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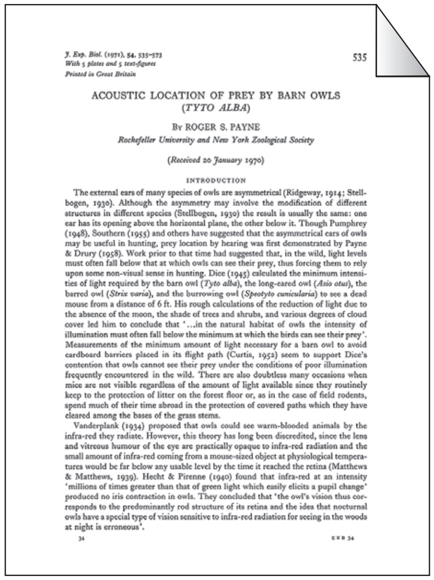
JEB Classics

WHY ARE BARN OWLS A MODEL SYSTEM FOR SOUND LOCALIZATION?



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ACOUSTIC LOCATION OF PREY BY BARN OWLS
(*TYTO ALBA*)

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INTRODUCTION

The external ears of many species of owls are asymmetrical (Ridgeway, 1914; Stellbogen, 1930). Although the asymmetry may involve the modification of different structures in different species (Stellbogen, 1930) the result is usually the same: one ear has its opening above the horizontal plane, the other below it. Though Pumphrey (1948), Southern (1955) and others have suggested that the asymmetrical ears of owls may be useful in hunting, prey location by hearing was first demonstrated by Payne & Drury (1958). Work prior to that time had suggested that, in the wild, light levels must often fall below that at which owls can see their prey, thus forcing them to rely upon some non-visual sense in hunting. Dice (1945) calculated the minimum intensities of light required by the barn owl (*Tyto alba*), the long-eared owl (*Asio otus*), the barred owl (*Strix varia*), and the burrowing owl (*Speotyto cunicularia*) to see a dead mouse from a distance of 6 ft. His rough calculations of the reduction of light due to the absence of the moon, the shade of trees and shrubs, and various degrees of cloud cover led him to conclude that '...in the natural habitat of owls the intensity of illumination must often fall below the minimum at which the birds can see their prey'. Measurements of the minimum amount of light necessary for a barn owl to avoid cardboard barriers placed in its flight path (Curtis, 1952) seem to support Dice's contention that owls cannot see their prey under the conditions of poor illumination frequently encountered in the wild. There are also doubtless many occasions when mice are not visible regardless of the amount of light available since they routinely keep to the protection of litter on the forest floor or, as in the case of field rodents, spend much of their time abroad in the protection of covered paths which they have cleared among the bases of the grass stems.

Vanderplank (1934) proposed that owls could see warm-blooded animals by the infra-red they radiate. However, this theory has long been discredited, since the lens and vitreous humour of the eye are practically opaque to infra-red radiation and the small amount of infra-red coming from a mouse-sized object at physiological temperatures would be far below any usable level by the time it reached the retina (Matthews & Matthews, 1939). Hecht & Pirenne (1940) found that infra-red at an intensity 'millions of times greater than that of green light which easily elicits a pupil change' produced no iris contraction in owls. They concluded that 'the owl's vision thus corresponds to the predominantly rod structure of its retina and the idea that nocturnal owls have a special type of vision sensitive to infra-red radiation for seeing in the woods at night is erroneous'.

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Laura Hausmann, Martin Singheiser and Hermann Wagner discuss Roger Payne's 1971 paper entitled: Acoustic Location of Prey by Barn Owls (*Tyto alba*).

A copy of the paper can be obtained from
http://jeb.biologists.org/cgi/content/abstract/54/3/535

In 1971, Roger Payne published the paper 'Acoustic Location of Prey by Barn Owls (*Tyto alba*)'. Payne had conducted the underlying experiments at Cornell University in partial fulfilment of the requirements for his PhD, which he obtained in 1961. When the paper was published, Payne, a zoologist, was a professor at Rockefeller University. By that time he was already famous for his discovery of songs in humpback whales. Payne later left academia and started to promote conservation of whales, an activity he still pursues today.

Despite this extraordinary career, Payne took the time to write the paper on the location of prey by the barn owls. This paper laid the ground for many subsequent studies on the barn owl's ability to catch prey in complete darkness, specifically on the auditory processing involved in this behaviour.

In the 1960s, model systems such as bats, electric fish and song birds were just emerging. Payne was attracted by the specific anatomical adaptations of the barn owl and started his paper with a note on the asymmetrically arranged ears and nocturnal lifestyle of owls. Others had noted these specializations before, but Payne was not convinced by the existing hypotheses that related the asymmetrically arranged ears, the ruff and the nocturnal lifestyle to possible acoustic mechanisms underlying the location of prey by barn owls.

