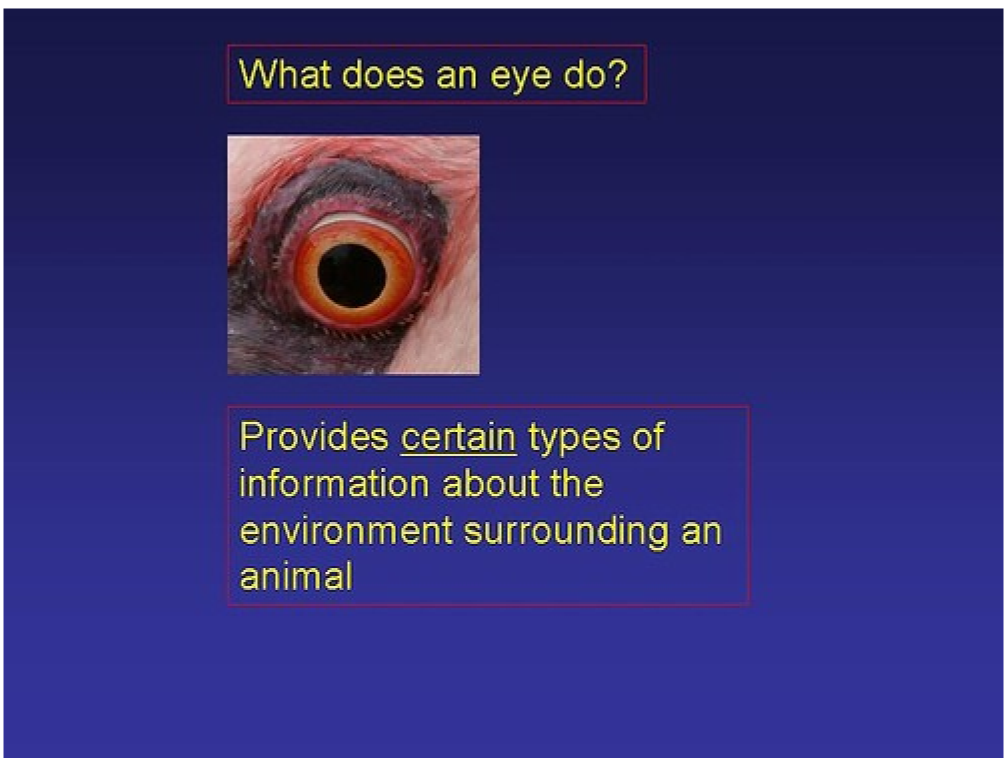


Why be interested in what a bird can see?

Because all vision is selective.

The information that you receive through your eyes is likely to be very different from that received by another animal when viewing the same scene.

We all live on the same planet but because of the differences in our senses we all live in different world.

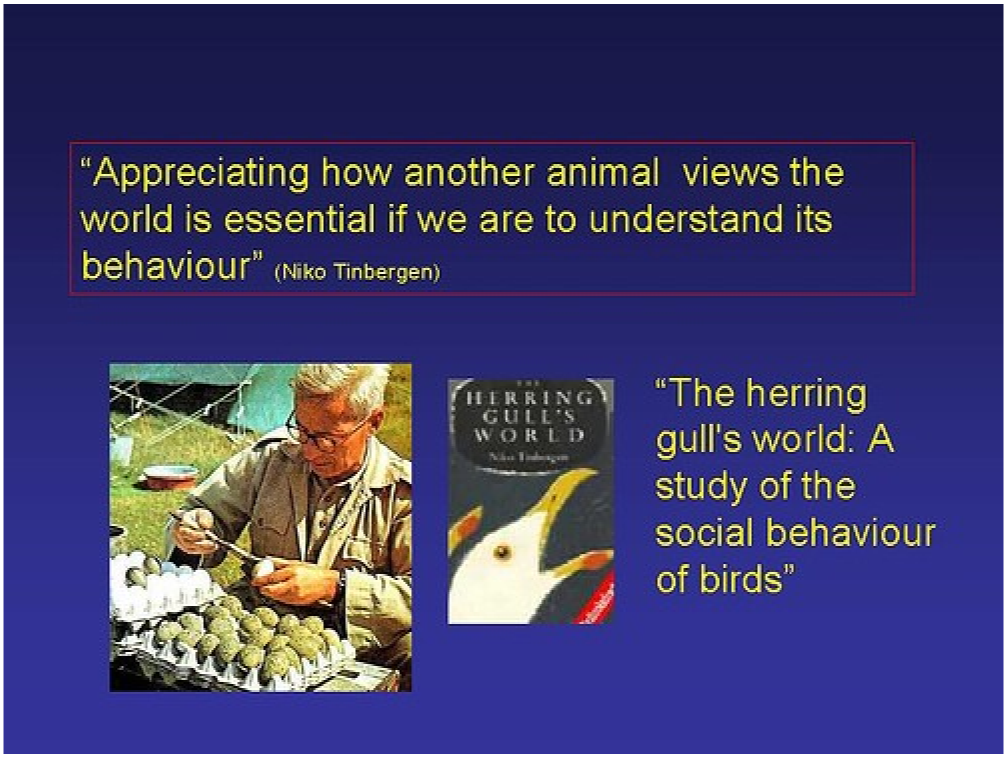
If we want to understand what controls another animal's behaviour we must know something about the information that is available to them.

For example, many animals, including many birds, can see in the Ultraviolet part of the spectrum.

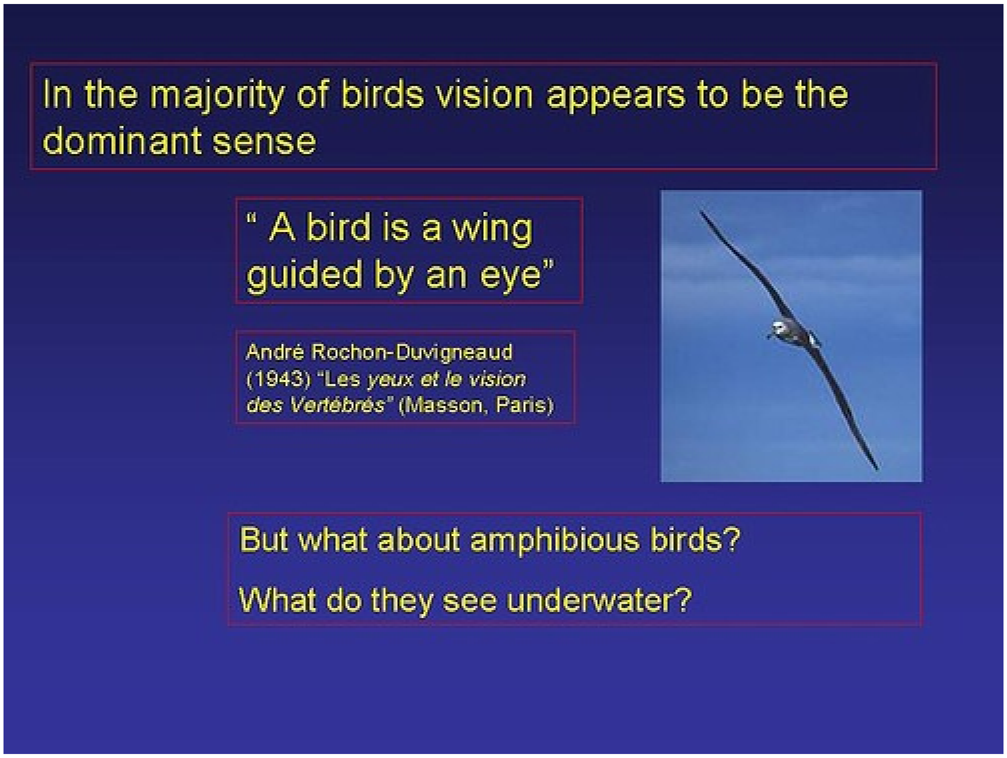
They can detect information of which we are totally unaware unless we use technology to detect it.

We have eyes on the front of our heads and tend to think that the world is out there, in front of us. But for the majority of animals, including most birds, eyes are positioned on the side of the head, and this gives a much wider field of view. Some birds, such as mallard ducks, for example, can see all around and above them. Clearly at any instant they can respond to information from a wider range of locations than we can.

You cannot creep up on a mallard without being detected



One of the most prominent people to recognise this in the world of birds was Niko Tinbergen, who won a Nobel Prize in recognition of his work in this area.



We popularly think that vision is the dominant sense of birds, and may think of birds as "A wing guided by an eye", but that picks out just one aspect of a bird's life. What about finding food, what about vision under water?

