

## Sensory capacities and the nocturnal habit of owls (Strigiformes)

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Behavioural studies show that in the eye of the Tawny Owl *Strix aluco* both absolute visual sensitivity and maximum spatial resolution at low light levels are close to the theoretical limit dictated principally by the quantal nature of light and the physiological limitations on the structure of vertebrate eyes. However, when the owl's visual sensitivity in relation to naturally occurring light levels is analysed, it is concluded that at night there will often be occasions when vision can only be used to control the owl's behaviour with respect to large objects.

Owls are capable of detecting and catching prey by hearing alone. However, absolute auditory sensitivity is not superior to that of mammals (including Man), but does appear to have reached the absolute limit on sensitivity in the aerial environment, which is dictated by the minimum ambient sound level.

An explanation of the owl's ability to be active at night based only upon high sensory sensitivity is thus untenable. Many features of the natural behaviour of the Tawny Owl (e.g., the high degree of territoriality, prey catching technique, dietary spectrum) may be interpreted as reflections of an additional requirement for the nocturnal habit beyond high sensory sensitivity: detailed knowledge of local topography.

The nocturnal habit amongst birds is rare. Probably less than 250 species (c. 3%) are regularly active outside daylight hours and the majority of these species, such as certain nightjars (Caprimulgidae), are best regarded as crepuscular rather than strictly nocturnal in their activity. Some bird species (swiftlets *Collocalia*, and the Oil Bird *Steatornis caripensis*) are able to guide themselves in the totally dark interior of caves, using echolocation (Griffin & Suthers 1970, Konishi & Knudsen 1979); however, such environments are structurally simple.

It is only amongst the Strigiformes (owls and barn owls) and the Caprimulgi-formes (frogmouths and their allies) that strictly nocturnal, non-echolocatory birds which fly in structurally complex environments, such as forests, are found. Not all species in these orders are nocturnal; indeed, probably less than 40 of the 135 species of owl may be regarded as strictly nocturnal, in that they are capable of completing all aspects of their life cycle between sunset and sunrise (Burton 1985).

The nocturnal environment would therefore seem to pose particular limiting problems for flying birds, and it is typically supposed that these problems are sensory in nature (Walls 1942, Tansley 1965). This paper presents available data on the visual and auditory capacities of owls and views these in the context of the ultimate limits on sensitivity and the critical features of the nocturnal environment. It is concluded that while the principal problems posed for the nocturnal behaviour of owls are indeed sensory, the solution to those problems involves more than sensory adaptations. Habitual nocturnal behaviour amongst birds would seem to be dependent upon behavioural, as well as sensory, adaptations.

The principal species discussed here is the Tawny Owl *Strix aluco*. The visual and auditory capacities of this species have been more comprehensively studied than those of any other bird, and many aspects of its natural history have been studied in detail. The Tawny Owl has a wide but discontinuous distribution in the palearctic and oriental zoogeographical regions. Its preferred habitat is closed canopy broad-leaved deciduous woodland, but it will inhabit coniferous and more open woodland types, parkland and the centres of large cities as long as mature trees are present (Beven 1956, Mikkola 1983). It is argued that the sensory adaptations of this and other nocturnal species are very similar and most of the problems discussed here concerning the Tawny Owl apply generally to nocturnal owl species.

## Vision at low light levels

### Absolute sensitivity

Field observations have long been interpreted as evidence that the visual sensitivity in owls is higher than in Man. Indeed the assumption of high sensitivity, coupled with evidence that owl retinae contain many rod photoreceptors was part of the original evidence used to support the duplicity theory of vision (Schultze 1867). The assumed high visual sensitivity of owls was correlated with the large size, tubular shape and frontal placement of owl eyes compared with those typically found in diurnal birds (Fig. 1), and these anatomical features became regarded as adaptations concerned with the nocturnal habit. However, how these particular features were supposed to facilitate high sensitivity was not discussed in detail (e.g., Walls 1942, Tansley 1965).

The assumption of high visual sensitivity in owls was questioned by evidence which suggested that the visual detection of infra-red radiation could mediate prey capture in the Tawny Owl (Vlinderplanck 1934). However, the ocular media of this

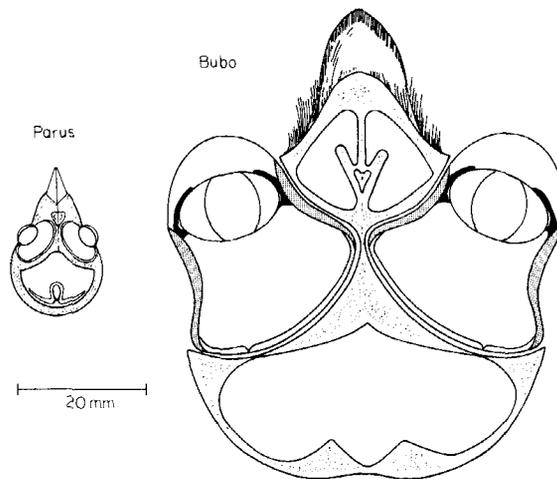


Figure 1. Drawings of horizontal sections through the head of the Black-capped Chickadee *Parus atricapillus* and the Great Horned Owl *Bubo virginianus*. Redrawn to scale from Wood (1917). In *Parus* eye shape, size and position are typical of diurnal Passeriforme species, in *Bubo* eye shape and position are typical of other owl species, and eye size is similar to that of the Tawny Owl.

bird were subsequently shown to be virtually opaque to infra-red radiation (Matthews & Matthews 1939).

