapid and precise visuo-motor tasks during prey capture, which implies retention of a sharp enough retinal image underwater (Katzir and Howland, 2003; Strod et al., 2004). The cornea is the principal refracting component of the eye in the air, yet upon submergence it is rendered virtually ineffective because its refractive index is similar to that of water. In amphibious species such as mergansers and cormorants the lens, now bearing the full refractive function (Levy and Sivak, 1980), is highly pliable and upon submergence undergoes a change in form that may well compensate for corneal loss of power (Hess, 1909; Walls, 1967; Levy and Sivak, 1980; Glasser and Howland, 1996; Kroger and Katzir, 2007). Consequently these species retain a state of emmetropia both in air and underwater (Katzir and Howland, 2003).

Visual detection and resolution have been little studied in amphibious avian species (Sivak et al., 1987). In great cormorants, visual resolution for high-contrast stimuli (square-wave gratings) in clear water was lower than in air (Strod, 2002; Strod et al., 2004). Cormorants' underwater resolution remained well within the mid to low range of other avian species in air and within the higher range reported for fishes and for diving mammals (Muntz, 1990; Guthrie and Muntz, 1993; Strod et al., 2004). Water turbidity was found to have a negative, linear effect on the cormorants' grating resolution at a given distance of testing. Most important, this effect was apparent at low turbidity levels (ca. 1 NTU; nephelometric turbidity units). Processes that underlie resolution differ, however, from those that underlie detection. Consequently, the capacity to visually detect prey (a fish) cannot be derived immediately from grating resolution. An example of this is that a target may be detected at resolution levels well below those required for determining their details.

We here determined visual detection of natural prey (fish) underwater in great cormorants. Because certain waterbirds employ mechano- and chemoreception to detect prey [e.g. Piersma et al. (Piersma et al., 1998); Tubinares – Procelariiformes], experiment I aimed at determining the role of vision in prey detection. Experiments II and III aimed at determining the effects on detection of prey size and distance, and thus of apparent prey size. In experiment II, apparent prey size was altered by keeping prey size constant while varying the viewing distance, whereas in experiment III, prey size was changed while viewing distance was kept constant. In both

experiments the subtending angle of the prey at the point of viewing was varied but in experiment III, although not in experiment II, this was accompanied by a change in the passage length of image-forming light. The effect of this passage length in air is mostly minimal yet underwater it has important consequences (see Lythgoe, 1979). Finally, in experiment IV we tested for the combined effect on prey detection of low-level turbidity and of prey distance.

## MATERIALS AND METHODS

### The birds

The cormorants (*Phalacrocorax carbo sinensis* Blumenbach 1798; 1 female, 5 males) were collected as nestlings from the Safari Park at Ramat-Gan, hand-reared individually. They were fed on fresh/live and defrosted fish (St Peter's fish, *Tilapia* sp., and carp, *Cyprinus carpio*). At the time of testing, three individuals were between 1 and 3 years old and three individuals were 4–5 years old. The birds were collected and maintained under license from the Israel Nature and National Parks Protection Authority and all experiments were performed under permission from the ethics committees of the Haifa University and of the Technion – Israel Institute of Technology. In experiment III, one cormorant showed no detection and was excluded from the analysis.

### The experimental setup

The experimental system comprised a water pool (5 m×8 m, 1.5 m in depth), divided into two sections by a concrete wall and covered by an opaque cover and an adjacent aviary (6 m in length, 5.4 m in width, 6 m in height). The setup for the tests (see Fig. 1) comprised a pre-test pool (1) and a test pool (2), inter-connected by an underwater trapdoor (3) with circulating freshwater. A Y-maze tunnel (4) of rigid mesh (50 cm×50 cm in cross-section) was placed on the pool's floor (depth 1–1.5 m), with its entrance at the trapdoor and with each Y-arm opening to one stimulus box (5). The maximal distance from the Y-junction to the prey boxes, as determined by the length of the experimental pool, was 3.1 m. In each trial, a bird would swim into the Y-maze, make a choice while in motion towards the Y-junction, continue through the chosen maze arm to the stimulus