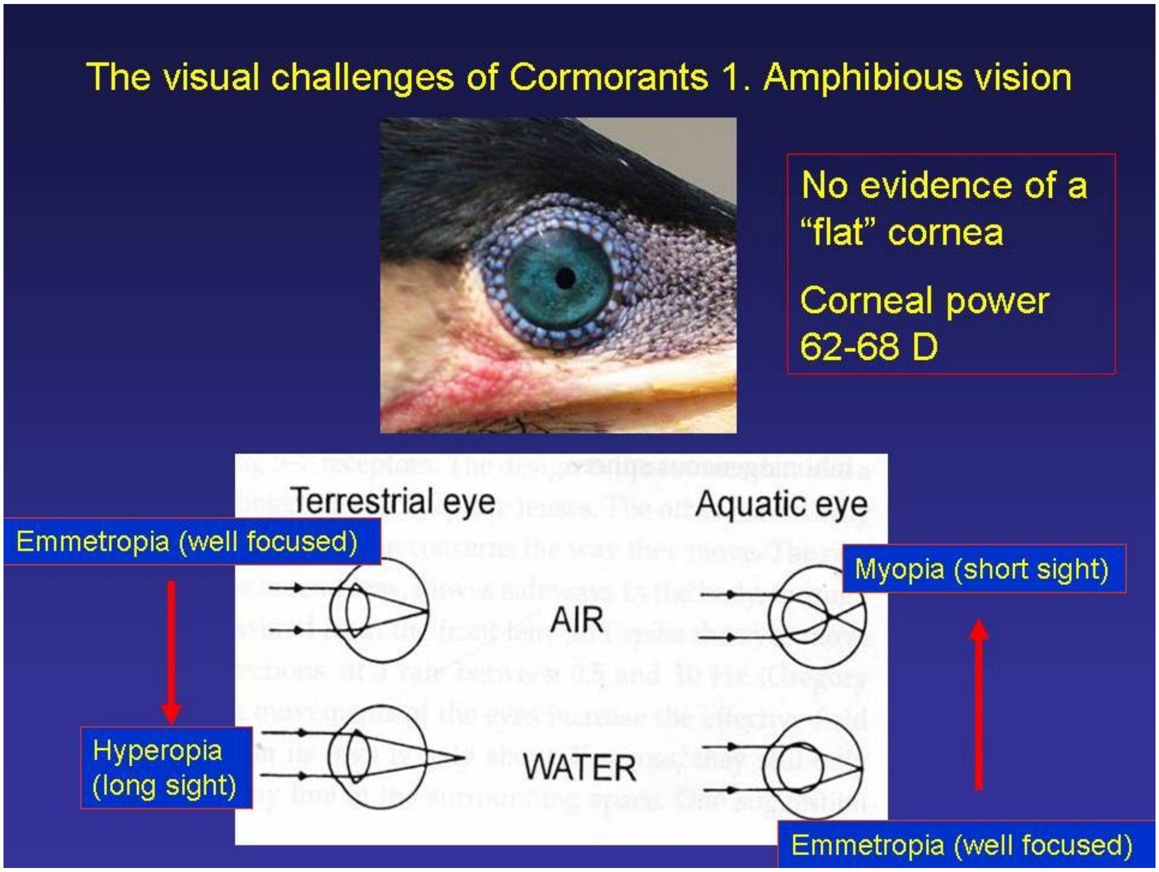
Many birds make their living by diving and finding prey: what do we know about their underwater world?

Great Cormorants are a prime species for investigation of this problem

The Great Cormorant is a diving predator of a wide range of fish: dives up to 30m deep in lakes, rivers, estuaries, coastal waters where the water quality ranges from clear to highly turbid

It has a world wide distribution from tropics to north of the Arctic Circle and is a highly efficient forager: brings them into conflict with human economic interests

Great Cormorants are birds that are seldom far from the news.
This front page story “Livelihood was eaten by seabirds” is from my local newspaper a month ago. It presented Great Cormorants as a devastating predator that needs to be controlled.



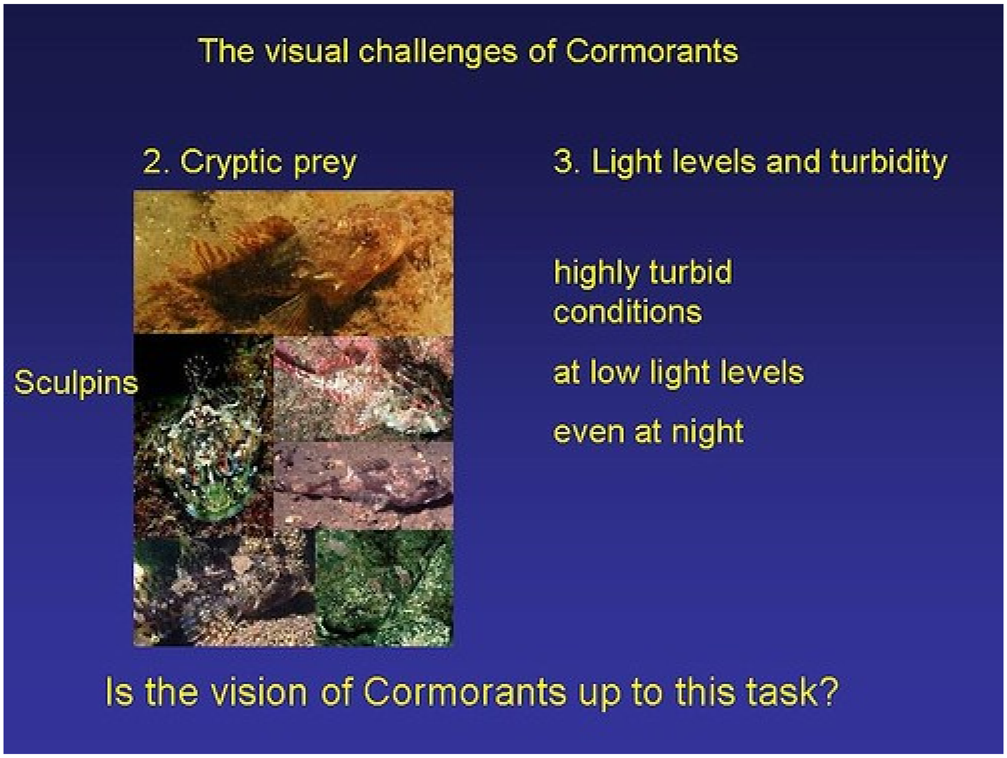
But what are the problems for a cormorant when it seeks its prey?

Problem one: going from air to water.

Crossing that boundary means that the cornea, at the front of the eye, no longer functions in focusing light on the retina. The cornea is a highly curved surface that in air separates two media of different refractive index and this gives it great optical power.

In water this power is lost. If you put your head under water and open your eyes, everything is blurred. This is because you have knocked out your cornea. Your eye goes from being well focused to being long sighted.

The reverse happens if you take a fish out of water, they become short sighted in air.

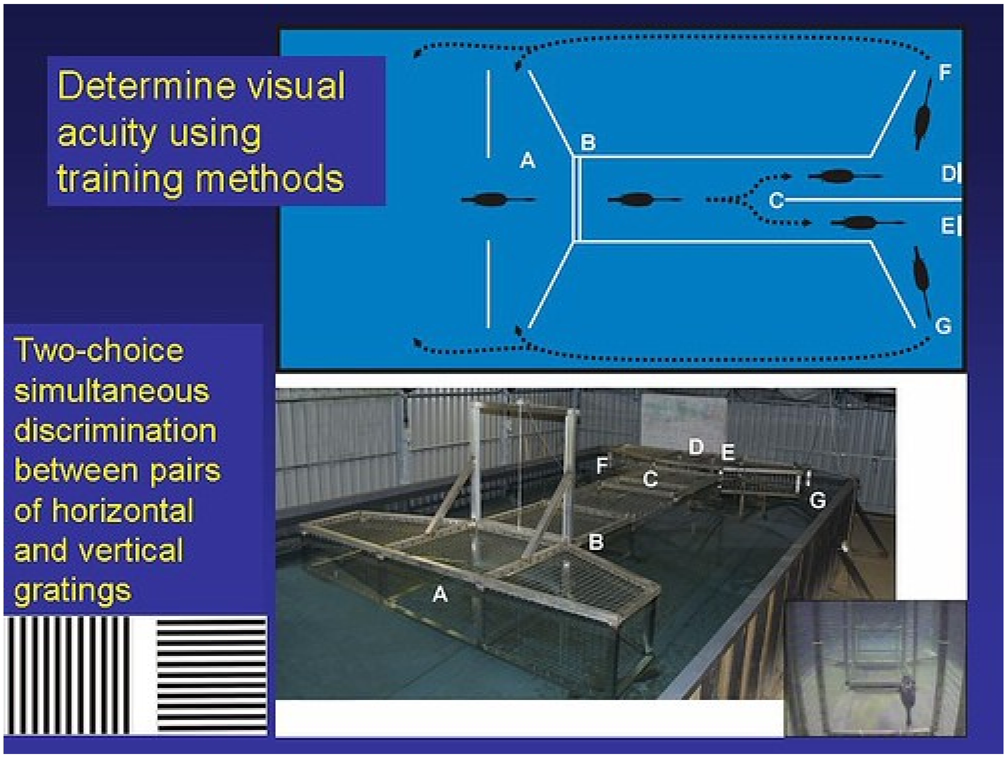


Cormorants have two further problems

The prey they search for are often very well camouflaged and lurk passive on the substrate and to our eyes are very difficult see, as in the example of these Sculpins. Prey may also hide away under rocks or tree roots

Also Comorants may forage in water that is very turbid, and they may forage at low light levels

So is cormorant vision up to the task?