The first experimental studies of visual sensitivity suggested that owl eyes were between 10 and 100 times more sensitive than that of Man (Hecht & Pirenne 1940, Dice 1945). However, neither of these studies measured absolute sensitivity directly, nor was it claimed that stimuli were calibrated with a high degree of accuracy. More recent analysis of visual sensitivity in Tawny Owls has led to a more modest conclusion in that absolute sensitivity in these birds was found to be higher than that of Man by an average of 2.5-fold (Martin 1977). This difference is within the normal, five-fold, range of absolute visual sensitivity found in the healthy human population and also within the range by which individual human thresholds may differ on a daily basis (Pirenne *et al.* 1957). Thus we might expect to find individual human subjects with visual sensitivity greater than that of individual Tawny Owls.

The 2.5-fold average difference in sensitivity between Owl and Man can be accounted for by a difference in the maximum brightness of the retinal image produced in the owl and human eye (Martin 1982). This suggests that the retinae of these two eyes are of similar sensitivity; there are good theoretical reasons for believing that this should be the case. For example, it has been argued that the human retina has attained the absolute limit of visual sensitivity, which is dictated by the quantal nature of light and the signal-to-noise limitations of extracting information from an array of photoreceptors which are responding at the limits of their sensitivity (Pirenne 1962, Barlow 1981). Since the rod photoreceptors of Man and Owl are very similar in respect of three parameters—dimensions, spectral sensitivity and specific absorbance of their visual pigments (Bowmaker & Martin 1978, Bowmaker & Dartnall 1980)—they would absorb a similar proportion of the light quanta that reaches them (Martin 1982). Therefore unless maximum retinal image brightness can be greatly increased over that of the human eye, visual sensitivity much in excess of that in humans is unlikely to be found in any owl species.

An hypothetical vertebrate eye with a focal length similar to that of the Tawny Owl [ $\approx 17$  mm; (Martin 1982)] but whose visual sensitivity was 10 or 100 times that of Man, would require entrance pupil diameters of 25 mm and 81 mm respectively. Clearly such eyes would have to be both absolutely large as well as peculiar in their general design—quite unlike the typical tubular shape of the owl eye (Fig. 1), and indeed quite unlike any vertebrate eye so far described (Martin 1983). Furthermore, it has been argued that a relatively long focal length, such as that found in the Tawny Owl's eye, is an essential feature of an eye designed to function throughout the naturally-occurring range of night time luminance levels (Martin 1982). This is because a long focal length will produce a large retinal image and thus permit flexibility in the way the retinal image is sampled by the photoreceptor array. Such flexibility is necessary to maximise the amount of information which can be extracted from the retinal image over a wide range of luminances (Snyder *et al.* 1977). [The naturally occurring nocturnal luminance range is discussed below]. Thus, given this constraint of a long focal length, it would seem that an owl eye with an image brightness even 10, let alone 100 times higher than that of Man, is unlikely to have evolved.

Absolute visual sensitivity in the Tawny Owl is approximately 100 times higher than that of the Pigeon *Columba livia* (Blough 1955) (Fig. 2), a strictly diurnal bird species. This difference can be attributed principally to differences in retinal neural mechanisms, since pigeon and owl eyes differ little in both the maximum brightness of their retinal image and in the parameters of individual rod photoreceptors (Martin 1982).