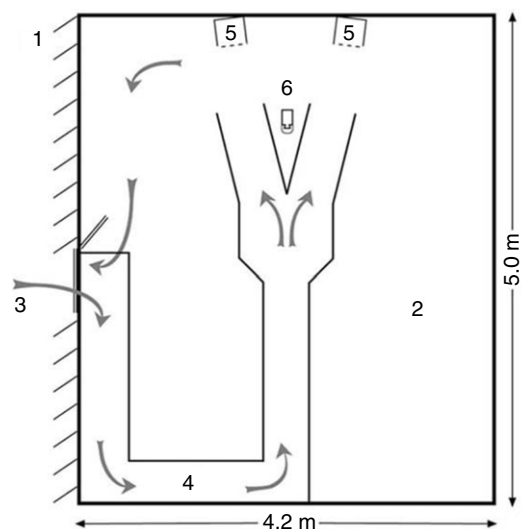


Fig. 1. Experimental setup. (1) Pre-test pool, (2) test pool, (3) underwater trapdoor, (4) Y-maze tunnel, (5) stimulus boxes, (6) video camera. Arrows depict the swimming paths of the cormorants. The position of the Y-junction could be moved towards or away from the targets.

Table 1. The experimental situations for prey detection

	Experiment I: role of vision	Experiment II: apparent prey size (varying fish distance)	Experiment III: apparent prey size (varying fish size)	Experiment IV: turbidity + distance
Prey box front	Opaque or transparent	Transparent	Transparent	Transparent
Y-junction distance (m)	1.4	0.8–3.1	3.1	0.8–2.8
Prey length (cm)	12	9	9–3	9
Prey height (cm)	5.11	3.75	3.75–1.04	3.75
Turbidity (NTU)	<0.5	<0.5	<0.5	0.3–4.5
Prey condition	Dead/alive	Dead	Dead	Dead
Critical value	0.75	0.75	0.75	0.77
No. of trials per bird	18	18	18	9
No. of individuals ( <i>N</i> )	6	6	5	5

Unless otherwise stated, fish (*Tilapia* species) body length was 9 cm.

box and return underwater to the pre-test pool. The stimulus boxes (32 cm×32 cm×25 cm depth) were of opaque meshed plastic with a transparent Perspex front pane (32 cm×32 cm) that could be moved up and down.

In experiment I, live fish were held in a semi-transparent, shallow mesh basket behind the front pane, which restricted the fish so that its body axis was parallel to the pane and at its centre. In experiments II, III and IV the positive stimuli were dead fish, impaled on the tip of a transparent, flexible plastic rod. Fish were separated into the required size groups and their length (between 3 and 9 cm) was finely set by cutting of the caudal peduncle.

#### Procedures

Training and testing procedures are provided in detail in Strod et al. (Strod et al., 2004) and in Table 1. On each test day nine trials for each tested individual were run. The order of presentation was pseudo-random (Zar, 1984) with the positive stimulus (fish) presented at the distal end of the respective arm of the Y-maze (Fig. 1). A restriction of no more than two consecutive presentations of a stimulus on any given side was imposed.

In experiment I, the front pane of the prey box was of visually opaque thin black fabric stretched on a Perspex frame. The prey was a live or dead fish (carp, *Cyprinus carpio*, or *Tilapia*), 12 cm in body length. In the control tests, the front doors were of transparent Perspex. The distance between the Y-junction and the prey boxes was 1.4 m, and the water was kept at maximal clarity (turbidity level less than 0.5 NTU).

In experiment II, the prey presented was a dead fish 9 cm in length and the water was kept at maximal clarity (turbidity level ca. 0.5 NTU). For each distance tested (i.e. between 0.8 and 3.1 m), between 1 and 3 days were required to reach the significant level of correct choice. For each bird, the results presented are those of the last 2 test days (i.e. final 18 trials). In experiment III, dead fish were presented at a distance of 3.1 m from the Y-junction. Based on their total length, the fish were assigned into groups of between 9 and 3 cm at 1 cm increments. In experiment IV, the positive stimuli were dead fish 9 cm in length. Water turbidity levels were experimentally controlled between 0.3 and 4.5 NTU, and distance to the target was from 0.8 to 2.8 m.