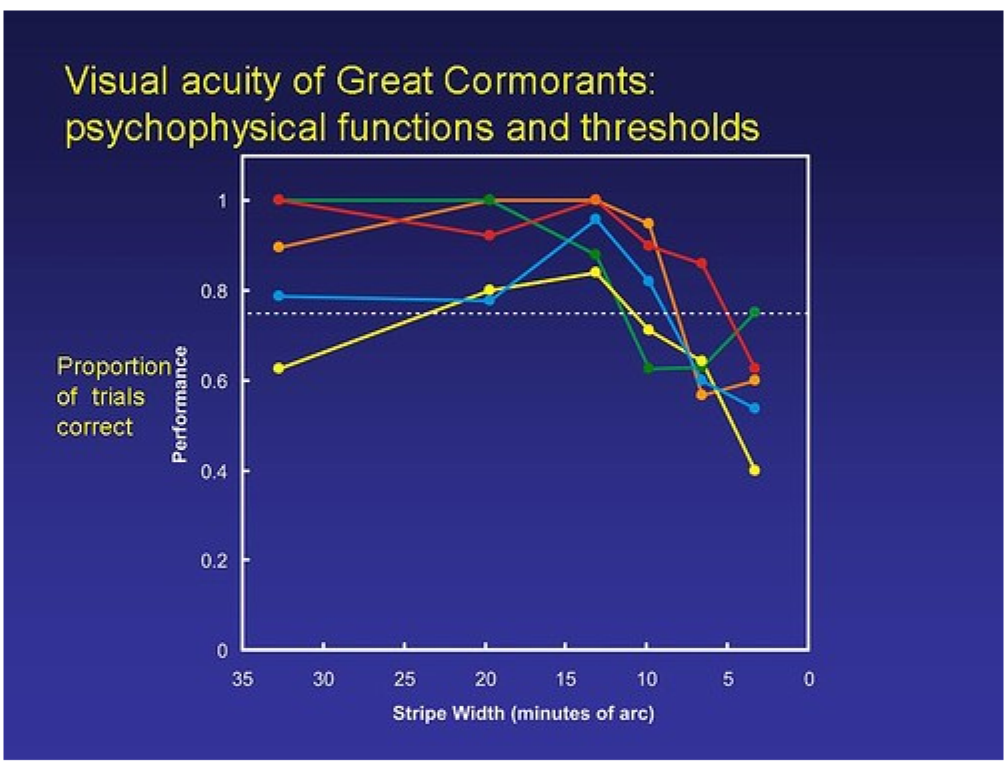
How do we find out?

Ask the cormorants what it sees.

We do this by training them to discriminate between pairs of patterns consisting of horizontal and vertical stripes. If they chose (say) the vertical stripes we reward them with a fish, chose the horizontal stripes and they get nothing. This way they soon learn to make a correct choice on every trail.

In our “Swimway” apparatus they start at A, the gate at B opens, they swim down to point C where they have to chose to go left or right depending upon whether the pattern of choice (D or E) is to the right or left of the barrier (which controls the distance from which they view the striped patterns). They then exit at F or G and go back to the start, ready for another trial.

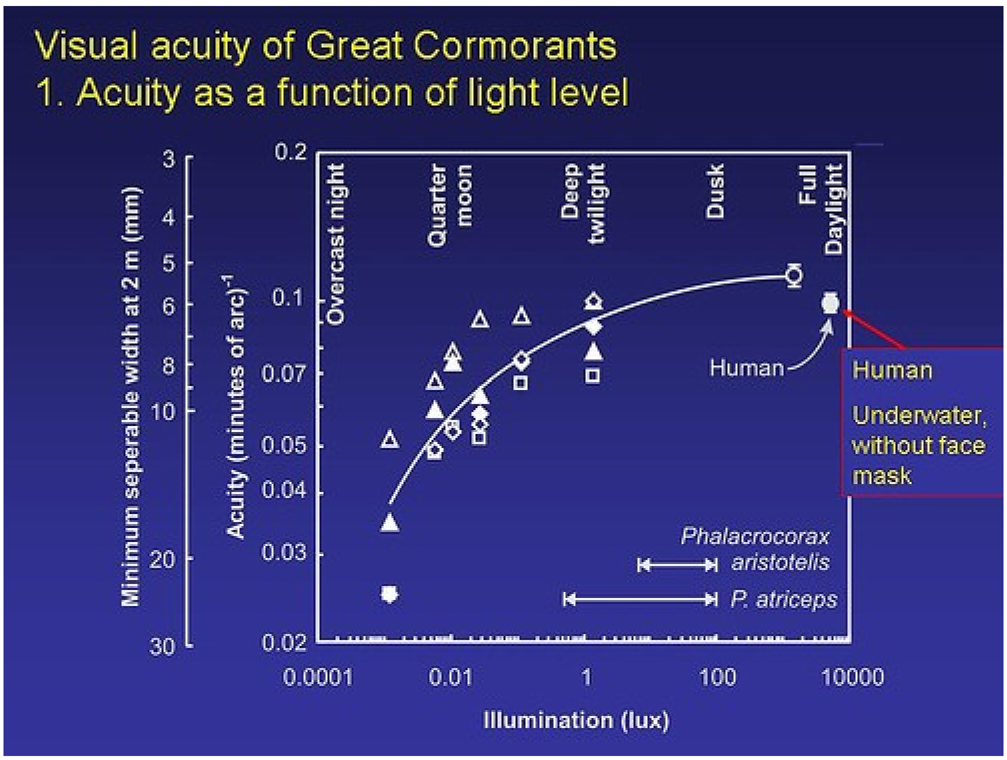
A cormorant's eye view of the apparatus



After many trials the birds get this choice 100% correct. If they were are just choosing randomly they would get 50% correct.

Look at the graph: each colour represents a different individual bird. If we start to vary the width of the stripes this discrimination performance of the birds starts to deteriorate, they make more errors as the stripes get narrower. So we get a “psychophysical function” which plots % correct as a function of stripe width.

We say that 75% correct is a measure of their threshold for detecting stripes width. The narrowest stripe pair that can be discriminated correctly on 75% of the occasions is used to define their “visual acuity threshold”.

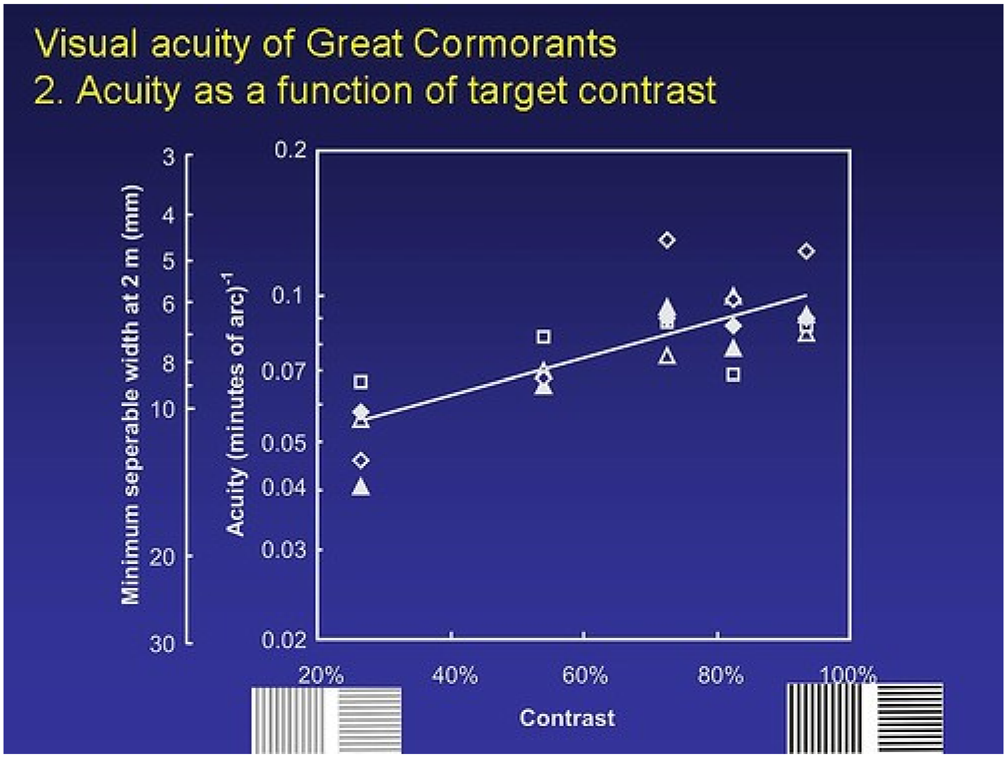


But visual acuity will vary with various features of the stimulus.