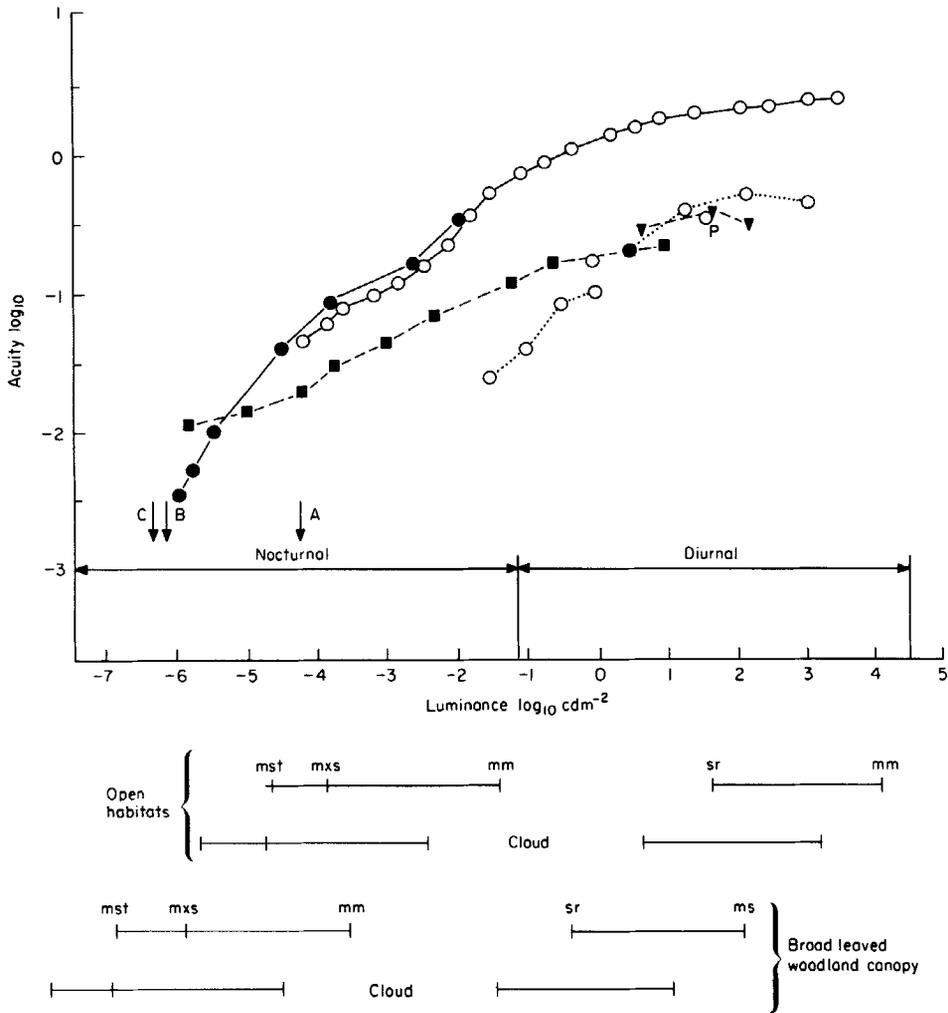


Figure 2. Top. Minimum separable visual acuity (expressed as  $\log_{10}$  of the reciprocal of the minimum separable angle) as a function of luminance in Man, Pigeon and two owl species ( $\text{cdm}^{-2}$ , candela per square metre).

Bottom. Naturally occurring luminance levels of a grass or leaf litter substrate during day-time and night-time. Luminance ranges within open habitats and under a broad leaved woodland canopy are shown. Each horizontal bar indicates the maximum likely range of luminance which can be experienced in the habitat under the conditions indicated. Day-time luminance levels (the four horizontal bars to the right) are for latitude  $50^\circ$  at the time of the summer solstice, and show the luminance range from sunrise (*sr*) to maximum midday sun (*ms*). Night-time luminance levels (the four horizontal bars to the left) show the range from maximum moonlight (*mm*) to minimum starlight (*mst*); maximum starlight without moon (*mxs*) is also indicated. Luminance levels experienced under maximum cloud cover are shown for both day- and night-time in the two habitat types. The total diurnal luminance range of  $5.6 \log_{10}$  units is the range which may be experienced between maximum sunlight without cloud cover in an open habitat, and at sunrise with cloud cover beneath woodland canopy. The total nocturnal luminance range of  $6.31 \log_{10}$  units is the range from maximum moonlight without cloud in an open habitat, to minimum starlight with cloud beneath the woodland canopy. Points A, B and C indicate the mean behaviourally-determined absolute visual threshold of Pigeon, Man and Owl respectively (modified from Martin, 1982). (●—●) Human; Pirene *et al.* (1957); (○—○) Human; Shlaer (1937); (■—■) Owl *Bubo*; Fite (1973); (▼—▼) Owl *Strix*; Martin and Gordon (1974); (○<sub>P</sub>) Pigeon; *Columba*, Blough (1971); (○...○) Pigeon; Hodos and Leibowitz (1977), Hodos *et al.* (1976).

### Spatial resolution

Theoretical considerations of retinal image analysis (Snyder *et al.* 1977) suggest that spatial resolution at low light levels in Man and Owls should be similar, and there is experimental evidence that this is so (Fig. 2). Spatial resolution of any image must decrease with luminance level regardless of the device (e.g., photoreceptors, photographic emulsion, photodiodes, etc) used to analyse the image. High spatial resolution of an image of low luminance is not possible theoretically, regardless of the degree of contrast in the image (Snyder *et al.* 1977).

There is commercially available equipment which serves to enhance human visual resolution at night; it does so either by increasing the size and brightness of the image, and/or by unemploying a non-visible part of the electromagnetic spectrum which is at a higher intensity than the visible wavelengths (e.g., infra-red). Because of the similarities in rod photoreceptor parameters in human and owl eyes, it may be seen that an owl could achieve spatial resolution superior to that of Man by employing only one element of the strategy used by the commercial devices, i.e., increased image-size and brightness. However, as argued above it would seem that there is little possibility that this can occur.