Fish total length was measured to the nearest 0.1 cm using calipers. The relationship of total length (*x*) to maximal body height (*y*) followed the equation:  $y=0.453x-0.323$ . The height of the stimulus fish was taken as indicative of visual resolution, providing the minimal dimension presented to the bird.

To determine the possible effect of the prey boxes, two experiments were run with prey held in transparent Perspex cylinders, radius 15 cm.

#### Illumination and turbidity

Tests were conducted under natural, diffuse, high-level illumination. Down-welling underwater illumination was measured at the Y-junction using a Li-Cor L-189 photometer (Lincoln, NE, USA) with a quantum sensor directed upwards and providing readings in  $\mu\text{Ein m}^{-2} \text{s}^{-1}$  units. Because the spectral sensitivity of the cormorants is not fully known (Hart, 2001), these readings were converted to human photopic lux units, based on the manufacturer's conversion table. The illumination levels in the tests ranged between 0.77 and 2.20 klx, well above the levels known to affect visual resolution in other birds (Hodos et al., 1976; Rounsley and McFadden, 2005; Ghim and Hodos, 2006). The level of water turbidity was controlled by suspending a measured amount of fine-grained soil in a double-layered fabric bag in the re-circulating water current of the experimental pool, 20 h prior to each trial. Water turbidity was measured daily, before, during and after the tests. Measurements were made by a portable turbidimeter (Hach 2100P, Loveland, CO, USA) having a range of 0–10 NTU and a resolution of 0.1 NTU. The contrast of fish to the background was  $0.46\pm 0.06$  (mean  $\pm$  s.e.m.), calculated as  $C=(I_F-I_B)/(I_F+I_B)$  where *I* is illuminance, *B* is background and *F* is fish.  $I_F$  and  $I_B$  were measured from underwater digitized photographs (Sony CCD-TR440E video camera, Japan), using Adobe Photoshop 5.0 software.

#### Analysis

The proportion of trials in which the positive stimulus side (i.e. the fish side) was chosen was taken as a measure of prey detection. Based on binomial distribution (Zar, 1984), the critical proportion (critical value) for significant detection was set at 0.75 for experiments with 18 trials, and at 0.77 for experiments with nine trials. If the proportion of correct choices exceeded these respective critical values it was taken as implying significant prey detection. These values are comparable to critical values commonly used in behavioural tests of visual detection (Schusterman and Balliet, 1970; Reymond, 1985; Hodos, 1994; Ghim and Hodos, 2006). The results for prey detection in clear water (experiments I, II and III) are from the first 2 consecutive days (i.e. 18 trials) during which a cormorant reached the criterion level (i.e. the critical value 0.75 of correct choices). If the bird failed to reach the criterion level, the results of the final 2 days of the experiment (i.e. days 4 and 5) were used in the analysis. The results presented for prey detection in turbid water (experiment IV) are for the single test day (9 trials). The limit of detection for each of the tested distances was determined from the intersect of the line depicting the critical value with the line connecting the last data point above it, and the first point below it.

Video analysis had shown (Strod et al., 2004) that when approaching the target underwater there was a distinct point at which

the cormorants most probably made their decision as to which target to choose (i.e. their 'reactive distance'). This was typified by a sharp turning of the head towards the target in the otherwise straight path. This point was  $67 \pm 3$  cm before the Y-junction. We used this value in our calculation of subtending angles at the point of detection. This value was not applied to the situation of turbid water because the point of head turning could not be observed.