So, as we decrease the overall light level, acuity gets lower, that is the cormorant can only see wider strips as things get dim. Just the same as us. This graph shows how average acuity changes with light level and I have indicated what these light levels are with respect to naturally occurring conditions, e.g. sunlight, twilight moonlight, and I have also indicated the range of light levels that some cormorant species are known to forage within.

Perhaps the most surprising finding is just how poor the acuity of Cormorants is.

Even at high light levels, their best performance is 60 times worse than that of an eagle. What is more telling is that cormorant acuity underwater is very similar to that of the very best human vision underwater without a face mask. If we open our eyes underwater, we see a blur, it seems that cormorants are no better than us.



As in other animals , including ourselves, the acuity of cormorants decreases as the contrast of the target decreases, So, not surpsingly, grey targets and less well seen that black and white targets

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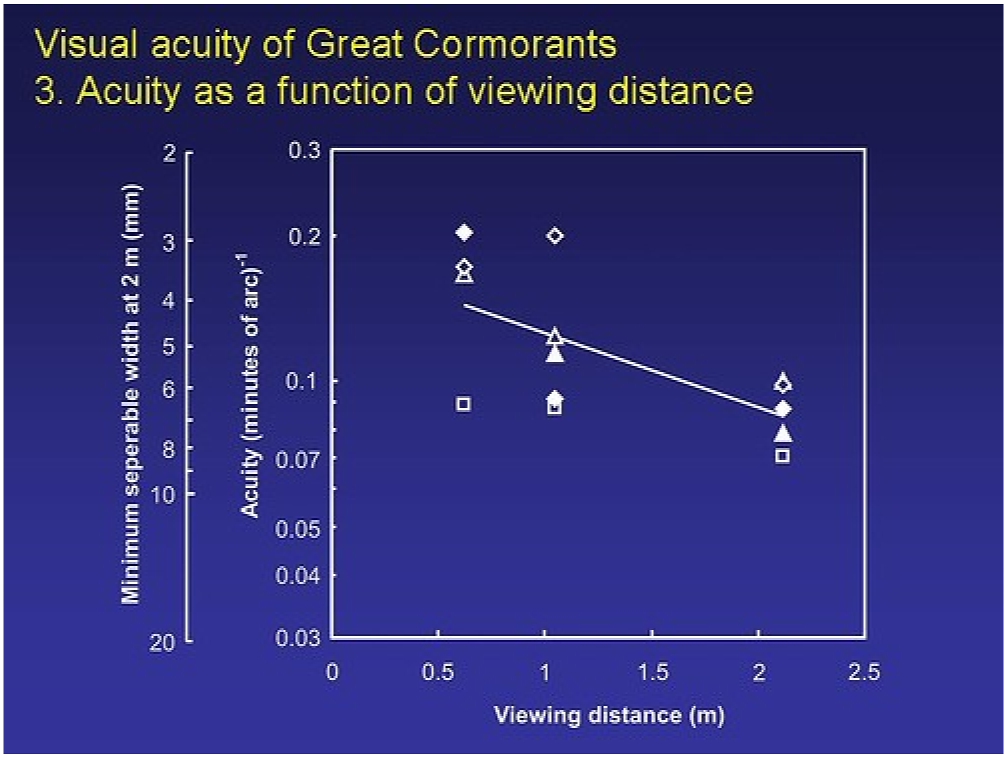
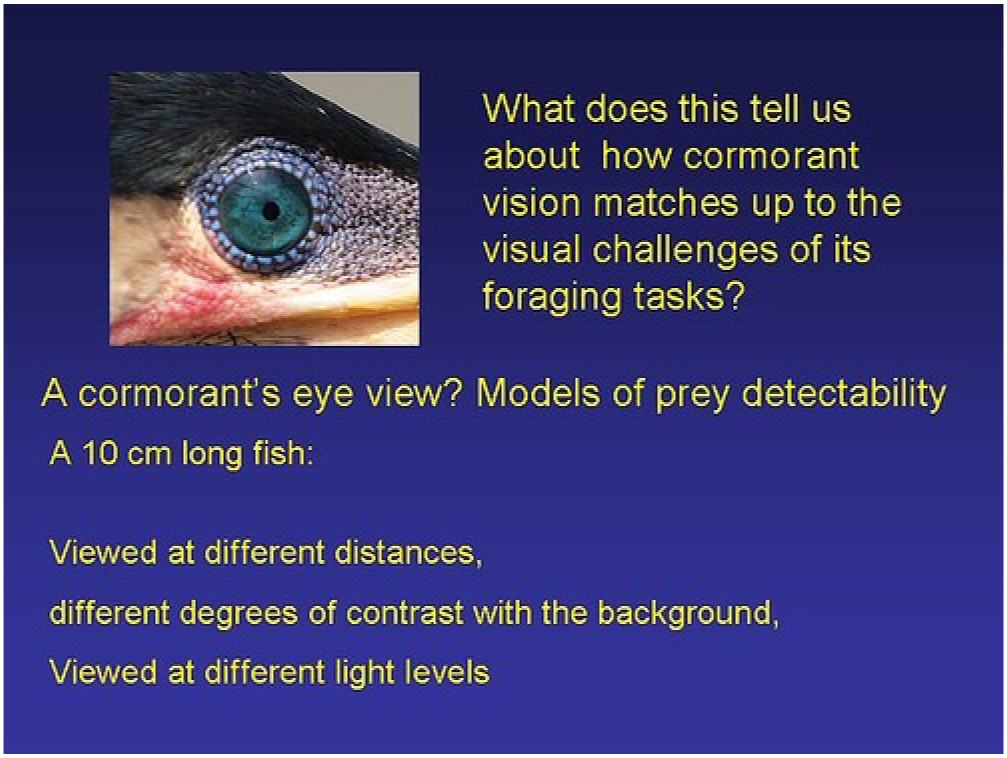


Also as viewing distance changes so acuity changes and here we show that if the cormorants are viewing the targets at half a metre, 1 m or 2 m does have a significant effect on its visual acuity.

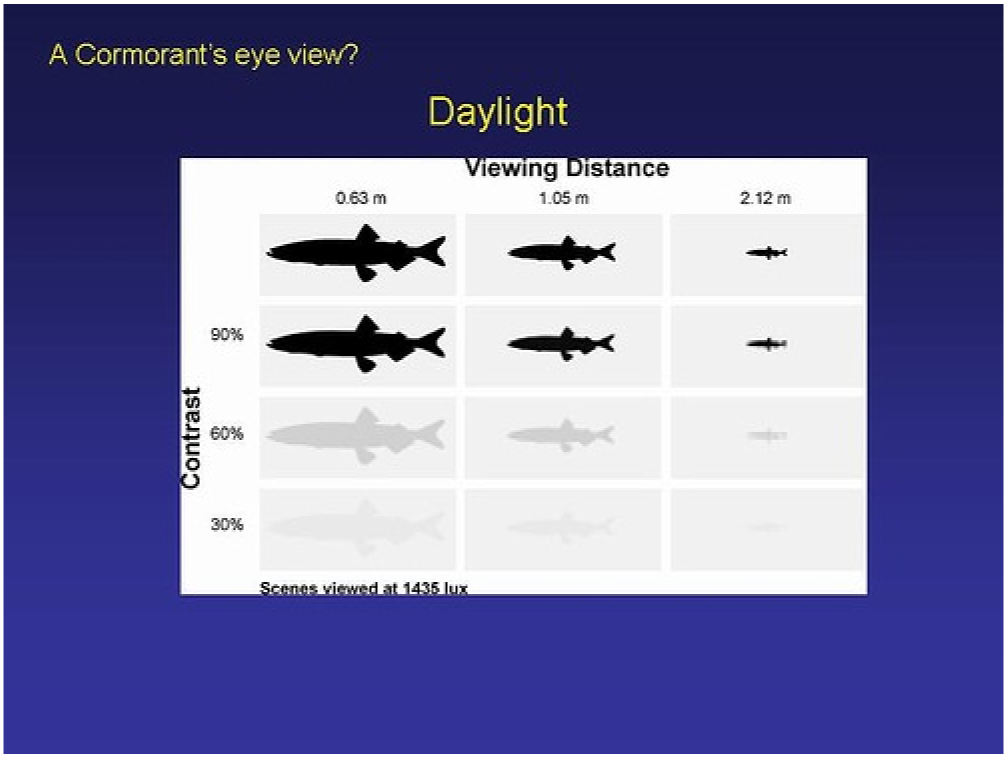


This data while important is a little dry, so how can we make it relevant to the task that faces a foraging cormorant in its natural environment?