### Vision at high light levels

Behavioural (Martin & Gordon 1974a,b), electrophysiological (Martin *et al.* 1975) and anatomical (Bowmaker & Martin 1978) studies all furnish evidence that the Tawny Owl visual system functions adequately at high, day-time, light levels. Evidence from analysis of the visual pigments of cone photoreceptors and their associated oil droplets (Bowmaker & Martin 1978) corroborates behavioural investigations of wavelength discrimination (Martin 1974) which suggest that the owl is not capable of such subtle wavelength discriminations as diurnal bird species such as the Pigeon *Columba livia* (Wright 1979). However, Figure 2 shows that maximum spatial resolution in two owl species—the Tawny Owl and the Great Horned Owl *Bubo virginianus*—and in the pigeon is very similar and is attained in all three species at a similar luminance level. This implies that, during the day-time, owls are not at a visual disadvantage compared with at least some obligate diurnal bird species, such as the Pigeon. All of these species are, however, inferior in their maximum spatial resolution compared with either man or with a diurnal bird of prey, the American Kestrel *Falco sparverius* (Hirsch 1982). Maximum resolution in these latter species is approximately five times higher than in the tawny owl at a similar high luminance level.

### Binocular vision

The owls in general are often regarded as having the most frontally placed eyes amongst the birds (Fig. 1) and that this has resulted in them possessing some of the largest binocular fields to be found in this vertebrate class. However, in the Tawny Owl the optic axes of the eyes are not parallel, but diverge by  $55^\circ$  and maximum binocular field width equals only  $48^\circ$  (Martin 1984a). By comparison, the optic axes in Man and Pigeon diverge by  $10^\circ$  and  $132^\circ$  respectively and the maximum widths of their binocular fields are approximately  $140^\circ$  and  $22^\circ$ . The function of binocularity and the factors which may account for the known interspecific differences in binocular field width amongst vertebrates has received much discussion, but there is little consensus on either of these topics (Martin 1984a). Thus it is not clear whether the relatively large binocular field of the owl compared with that of the Pigeon can be

correlated directly with the nocturnal habit, as has often been assumed (Walls 1942, Tansley 1965, Mikkola 1983, Burton 1985).

### **Vision in relation to naturally occurring light levels**

Figure 2 shows that the light levels which may be experienced within the nocturnal environment are highly variable. Depending upon such factors as the degree of vegetation cover, the altitude and phase of the moon and the presence of cloud, incident light levels at night may differ by over one million-fold. In addition, the reflectance of natural substrates can differ by a factor of up to 100-fold [e.g., fresh snow compared with black soil (Krinov 1947)] so the range of luminance levels an eye might be exposed to after sunset may cover eight orders of magnitude. Thus, for the purposes of understanding the sensory problems of the nocturnal habit the simple 'nocturnal' label can be misleading. For example, nocturnal bird species which live in predominantly open habitats such as the majority of the Caprimulgiformes (nightjars, etc.), and some owls, may never experience the lowest naturally occurring luminance levels to which the nocturnal woodland owls are frequently exposed.

Figure 2 indicates that, even under cloud cover, the sky itself should always be visible to both Man and Tawny Owl (though not to the Pigeon) and thus some kind of pattern vision should be possible by viewing objects in silhouette against the sky. However, under a woodland canopy the minimum natural luminance even of grass or leaf litter, let alone black earth or similar low reflectance substrates, is low enough to render these substrates invisible both to Man and to Tawny Owl. Also, because the reflectances of many natural substrates and objects are very similar (Krinov 1947), the visual scene will be of low contrast. So there will be many occasions, especially under a vegetation canopy, when even large objects will be invisible despite being viewed at average luminance levels which are above absolute visual threshold. While this invisibility of natural objects can be readily verified by personal 'observation', predicting the nature, size and distance at which various objects might just be detected at a given luminance is problematic, principally because there is little information on spatial resolution beyond measures of minimum separable acuity (involving high contrast stimuli) at low luminance levels. However, something of the problem can be appreciated by the following prediction which can be made from the data of Figure 2: at a luminance level approximately 10 times higher than absolute visual threshold (i.e., in the middle of the luminance range which commonly occurs under a broad-leaved woodland canopy at night) even a dark-coloured rodent 60 mm in length walking across snow will be invisible to both Man and owl until within a viewing distance of 3 m.

It would seem, therefore, that at the lower naturally occurring light levels the visual system can only be used both by Man and Owls to control behaviour with respect to large objects, and cannot detect such objects as small branches or prey items.

## **Audition**

### **Auditory localization**

It has been clearly demonstrated that audition can play an important part in prey capture by owls. Barn Owls *Tyto alba* can detect and capture live rodent prey by pouncing from a perch in total darkness, guided only by the sound that the animal

produces as it moves through leaf litter (Payne 1971). The outer ears of many owl species are large, and exhibit complex bilateral asymmetry in size, shape and position (Norberg 1977). It has been proposed that these anatomical features are an essential part of the auditory localization system, functioning principally in the vertical location of sounds in the frontal plane (Norberg 1978, Knudsen & Konishi 1979). While studies of auditory localization in the Barn Owl (Knudsen *et al.* 1979), make it clear that audition itself is sufficient to mediate prey capture, it is also clear that the Barn Owl's ability to localize white noise sound sources (which approximate leaf litter rustle) is not superior to that of Man (Mills 1958, Roffler & Butler 1968).