## RESULTS AND DISCUSSION

### Experiment I: the role of vision in the detection of natural prey

When vision (but not chemo- or mechanoreception) was obstructed, the cormorants' choice of the prey box and the no-prey box did not differ ( $P > 0.05$ , Fig. 2), indicating no prey detection. In the control tests, when the prey was presented behind a transparent partition, the choice of prey side was significantly higher than that of the non-prey side ( $P < 0.05$ , Fig. 2), indicating significant detection. Furthermore, on the first three tests of the experiment there seemed to be a clear trend of improvement of choice of prey side, while without visual information no such trend was observed over the 5 consecutive test days (Fig. 2). Thus, for great cormorants, visual information is critical for the detection of live prey underwater. This supports the observation that while floating on a pool containing fish, cormorants seem to be unaware of the presence of fish and will commence underwater pursuits only after having submerged their head (T.S., unpublished observation).

While birds are predominately diurnal and highly dependent on vision, the use of mechanoreception and chemoreception is not uncommon. It has been demonstrated that waders (Piersma et al., 1998; Elner et al., 2005), wood storks (*Mycteria americana*) and Eurasian spoonbills (*Platalea leucordia*; G.K., unpublished data) use mechanoreception to detect prey in sand, mud or water. Olfaction is used by petrels and other Procellariiformes for prey detection as well as for locating their burrows, and in pigeons (*Columba livia*) it is used in close range for homing (Papi, 1990). The above examples are all of foraging situations in which the eyes are kept above the water, and vision is impaired by turbidity (ducks, spoonbills), substrate opaqueness (sand in plovers, e.g. *Charadrius*) or low light levels (e.g. nocturnal activities in Procellariiformes), while examples of chemoreception are for airborne volatiles.

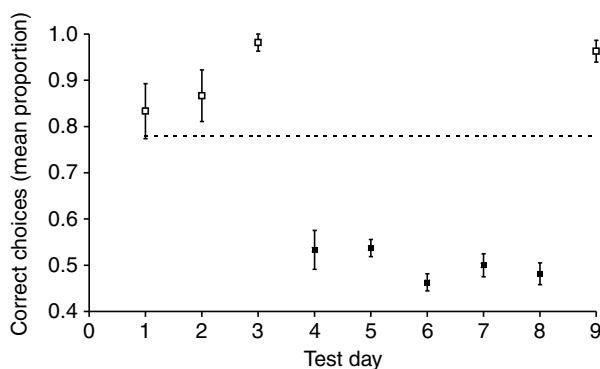


Fig. 2. Choice of prey as a function of visual occlusion (experiment I). Each data point is the proportion (mean  $\pm$  s.e.m.;  $N=6$  birds; 9 trials per bird per day over 2 days) of choice of prey side ('correct choice'). The prey (live or a dead fish, 12–15 cm in length) was presented behind a transparent Perspex door (open squares) on days 1, 2, 3 and 9, or behind a visually opaque fabric door (solid squares) on days 4 to 8. Targets were 1.4 m from the Y-junction. Broken line indicates the critical value for significant choice (0.78).

However, despite their potential advantage, there are no current indications of the use of these modalities in the underwater pursuits of diving birds.

### Experiment II: the effect on detection of apparent prey size (a)

In this experiment, apparent prey size was altered by keeping prey size constant while varying the viewing distance. The results show that prey detection was significant ( $P < 0.05$ ) to a distance of 2.8 m for all six cormorants, while at 3.1 m it was significant in five of the birds (Fig. 3). The bird that failed at 3.1 m had achieved the highest visual resolution score when previously tested on square-wave gratings (Strod et al., 2004). As its failure here seemed not to stem from perceptual incapacity, it was excluded from the analysis of the 3.1 m distance.