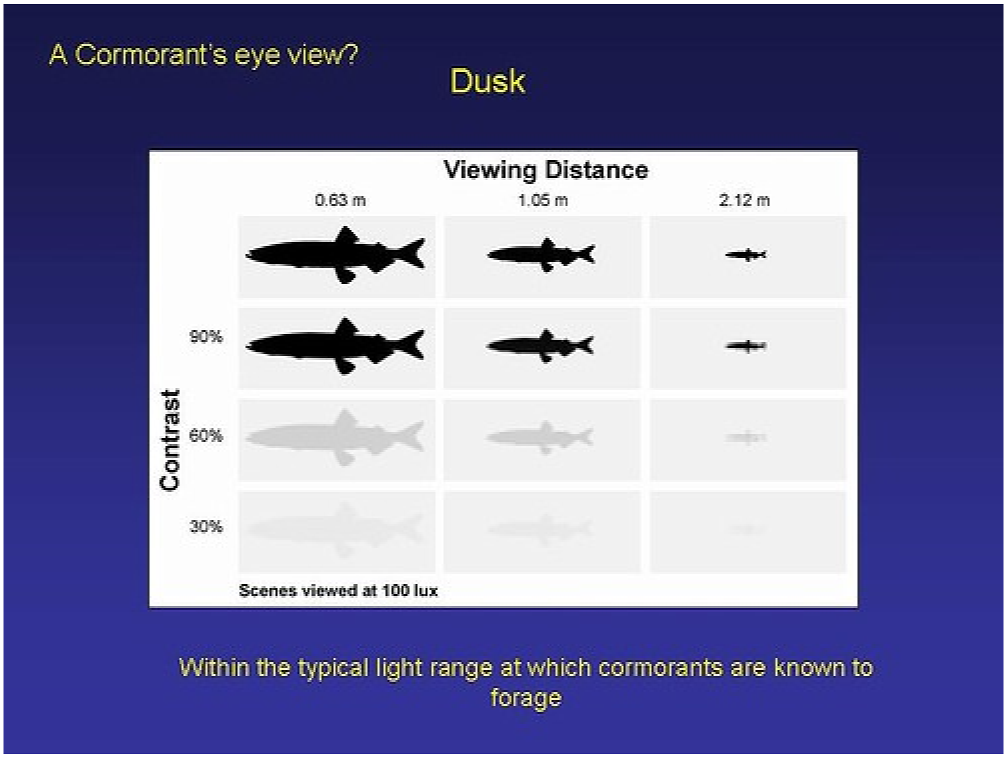
What is the "cormorant's eye view"?

We can try to model this by using all the data which you have just seen and from it build a " filter" that enable us to simulate the view of a standard target as a function of light level, contrast and viewing distance.

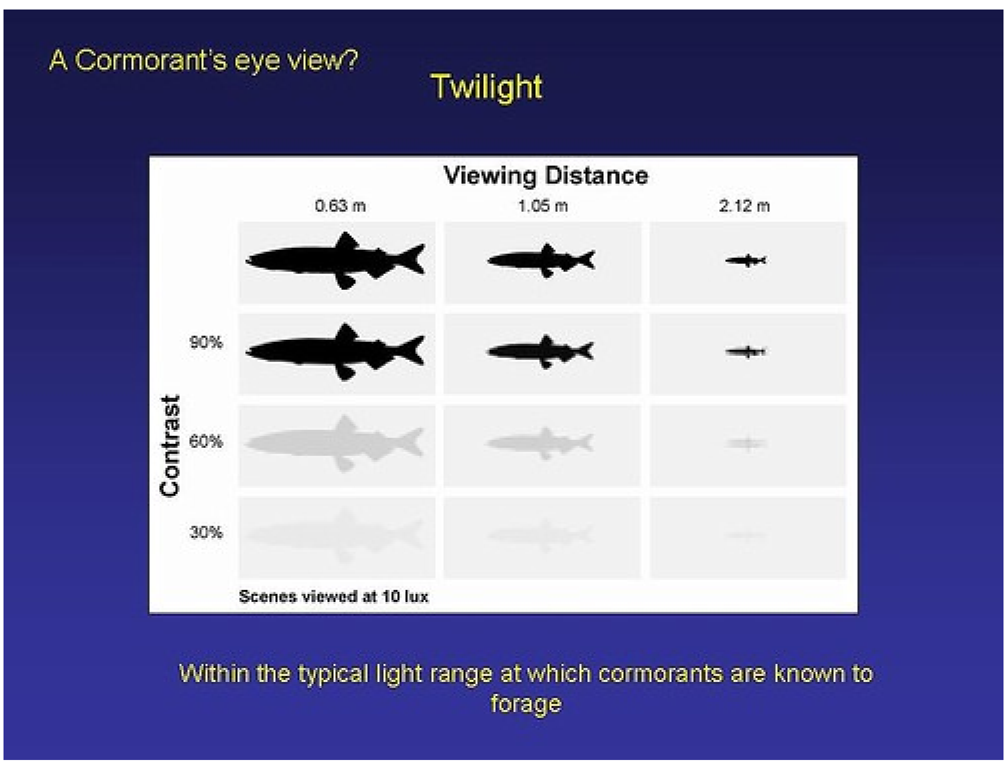
The next three slide show some examples of this



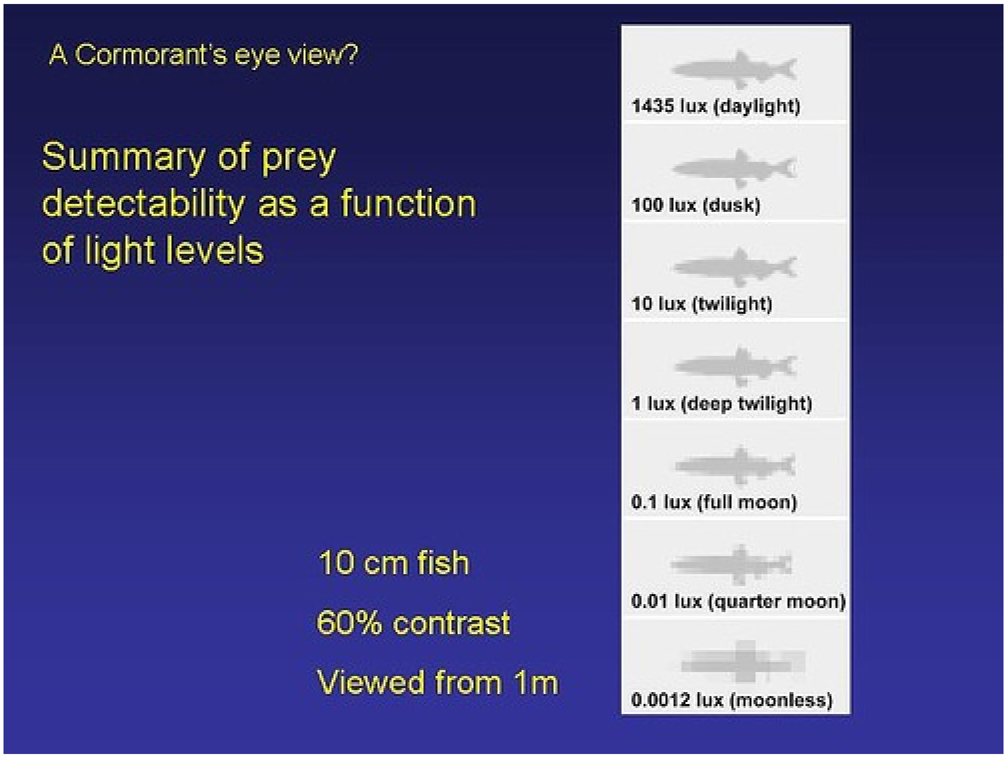
Here we have a Cormorant's eye views of a 10 cm fish which contrasts at different levels with the background and when viewed from different distances at high natural light levels