After describing the anatomy of the ear in detail, Payne reports an experiment to determine possible sensory cues that the owls could use for sound localization. In this experiment the barn owl first learned to strike live mice in complete darkness in a free-flight room, the floor of which was covered with a layer of dry leaves. Sometimes a mouse-sized wad of paper was dragged on the floor instead of a mouse. The owl successfully struck this artefact, thus excluding both visual and infrared detection as the crucial cues to locating its prey. Since the paper also did not smell like any prey, Payne concluded that the owls must use auditory cues. He, and later Mark Konishi (Konishi, 1973), also confirmed this conclusion by letting the mouse tow a rustling piece of paper. Guess what, the barn owl struck the paper and not the quietly walking mouse.

After this initial clarification that owls hunt using acoustic cues, Payne tested the geometrical parameters underlying prey capture such as distance, motion direction and horizontal and vertical angles. He took motion pictures of an animal flying in total darkness. The camera triggered a stroboscope that produced infra-red flashes. By analysing the film sequences Payne found out that the owls flew slower in darkness than they did in light. Payne also observed that the owl 'whirled' its head towards a sound source, a fixation response that occurs before the owl flies at the mouse. Payne also analysed striking precision by measuring the impact of the talons on the floor, demonstrating that the owl could locate a sound-emitting target within approximately 1 to 3 deg in both the horizontal and vertical directions. Later on, the head-fixation behaviour was quantified with magnetic tracking systems revealing a similar precision.

Payne's experiments did not lead to a firm conclusion about the ability of the owl to discriminate distances by listening to sound emitted by a loudspeaker, and this issue is not resolved as of today. On the other hand, Payne observed that the long axis of the barn owl's talons' oval strike pattern was parallel to the long axis of the mouse. Thus, the barn owl might extract information about the mouse's motion direction from acoustic information. Again, the issue of passive acoustic motion-direction detection is still a matter of debate today.

The experiments described so far did not reveal which sound parameters the barn owl uses for sound localization. Payne specifically tested the influence of frequency on localization behaviour. Sound frequencies above 5 kHz seemed to be most important. To quantify how this frequency dependence may be related to the asymmetrically arranged ear openings, Payne measured the directional sensitivities of the barn owl's ears. This method of using so-called head-related transfer functions is now the basis for many quantitative experiments (Keller et al., 1998). Payne had already related the increased precision at frequencies above 5 kHz to the more complex directional-sensitivity patterns measured at the ear drum in this frequency region. He also considered intracranial sound transmission, effectively asking the question of whether the owl's ears work as a pressure receiver or as a pressure-difference receiver. This question is also still unresolved, although the existing evidence clearly favours the pressure receiver. Finally, Payne measured cochlear microphone potentials. He used the owls' sensitivity as a rough estimate of their hearing range.

Payne himself summarized his findings by stating that 'barn owls (*Tyto alba*) can locate prey in total darkness using only the sense of hearing'. The error in both the vertical and horizontal planes is between 1 and 3 deg and frequencies above 5 kHz are particularly important for owls to locate their prey.

This short review may demonstrate that Payne asked many important questions and opened several fields of research by his experiments. The only approach that Payne did not try was to record neural activity from the barn owl's brain. However, Payne's experiments pointed towards the questions to be asked in such experiments. For example, electrophysiological recordings by Moiseff and Konishi (Moiseff and Konishi, 1981) demonstrated that the owl is able to use the interaural time difference at frequencies above 5 kHz for azimuthal sound localization. This came as a surprise, because it was thought at that time that the use of interaural time difference from the carrier was limited to frequencies below 4 kHz. Many laboratories continue to use the barn owl as a model system for neuroethological research as well as for basic questions in neuroscience, such as plasticity in neural systems. Whereas the barn owls' free-flight behaviour had received little attention in three decades following Payne's paper, several recent studies have used modern technology to analyse the owl's prey capture in controlled free-flight experiments (Fux and Eilam, 2009; Hausmann et al., 2009; Singheiser et al., 2010). The questions asked in these papers and many others may be traced back to Payne's classic experiments. A next step forward in owl research would be to create a transgenic owl so that the advantages of manipulating genes that have made mouse research so successful can be used to study the genetic basis of the underlying specific anatomical adaptations.

Payne's paper almost reads like a novel, at no expense to its high scientific quality. Payne performed hypothesis-driven experiments and presents a clear line of argument based on his observations. This work has inspired our research on owl's localization behaviour. The work by Roger Payne certainly has the potential to inspire future generations of researchers.

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