### **Auditory sensitivity**

As is the case with visual sensitivity, it was proposed that owls were markedly superior to man in their absolute auditory sensitivity (Konishi 1973). However, this conclusion was based upon the result obtained from a single subject, and it is known (Sivian & White 1933, Masterton *et al.* 1969) that measures of minimum auditory thresholds exhibit large variability due to both intraspecific and procedural differences.

More detailed interspecific comparisons of auditory thresholds in birds and mammals have led to the conclusion that both owls and mammals, including Man, have similar absolute auditory sensitivity and that this sensitivity coincides with the auditory masking level produced by minimum naturally occurring ambient sound (Martin 1984b). This suggests that the ultimate limit on auditory sensitivity in vertebrates is determined not by physiological factors, such as thermal agitation of fluids within the cochlea (Harris 1967), or 'self-noise' (Diercks & Jeffress 1962), but by a source common to all non-aquatic vertebrates: the minimum ambient sound level. Auditory sensitivity greater than that dictated by the minimum ambient sound is unlikely to evolve, since sounds below this minimum will always be inaudible due to the auditory masking produced by the ambient noise.

It may be concluded, therefore, that under any given environmental conditions the ability of both owls and man to detect and locate a particular sound is likely to be very similar.

### **The sensory problem of nocturnality**

The conclusion to be drawn from the above discussion of both the visual and auditory capacities of owls is that an explanation of the ability of these birds to be active at night, based only upon high sensory sensitivity, is untenable. Owls possess a visual system whose absolute sensitivity and resolution approach the theoretical maxima (dictated principally by the quantal nature of light). Even so, vision cannot function adequately to mediate prey detection or flight in the spatially complex environment of a woodland habitat under the full range of nocturnal light conditions. Also, although auditory sensitivity in owls appears to have reached the ultimate limit possible in the aerial environment, audition cannot of itself permit the detection of obstacles, although it can clearly serve in the detection of prey items which either emit sounds or make sounds as they move.

It has been hypothesized that much, if not all, human perception is dependent upon cognition as well as immediate sensory input (see, for example, Gregory (1974), Frisby (1979)). This is exemplified by studies of car-driving at night-time. In completing this task people frequently, sometimes habitually, drive in a manner which is beyond the control of information immediately available via their visual system (Hills 1980). Accidents are usually avoided, however, since the visual

information that is available (e.g., detection of road markings and lights on other vehicles) is supplemented by general knowledge of the nature of roads and traffic and specific knowledge of local topography.

Since both Man and Tawny Owl are equally restricted in their main tele-receptive sensory capacities, a similar analysis would seem applicable to the nocturnal behaviour of the Tawny Owl. Thus, it may be proposed that knowledge of both the general characteristics of the environment and specific details of the local topography are important for the mediation of the bird's behaviour under nocturnal conditions. The nocturnal habit of owls must be dependent upon behavioural and cognitive adaptations, as well as sensory adaptations.

### Natural history of the tawny owl

Long-term studies of the natural history of Tawny Owls (Southern 1970, Hirons 1976, 1985, Hardy 1977) have shown that this species exhibits a number of unusual behavioural traits. Perhaps the most important single feature of the Tawny Owl's natural history is its sedentary habit which is manifested by its high degree of territoriality.

The birds are territorial throughout the year and territorial boundaries alter little, if at all, during a bird's life time. The defended area supplies all of the food requirements of the individual bird. Also, both male and female share the same territory throughout the year, although there is some evidence that females occasionally move territories. In these features the Tawny Owl differs not only from the majority of bird species, including sympatric diurnal raptors of similar habitat preferences (e.g., the Sparrowhawk *Accipiter nisus* and Goshawk *A. gentilis* (Newton 1979, Marquiss & Newton 1981, Kenward 1982)), but also appears to differ from the majority of other owl species.

No other owl species has received such detailed study as the Tawny Owl, but summarised data for Western Palearctic species of owl (Cramp 1985) indicates that only in the Ural Owl *Strix uralensis* do individuals behave like the Tawny Owl and typically defend an exclusive hunting and breeding territory throughout the year. Both the Tawny and Ural Owls are nocturnal, with extensive woodland the preferred hunting and breeding habitat.

There are, however, species in which individuals or pairs have, on occasion, been reported as maintaining a territory throughout the year (Barn Owl, Eagle Owl *Bubo bubo*, Little Owl *Athene noctua*, Long-Eared Owl *Asio otus*, Tengmalm's Owl *Aegolius funereus*). These species are also regarded as nocturnal but they prefer habitats which are essentially more open than those frequented by the Tawny and Ural Owls, with scattered trees or woodland glades and margins an essential component. It would be of interest to know more detail of the particular circumstances (especially habitat characteristics) which are correlated with the occurrence of a sedentary habit in certain individuals of these species.

No diurnal and/or crepuscular species of Western Palearctic owl (Snowy Owl *Nyctea scandiaca*, Pygmy Owl *Glaucidium passerinum*, Hawk Owl *Surnia ulula*, Great Grey Owl *Strix nebulosa*, Short-Eared Owl *Asio flammeus*) appears to be as territorial as the nocturnal owls. In these species the majority of pairs maintain a territory (which need not coincide with the hunting range) during the breeding season only.