Here we have the same thing at lower light levels



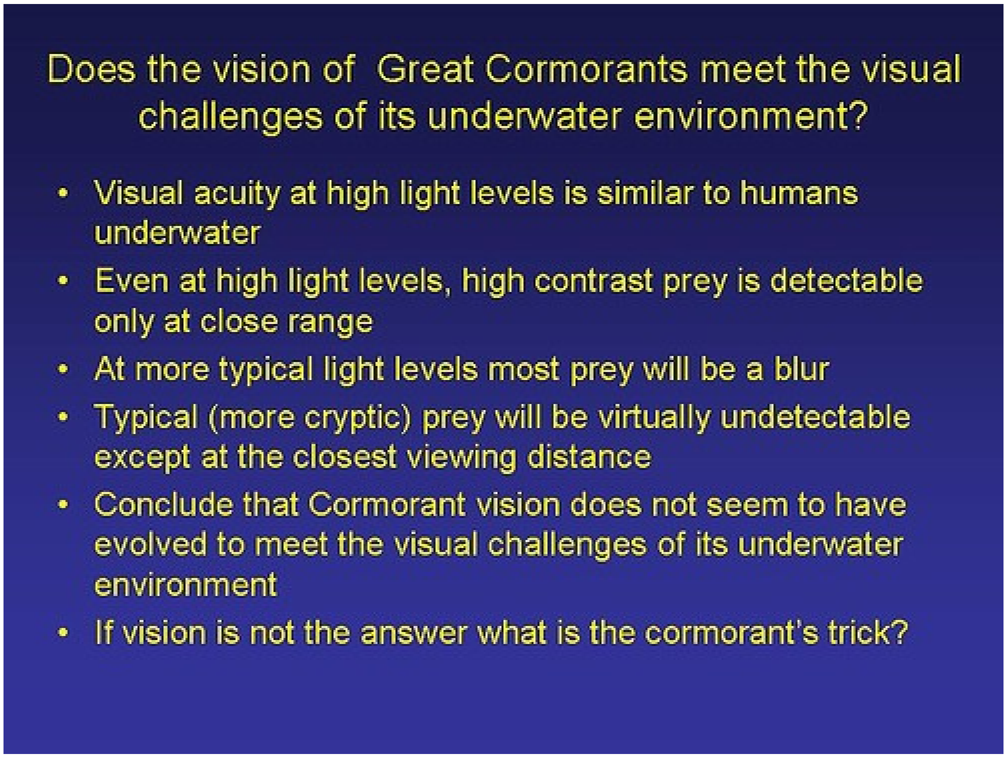
And the same thing at even lower light levels. These are equivalent to twilight, which is well within the range of light levels that cormorants are known to forage at.



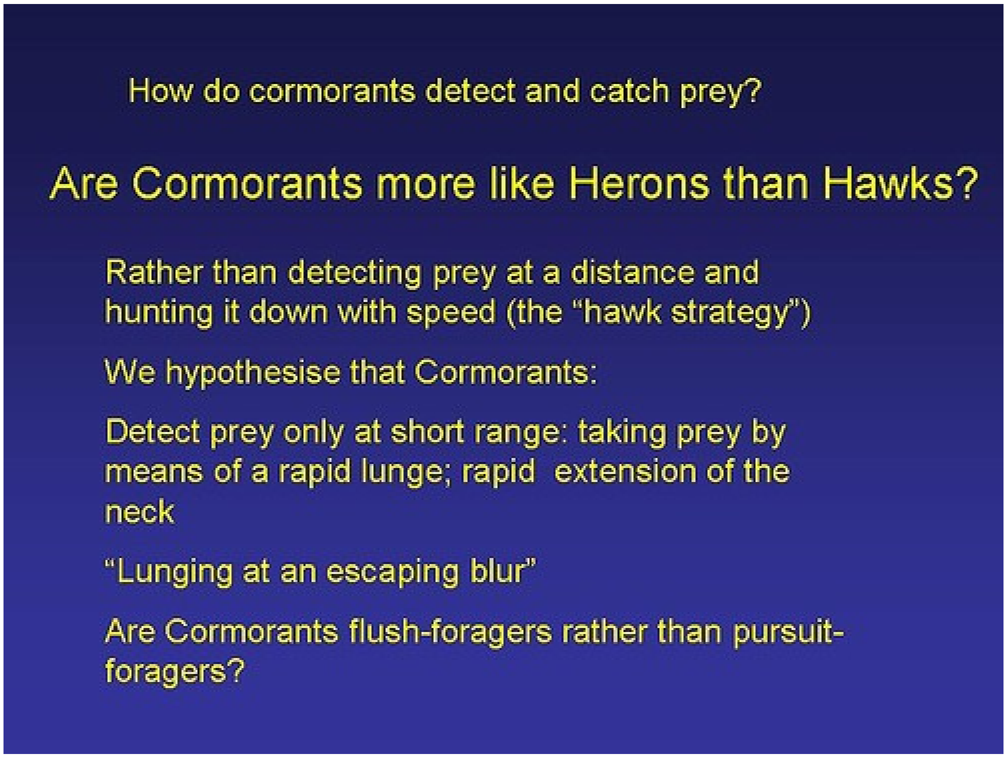
What does this really tell us?

This slide summarizes the cormorant's eye views of a standard fish of medium contrast, viewed from a distance of 1 metre, as a function of light levels.

It is clear that even with this kind of target (and remember that many fish will be far more cryptic) the cormorants can see only a blur, an indistinct outline.



I think it is safe to conclude that cormorant vision has not evolved to meet the perceptual challenges of its environment. We would have expected far better vision than this in a visually guided predator.

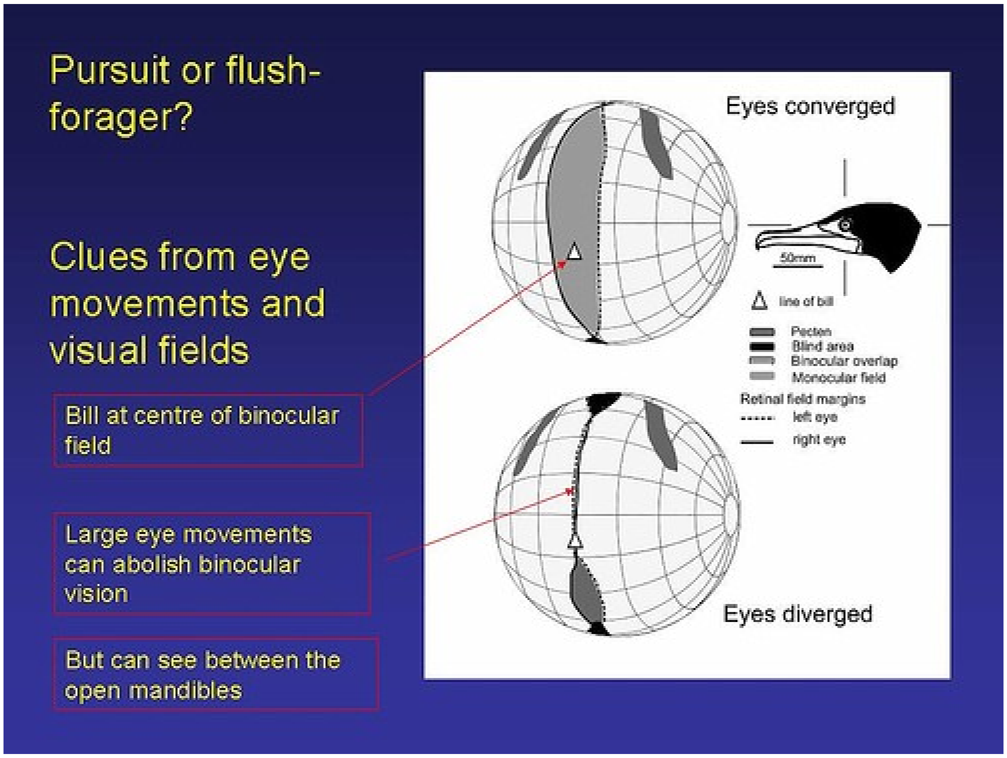


So how do cormorants catch their prey?

Are they more like herons than hawks?

Do they detect prey at a distance and pursue it (the hawk strategy) or do they disturb it a close range and take it with a rapid lunge of their long neck (the heron strategy)?

I would suggest they are “flush-foragers” like herons; forcing prey out from hiding places, perhaps by chance disturbance and then they catch a “moving blur”. That blur probably cannot be properly identified, but it has a high chance of being food.