The smallest subtending angle on which the cormorants were tested in experiment II was  $41.6'$ , and when corrected for the 'point of decision' (head flip at 3.77 m; prey height 3.75 cm) the calculated subtending angle was  $34.2'$  (Fig. 3). At all distances tested the mean detection was significantly higher than chance level. However, the probability of correct choices declined significantly with increased distance, with Detection success =  $-0.034D + 1.021$  (where  $D$  is the detection distance in m,  $r^2 = 0.5$ ,  $N = 70$ ,  $P < 0.001$ ). Also, an increase in variance was observed with increased distance. This may be the result of an increase in perceptual difficulty or of an increased physical difficulty in performing the experimental task in the setup (i.e. the short distance of straight path before the Y-junction, Fig. 1). Similarly, a significant decline in visual resolution as a function of distance was reported for great cormorants tested on high-contrast, square-wave gratings, under mid to low ambient illumination levels and turbidity levels of ca. 1 NTU (White et al., 2007), in contrast to the results of Strod et al. (Strod et al., 2004).

### Experiment III: the effect on detection of apparent prey size (b)

In this experiment, apparent prey size was altered by varying prey size while keeping the viewing distance constant. The results of this experiment show that all prey sizes (i.e. 9 to 3 cm in length) were significantly ( $P < 0.05$ ) detected by four of the cormorants (Fig. 4) while one individual failed to detect the smallest sized fish. Thus,

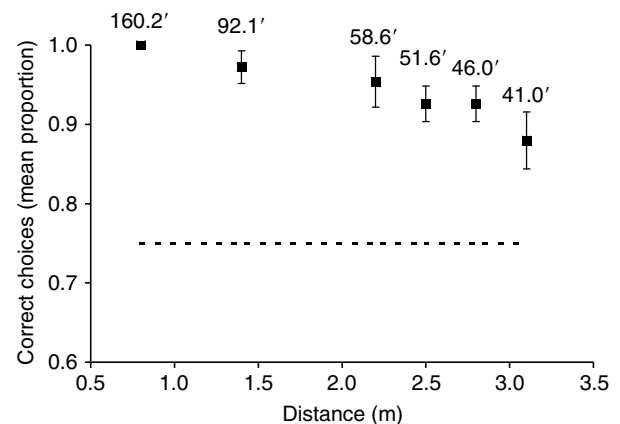


Fig. 3. Choice of prey as a function of prey distance (experiment II). Each data point represents the overall mean proportion of choices for the prey side (mean of means  $\pm$  s.e.m.;  $N=6$  birds; 9 trials per bird per day over 2 test days). Values above data points are corresponding subtending angles of the prey's height. Broken line indicates the critical value for significant choice of the prey side (0.75). Prey (dead fish) were 9 cm in length at all distances except 2.8 m, at which they were 10 cm in length.

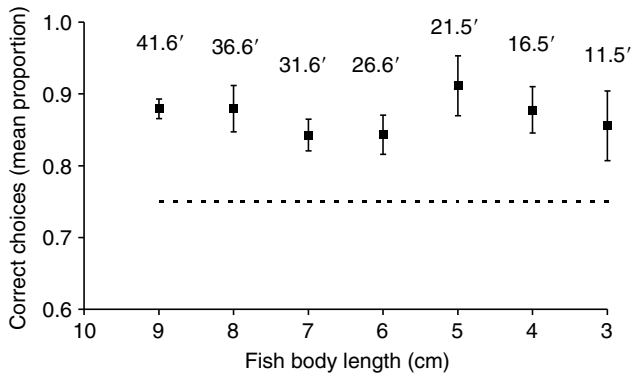


Fig. 4. Choice of prey as a function of prey size (experiment III). Each data point represents the mean individual proportion of choices for the prey side (mean of means  $\pm$  s.e.m.; 9 trials per bird per day; 2 test days; target distance to Y-junction 3.1 m). For a prey length of 5 cm, the results for three birds are for nine trials only. Broken line indicates critical value for significant choice of the prey side (0.75).

the cormorants could detect a 3 cm long (i.e. 1.03 cm in height) fish at a distance of 3.1 m. This provides a minimal subtending angle at detection of 11.5'. As the use of fish smaller than 3 cm in length was technically not possible, and correcting for added distance at the point of head flip, the minimal subtending angle at detection was  $\leq 9.45'$  (3.17 cycles per degree). It is clear that in this experiment the cormorants had not yet reached their detection limit as the prey was large enough and the visual distance in the water short enough to allow prey detection.