Of the Western Palearctic species only the Scops Owl *Otus scops* presents an exception to these general conclusions in that the species is regarded as essentially nocturnal, but there are no records of sedentary individuals or pairs. Scops Owl requires the cover of trees for roosting and nesting but hunt large insect prey over

open ground. Northern populations of the species are migratory, while southern ones are partially migratory or resident. However, it is not known whether any of the resident individuals maintain a territory outside the breeding season although local populations are known to be gregarious at this time.

In the case of the Tawny Owl, possession of a territory seems essential for the survival of the bird during the annual cycle. A high proportion ( $\approx 60\%$ ) of young birds die each year, many of starvation, and it is believed that the majority of these birds do not hold territories and that their starvation is directly attributable to this factor (Hirons *et al.* 1979, Hirons 1985). Mortality amongst territory holders is less than 15% per annum. Once established in its territory (in Southern England, in the preferred habitat type, approximately 12 ha) an individual owl (both male and female alike) is likely to remain in that area all of its life (average life expectancy, 5+ years: oldest ringed bird, 18 years 7 months). Territorial boundaries are defended vigorously against neighbours and non-territorial intruders are excluded from territories. However, if a territory becomes vacant it is normally re-occupied before the adjacent resident birds expand into it.

The dietary spectrum of the Tawny Owl is broad. It seems that since Tawny Owls forage exclusively within the boundaries of their territory, they must turn to alternative prey items during the annual cycle. Thus, unlike the owls of similar body weight, but which live in open habitats and tend to be specialist feeders (e.g., the Short-Eared Owl), the Tawny Owls' response to a shortage of prey of optimum size (small mammals and birds) is not to forage further afield, but to forage within its territory for smaller items, such as earthworms, which at certain times of the year can form a substantial proportion of the diet (Southern 1970).

Not only do the birds remain in their territory throughout their life, but they are also consistent in the way that the territory is used (Hardy 1977). Thus, hunting, roosting and feeding tend to take place at regularly-used perches. The hunting technique is predominantly 'perch-and-pounce', where the owl waits for prey to come into the vicinity of the chosen perch. It does not quarter for prey on the wing as do owls of open habitats (e.g., the Short-Eared Owl) although hunting Tawny Owls have been recorded as flying into a roost of small passerines (Cramp 1985). Hunting on the wing has been recorded in the Tawny Owl but this was apparently anomalous behaviour (Nilson 1978). It was recorded in summer at a high latitude when light levels were higher than the normal nocturnal range.

It is also noteworthy that Southern *et al.* (1954) concluded that young Tawny Owls, during the protracted period of dependence on their parents (approximately  $2\frac{1}{2}$ –3 months post fledging), make little or no effort to feed themselves, but concentrate on learning their way about the parental territory. Also, there is evidence that even adult Tawny Owls may not always be able to negotiate obstacles within their territory. Thus, when disturbed or surprised at night, Tawny Owls have been known to fly into branches and even tree trunks (Hirons, pers. com.) thus suggesting that vision was not sufficient to guide these birds about obstacles.

## Conclusion

### Territoriality and the nocturnal habit

Many features of the natural history of the Tawny Owl becomes explicable in the light of the sensory limitations and the behavioural and cognitive aspects of nocturnality discussed above. Thus, the high degree of territoriality may be interpreted as essential to permit prey capture and general mobility when light levels become limiting for the immediate visual guidance of flight and other behaviour. To

stray out of the territory (for example in response to a shortage of optimal sized prey) is of no advantage since it is specific knowledge of landmarks and the regularly used perches that is essential for prey capture and movement under restricted sensory input. For similar reasons invasion of an adjacent territory is of little value. The use of the 'perch-and-pounce' hunting technique, employing a limited number of perches, is also comprehensible, since the use of these regular perches will facilitate the accumulation of the topographical knowledge required to mediate prey capture using audition alone.

### **The value of topographical knowledge**

The adaptive function of avian territoriality is not generally understood. This is because the proximate and ultimate factors underlying territoriality are not the same in all species and indeed more than one factor may be operating simultaneously (Wilson 1975, Davies 1978). Hinde (1956: 349) proposed that 'familiarity with food sources and refuges from predators', could be regarded as one of the functions of territorial behaviour. However, most recent work on territoriality has tended to favour analyses using metaphors drawn from economics in which emphasis has been upon the costs and benefits involved in the defence of resources within the territory.

Familiarity with food sources and refuges from predators are likely to be benefits which accrue as the result of protracted residence in any one site. However, in the case of the Tawny Owl it would seem that to be an habitual nocturnal species, detailed topographical knowledge, gained through protracted residence in a restricted area, is essential for survival. If an economical metaphor is to be employed, then rather than regard the high degree of territoriality in the Tawny Owl as involving only the defence of a resource (average territory size in Tawny Owls is related primarily to average abundance of prey within an area (Southern 1970, Hirons 1976, Hardy 1977, Hirons 1985), and nest sites may sometimes be a limited resource (Lundberg 1979, Wardhough 1984)), it might be convenient to view the situation as also involving the 'protection of an investment'.