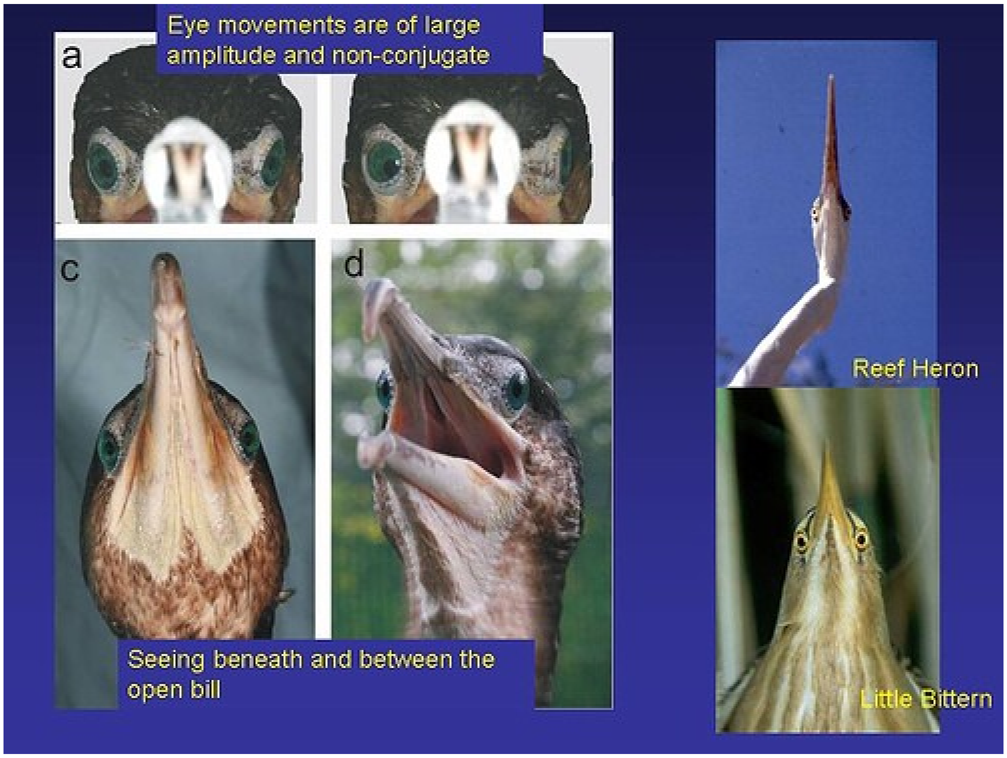


We can get some more clues to this from information on the visual fields of cormorants.

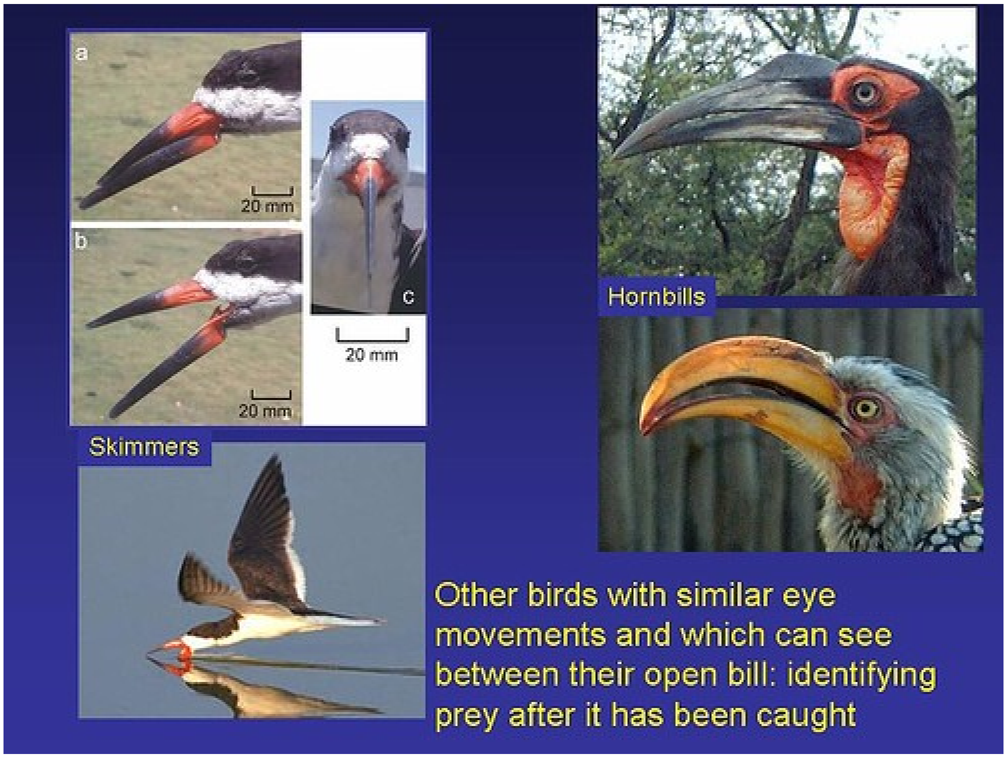
These diagrams show the visual field of cormorants. It plots on the surface of sphere surrounding the bird's head the position of the area of binocular vision and the projection of the bill.

We can see that the bill lies close to the centre of the binocular field and we know from studies with other birds, that this indicates that the bill may be controlled accurately by vision.

But unlike many birds cormorants also have large eye movements which can completed abolish binocular vision, but also allow the eyes to search around for prey.



The eyes can move independently of each other, as shown in these photographs. Also they can not only look directly below the bill (like herons) but they can also see between the opened mandibles. Many birds see just beyond their bill and cannot see what they are holding in the bill, cormorants can see what they are holding.

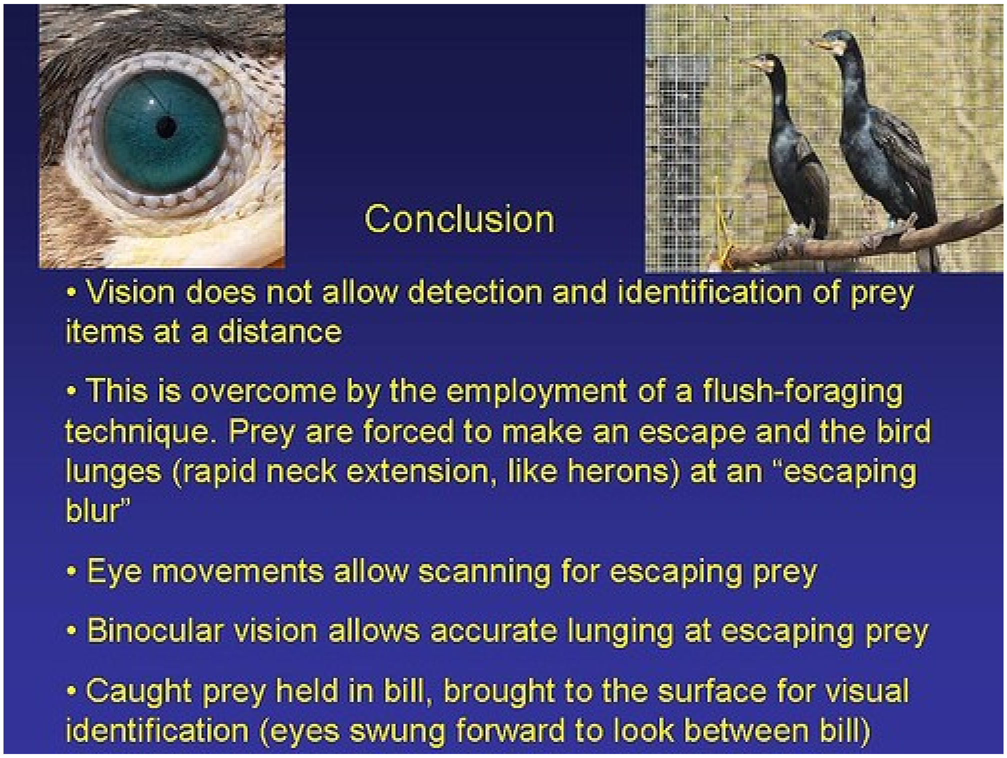


This type of visual field arrangement is found in other birds that also either flush-forage , such as the hornbills shown here, that disturb and grab prey at short range. Seeing between the mandibles is also found in Skimmers. These birds “trawl blindly” through the upper surface of water and grab anything that their mandible hits. All of these birds need to check, take a look at, what they have just caught, since it may not be edible!

Cormorants are known to always bring their prey to the surface before ingestion.