Underwater visual resolution for high-contrast, square-wave gratings determined for these same cormorants under high natural (sunlight) illumination was *ca.* 6.3' (Strod et al., 2004). This is a smaller subtending angle than that achieved here for the single target (prey fish). Comparably, White et al. (White et al., 2007) provide a resolution value of 11.8' for great cormorants tested on high-contrast square-wave gratings, under artificial ambient illumination of 1.4 lx and turbidity levels of  $\sim 1$  NTU. [Note that in figure 4 of White et al. (White et al., 2007) the cormorants resolved a *ca.* 4 mm grating at a distance of 2 m, which corresponds to a subtending angle of *ca.* 6'.]

A comparison between the detection of a real prey and the resolution of square-wave gratings is not applicable. This is because it is not possible to determine the minimal angular resolution, which is the distance between two points that can just be visually discerned, from a single object. The differences in target dimension (length, height) will result in the birds being presented with a range of spatial frequencies, and increasing the distance (experiment II) will decrease the contrast while raising the spatial frequency spectrum. Also, a single small object contains quite low spatial frequencies, making it possible to detect it without resolving it. Moreover, differences between the situations are also expected because (i) in the experiments above the cormorants had not reached their maximal capacity of detection and (ii) the contrast of the prey to the background in the present experiments was considerably lower than that for the gratings used by Strod et al. (Strod et al., 2004).

#### Experiment IV: the effects on prey detection of low-level water turbidity and prey distance

Underwater visibility is known to decrease with an increasing concentration of suspended material (Gazey, 1970; Duntley,

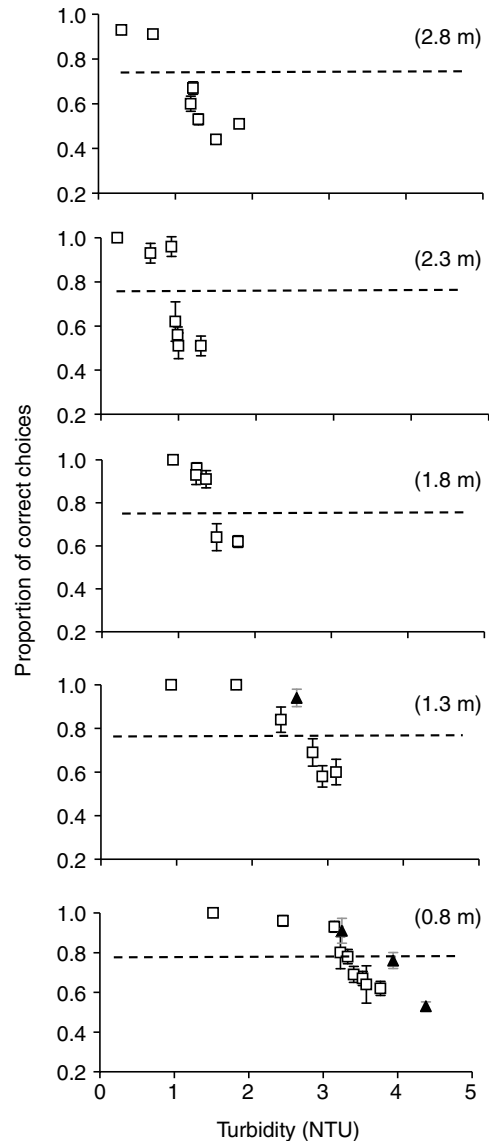


Fig. 5. Choice of prey as a function of water turbidity and distance (experiment IV). Each data point is the individual proportion of choices (mean  $\pm$  s.e.m.; 9 trials per bird per day;  $N=5$  birds) of choosing the prey side. Target distance to Y-junction is given in parentheses; solid triangles, controls (prey in transparent cylindrical boxes). Prey in all tests were *Tilapia* species, length 9 cm. Broken line indicates critical value for significant choice (0.77).