Defence of a resource implies that some commodity within the territory has a value which can be readily appropriated by other individuals. However, topographical knowledge of a territory has value to the resident individual only. It cannot be transferred to another individual nor can it be transferred by the resident to another site. However, topographical knowledge, and hence the value of holding a particular territory is likely to increase with length of residence in the same way that an investment increases its value over time. (In the Tawny Owl Southern & Lowe (1986) have argued that continued occupancy of a territory results in greater hunting skill. This is reflected in the data of Southern (1970) which suggest that the probability of successful breeding increases with the length of time that the territory has been occupied.) At some point the value of this investment may come to outweigh that of the defended resources. Whether it does so for a particular species or individual will depend upon many factors concerning the quality of the defended resources and the value of topographical knowledge in the natural behaviour of the species.

In the Tawny Owl, because of the necessity of detailed topographical knowledge for nocturnal mobility and prey capture throughout the year, the point at which the value of this knowledge exceeds the value of the defended resources may be reached frequently. The observations that resident Tawny Owls remain on territory and accept a diversity of prey items, many of which are below optimal size, e.g., earthworms and beetles (Southern 1970) and/or use less favoured nest sites (e.g., a

scrape on the ground rather than a hollow tree (Mikkola 1983) may both be explained in these terms.

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### References

- BARLOW, H.B. 1981. Critical limiting factors in the design of the eye and visual cortex. *Proc. R. Soc. Lond. B.* 212: 1–34.
- BEVEN, G. 1956. The food of Tawny Owls in London. *London Bird Rep.* 29: 57–72.
- BLOUGH, D.S. 1955. Method for tracing dark adaptation in the pigeon. *Science* 121: 703–704.
- BLOUGH, P.M. 1971. The visual acuity of the pigeon for distant targets. *J. exp. Anal. Behav.* 15: 57–68.
- BOWMAKER, J.K. & DARTNALL, H.J.A. 1980. Visual pigments of rods and cones in a human retina. *J. Physiol. (Lond.)* 298: 501–511.
- BOWMAKER, J.K. & MARTIN, G.R. 1978. Visual pigments and colour vision in a nocturnal bird, *Strix aluco* (Tawny Owl). *Vision Res.* 18: 1125–1130.
- BURTON, J.A. 1985. *Owls of the World* (Second Edition). London: Lowe.
- CRAMP, S. (ED.). 1985. *The birds of the Western Palearctic*, Vol. 4. Oxford: Oxford University Press.
- DAVIES, N.B. 1978. Ecological questions about territorial behaviour. *In* Krebs, J.R. & Davies, N.B. (eds), *Behavioural Ecology: An Evolutionary Approach*: 317–350. Oxford: Blackwell.
- DICE, D.L. 1945. Minimum intensities of illumination under which owls can find dead prey by sight. *Am. Nat.* 79: 384–416.
- DIERCKX, K.J. & JEFFRESS, L.A. 1962. Interaural phase and the absolute threshold for tone. *J. Acoust. Soc. Am.* 34: 981–984.
- FITE, K.V. 1973. Anatomical and behavioural correlates of visual acuity in the Great Horned Owl. *Vision Res.* 13: 219–230.
- FRISBY, J. 1979. *Seeing, illusion, brain and mind*. Oxford: Oxford University Press.
- GREGORY, R.L. 1974. *Concepts and mechanisms of perception*. London: Duckworth.
- GRIFFIN, D.R. & SUTHERS, R.A. 1970. Sensitivity of echolocation in cave swiftlets. *Biol. Bull.* 139: 495–501.
- HARDY, A.R. 1977. *Hunting ranges and feeding ecology of owls in farmland*. PhD Thesis, Aberdeen University.
- HARRIS, G.G. 1967. Brownian motion in the cochlear partition. *J. Acoust. Soc. Am.* 44: 176–186.
- HECHT, S. & PIRENNE, M.H. 1940. The sensitivity of the nocturnal Long Eared Owl in the spectrum. *J. Gen. Physiol.* 23: 709–717.
- HILLS, B.L. 1980. Vision, visibility and perception in driving. *Perception* 9: 183–216.
- HINDE, R.A. 1956. The biological significance of the territories of birds. *Ibis* 98: 340–369.
- HIRONS, G.J.M. 1976. A population study of the Tawny Owl (*Strix aluco*) and its main prey species in a woodland. D Phil Thesis, Oxford University.
- HIRONS, G.J.M. 1985. The effects of territorial behaviour on the stability and dispersion of Tawny Owl (*Strix aluco*) populations. *J. Zool. Lond.* (in press).
- HIRONS, G., HARDY, A. & STANLEY, P. 1979. Starvation in young Tawny Owls. *Bird Study* 26: 59–63.
- HIRSCH, J. 1982. Falcon visual sensitivity to grating contrast. *Nature (Lond.)* 300: 57–58.
- HODOS, W. & LEIBOWITZ, R.W. 1977. Near-vield visual acuity of pigeons: effects of scotopic adaptations and wavelength. *Vision Res.* 17: 463–467.
- HODOS, W., LEIBOWITZ, R.W. & BONBRIGHT, J.C. 1976. Near-field visual acuity of pigeons: effects of head position and stimulus. *J. Exp. Anal. Behav.* 25: 129–141.
- KENWARD, R.E. 1982. Goshawk hunting behaviour, and range size as a function of food and habitat availability. *J. Anim. Ecol.* 51: 69–80.
- KNUDSEN, E.I. & KONISHI, M. 1979. Mechanisms of sound localization in the Barn Owl (*Tyto alba*). *J. Comp. Physiol.* 133: 13–21.
- KNUDSEN, E.I., BLASDEL, G.G. & KONISHI, M. 1979. Sound localization by the Barn Owl (*Tyto alba*) measured with the search coil technique. *J. Comp. Physiol.* 133: 1–11.
- KONISHI, M. 1973. How the owl tracks its prey. *Am. Sci.* 61: 414–424.
- KONISHI, M. & KNUDSEN, E.I. 1979. The oil bird: hearing and echolocation. *Science* 204: 425–427.
- KRINOV, E.L. 1947. Spectrol, naye otrazhatel 'naya sposobnost' prirodnykh obrazovani. Izadaltel'sto Akad. U.S.S.R. (translation by G. Belkov, National Research Council, Canada. Technical Translation TT-439, 1953).
- LUNDBERG, A. 1979. Residency, migration and a compromise: adaptations to nest-site scarcity and food specialization in three Fenoscandian owl species. *Oecologia. (Berl.)* 41: 273–281.