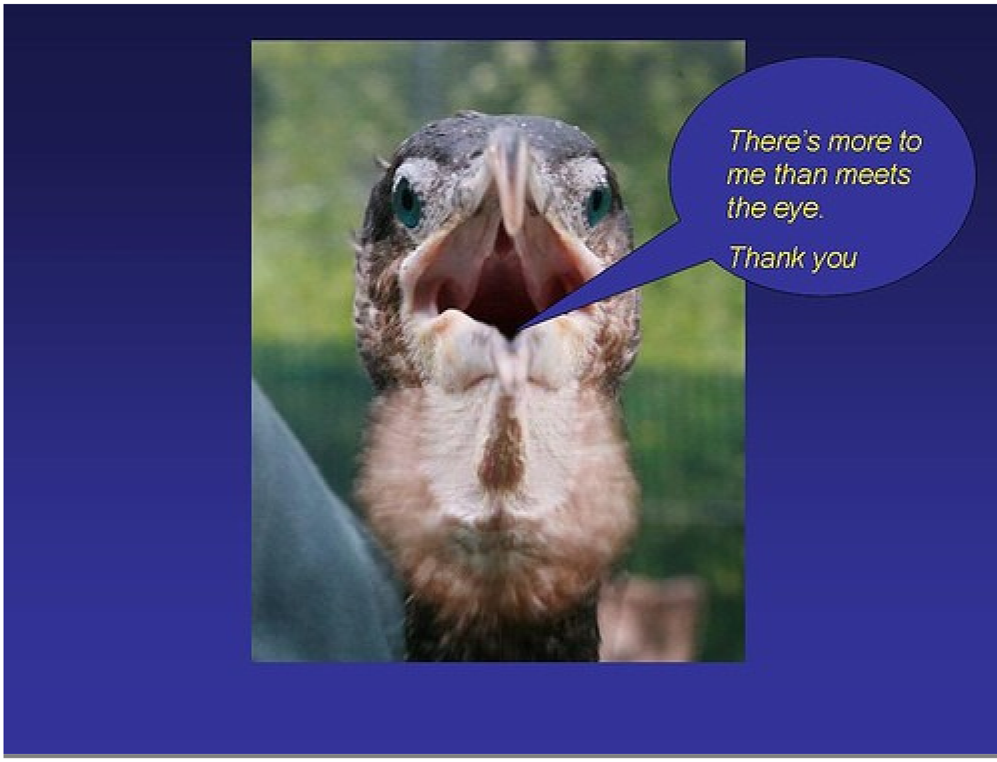
So it looks as though their visual fields will allow then to inspect items which have been caught somewhat blindly below water.

A rapid lung of their long neck secures the indistinct prey, but vision at the surface may be used to check what it is they have caught



So here are the conclusions.

Clearly vision on its own is not the answer to successful foraging in cormorants. The general lesson is that senses are always limited but often behaviour has evolved to work within those limits to provide the intriguing behaviours that we often take for granted.



There then followed a discussion:

Fletcher Pinion: why would behavior evolve rather than structure?

GrahamM Applemoor: I think the answer lies in the extreme variability of the water conditions in which cormorants have evolved to forage – if we actually look at coastal or esturine water, there really isn't much information, even if you had excellent vision, so it would be unlikely that natural selection could have acted. They must have evolved early on to overcome the limitations of their senses

Fletcher Pinion: But the structure had to exist in order to enable the behavior, right?

GrahamM Applemoor: Certainly. These birds are clearly very adept at flight – they're very accurate, so their vision is adapted primarily for aerial conditons and aquatic is a secondary adaptation. What we need to know is how good their vision is in air, because it looks as though they just haven't evolved a visual system to overcome the problems of going into water. The birds forage in relatively short intensive bouts, lasting probably only 15 mins at a time, so seems likely that air vision is the important thing

Fletcher Pinion: Why do they need good vision in air? Have other diving birds developed underwater eyes?

GrahamM Applemoor: Yes, they have. But nobody has actually measured visual acuity in any other diving birds. There is some evidence that birds like penguins (which are more aquatic-adapted) do have better underwater vision but we can only assume that from the much flatter cornea which seems to be an adaptation for going from air to water

Fletcher Pinion: Do we see similar adaptations in non-birds that eat the same way?

GrahamM Applemoor: Again, we just don't know. Measuring acuity takes a long time – this work took about 9 months – because it takes so long to train and test the birds, so people have tended to not find out. There have been measures of acuity in some seal species, which suggest they have reasonable acuity underwater. They certainly have flat corneas which seems to be the primary adaptation for underwater foraging. But we don't know much about any other animals.

Fletcher Pinion: are there other animals that can see what's in their mouths, I think was was I really wanted to ask

GrahamM Applemoor: Well, the only species I know of are the hornbills, herons and the skimmer, which certainly can see what's between the mandibles. Most birds see beyond the bill, not what's in it, so it does seem to be a particular specialisation

Hiro Sheridan: Have you studied how they react to movement?

GrahamM Applemoor: No. But that is obviously one of the things that we should do. Even if it's a blur, they need to detect it's a moving blur and we need to find out more about movement detection in these birds. However, it is very difficult to actually think of a suitable test of movement detection, to really see what is the fastest or slowest object they can detect. But we're working on it

Peace Furst: Is there a family structure in cormorants similar to crows to teach behavioural skills like these?

GrahamM Applemoor: Peace, the simple answer is I don't know, but to elaborate, I've got a colony of 14 tame cormorants which is the only one in the UK, maybe the only one in the world, where it's possible to study them in such detail. And one thing that struck us in the last couple of years is they do have a very elaborate social structure, and there is a fairly long period of dependance on the adults, but we have no information at all about how the young actually learn to find and catch prey.

Ada Meerson: Captive penguins will chase fish-shaped light beams projected underwater in their habitats, so they certainly see movement.

GrahamM Applemoor: Ada, yep, that does indicate they can see movement, but we really need to somehow quantify how they can see movement to be able to compare species and to see if cormorants have any special abilities.

Fletcher Pinion: Do you have any thoughts on the evolution of the relationship between the eye muscles (which enable the bird to see what it's grabbed) and the behavior of "lunge and grab"? I mean, "If it moves, see what it tastes like" has survival value, but it's risky… ;-)

GrahamM Applemoor: Fletcher, yes, I have some thoughts. Some birds have no eye movements at all, other birds have really large eye movement. It's possible that the eye mvements evolved for scanning around the birds, and secondarily it's enabled the birds to actually see what they have caught. Yes, "if it moves, what does it taste like" is definitely risky, but when you consider how cryptic some of those fish are, they won't be able to detect it until it moves and if it does move, the grabbing-then-checking philosophy must be a successful one.

Fletcher Pinion: but other birds are successful with grab-and-swallow, right?

GrahamM Applemoor: Fletcher, I'm not sure if other birds do have success with grab-and-swallow rather than grab-and-check. A lot of birds do decide before they peck at it

Troy McLuhan: Do the cormorants have predators? How do they evade them?

Fletcher Pinion: Good question, Troy – that woudl drive the scanning eyeball

GrahamM Applemoor: Troy, cormorants do have some predators. The main predators are likely to be seals. In air, we don't know of any particular predators, but these are large birds (2-3kg) so they don't have many air predator problems. It's really large aquatic mammals which pose a problem

Fletcher Pinion: if that's the case, then scanning doesn't really help, does it? Or does scanning help in seeing evading blurs?

GrahamM Applemoor: I'm suggesting that scanning is for looking for prey, not predator driven. They have very wide visual fields and have a relatively small blind area behind the head, so scanning might help in detecting something which would otherwise be in the periphery, then you can turn your head to grab it.

Fletcher Pinion: so perhaps being able to see what you're grabbed is a lucky accident of being able to scan? A bit of langniappe?

GrahamM Applemoor: Fletcher, I agree – we don't really know enough to be sure. It may be a lucky side-effect, yes

Troy McLuhan: I had one more question – about the difference in acuity between peripheral and central vision

GrahamM Applemoor: Troy, again we just don't know anything about it. All we've managed to do so far is measure acuity and get the results I've just presented. Certainly we might predict there'd be differences between peripheral and central acuity, but we just don't know

Hiro Sheridan: I noticed that the data you collected was not uniform between birds, do they have different levels of eyesight like humans?

GrahamM Applemoor: Hiro, yes, certainly. What I was presenting to you was average resulted based on a five-bird sample, but of course all sensory systems will vary between individuals and som will be better than others. All we can do is talk about the average cormorant as we talk about the average human

Hiro Sheridan: So when you collected your colony, were they from different locations? To avoid families of short-sighted birds?

GrahamM Applemoor: Yes, we've got birds 2 years running from 2 different colonies, probably 50-60 miles apart. Not entirely random but we've done something in that direction

Jorge Arida: Apart from your 14 cormorants, are there other places where people have lived with cormorants for a long time and got to know their behaviour? Not necessarily scientists…

Fletcher Pinion: Jorge, fishermen in Indonesia (iirc) use them.

GrahamM Applemoor: There was another colony in Britain that was disbanded a few years ago, but I don't know of any in zoos, as they normally just have one or two rather than a colony

Troy McLuhan: I don't think that any of the 13 colonies were cormorants

GrahamM Applemoor: It's not just in Indonesia – it's a tradition in China and Japan to use tame cormorants to catch fish, and there is some evidence that it used to be done in Britain a few hundred years ago

Fletcher Pinion: something in medieval texts?

GrahamM Applemoor: Yes, it's some illustrations in a medieval text

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