1974; Abrahams and Kattenfeld, 1997; Horppila et al., 2004), especially under direct light (Jagger and Muntz, 1993). In experiment IV, a rapid decrease in prey detection with increased turbidity for each tested distance was observed (Fig. 5). The effect of turbidity on detection seems to be not linear but rather a step-wise function. The combined effect of turbidity and distance on the probability of detection success was significant, with both variables having a negative effect: Detection success =  $-0.286D - 0.224Tu + 1.691$  (where  $Tu$  is turbidity in NTU,  $r^2=0.68$ ,  $N=144$ ,  $P<0.001$ ). The maximal turbidity at which a significant detection was retained for each distance was determined by interpolation. Plotting the cut-off values for all distances against turbidity yielded an exponential decrease in detection distance:  $D=3.79e^{-4.55Tu}$  (Fig. 6).

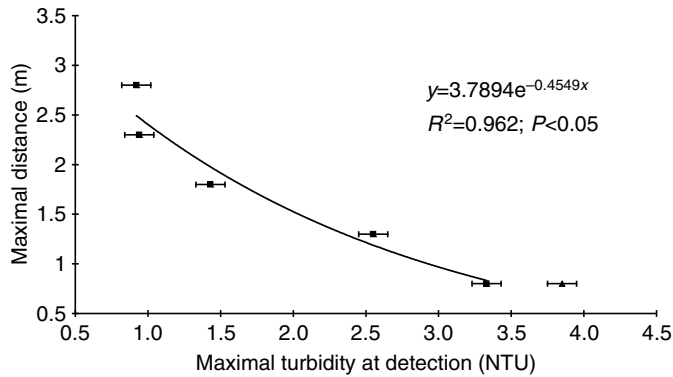


Fig. 6. Maximal distance of prey detection as a function of water turbidity. The results are the mean cut-off points ( $\pm$ s.e.m.;  $N=5$ ) from Fig. 5. Solid triangle, control test (no prey in boxes).

The effects of turbidity levels lower than 5 NTU on underwater visual capacities have been little studied. However, the results here clearly indicate that at levels lower than 1 NTU the cormorants had already lost more than 25% of their potential detection distance, and at 3.3 NTU a 74% decrease would be suffered. Levels of between 0 and 1 NTU are mostly regarded as 'clear water' and behavioural tests in which turbidity levels are >5 NTU or even an order of magnitude higher are common (but see Vogel and Beauchamp, 1999). This calls for greater caution with regard to turbidity levels in future experimental procedures that are biologically meaningful. The decline observed here was steeper than that found for fish (~82% at 5 NTU) (Miner and Stein, 1996). When the prey was better lit (in the transparent prey boxes) the maximal turbidity under which detection was still retained was higher by only 0.5 NTU (Fig. 5), indicating that the results in this set-up could change little under higher illumination (Vogel and Beauchamp, 1999). When turbidity approached the 'detection limit', the increased difficulty in the birds' decision making was expressed in the increased variance in the proportion of correct choices.

Measurements of turbidity by light attenuation may not suffice for experiments on visually guided tasks. This is because at low-level turbidities, visibility may deteriorate if the scattering coefficient of the particles is high and the absorption coefficient is low. Underwater visibility is especially affected by turbidity under direct light (Jagger and Muntz, 1993) and it is possible that the intensity of the underwater ambient light will increase at low-level turbidities due to light reflection by suspended particles, as is the case with light fog in air. The contrast will be reduced through increased ambient light levels between the eye and the object, and thus visibility will decline. Reduced prey detection under turbid conditions, shown in the present study, lends further support to the role of vision in aquatic predator-prey interactions. Turbidity may alter the colour of both predator and prey, reduce fish reactive distance to their prey (Vinyard and O'Brien, 1976; Barret et al., 1992; Miner and Stein, 1996; Gregory and O'Brien, 1983; Abrahams and Kattenfeld, 1997) and, most probably, has a role in the choice of foraging sites by cormorants (Van Eerden and Voslamber, 1995).

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