- MARTIN, G.R. 1974. Color vision in the Tawny Owl (*Strix aluco*). J. Comp. Physiol. Psychol. 86: 133-142.
- MARTIN, G.R. 1977. Absolute visual threshold and scotopic spectral sensitivity in the tawny owl, *Strix aluco*. Nature (Lond). 268: 636-638.
- MARTIN, G.R. 1982. An owl's eye: schematic optics and visual performance in *Strix aluco*. L. J. Comp. Physiol. 145: 341-349.
- MARTIN, G.R. 1983. Schematic eye models in vertebrates. In: Ottoson D. (ed). Progress in Sensory Physiology, Vol. 4: 43-81. Berlin, Heidelberg, New York: Springer.
- MARTIN, G.R. 1984a. The visual fields of the Tawny Owl, *Strix aluco* L. Vision Res. 24: 1739-1751.
- MARTIN, G.R. 1984b. An environmental limit on absolute auditory sensitivity in non-aquatic vertebrates. Behav. Process. 9: 205-221.
- MARTIN, G.R. & GORDON, I.E. 1974a. Increment-threshold spectral sensitivity in the Tawny Owl (*Strix aluco*). Vision Res. 14: 615-620.
- MARTIN, G.R. & GORDON, I.E. 1974b. Visual acuity in the Tawny Owl (*Strix aluco*). vision Res. 14: 1393-1397.
- MARTIN, G.R., GORDON, I.E. & CADLE, D.R. 1975. Electroretinographically determined spectral sensitivity in the Tawny Owl (*Strix aluco*). J. Comp. Physiol. Psychol. 89: 72-78.
- MARQUISS, M. & NEWTON, I. 1981. A radio-tracking study of the ranging behaviour and dispersion of European Sparrowhawks *Accipiter nisus*. J. Anim. Ecol. 51: 111-133.
- MASTERTON, B., HEFFNER, H. & RAVIZZA, R. 1969. The evolution of human hearing. J. Acoust. Soc. Am. 45: 966-985.
- MATTHEWS, L.H. & MATTHEWS, B.H.C. 1939. Owls and infra-red radiation. Nature (Lond). 143: 983.
- MIKKOLA, H. 1983. Owls of Europe. Calton: Poyser.
- MILLS, A.W. 1958. On the minimum audible angle. J. Acoust. Soc. Am. 30: 237-246.
- NEWTON, I. 1979. Population Ecology of Raptors. Berkhamstead: Poyser.
- NILSSON, I.N. 1978. Hunting in flight by Tawny Owl *Strix aluco*. Ibis 120: 528-531.
- NORBERG, R.A. 1977. Occurrence and independent evolution of bilateral ear asymmetry in owls and implications on owl taxonomy. Phil. Trans. R. Soc. Lond. B. 280: 375-408.
- NORBERG, R.A. 1978. Skull asymmetry, ear structure and function, and auditory localization in Tengmalm's owl, *Aegolius funereus* (Linne). Phil. Trans. Roy. Soc. Lond. B. 282: 325-410.
- PAYNE, R.S. 1971. Acoustic location of prey by Barn Owls (*Tyto alba*). J. Exp. Biol. 54: 535-573.
- PIRENNE, M.H. 1962. Absolute thresholds and quantum effects: In Davson H (ed) The Eye, Vol 2: 123-140. New York: Academic Press.
- PIRENNE, M.H., MARRIOTT, F.H.C. & O'DOHERTY, E.F. 1957. Individual differences in night vision efficiency. Med. Res. Council. GB. Spec. Rep. Ser. 294.
- ROEFFLER, S.K. & BUTLER, R.A. 1968. Factors that influence the localization of sound in the vertical plane. J. Acoust. Soc. Am. 43: 1255-1259.
- SCHULTZE, M. 1867. Uber Stabchen und Zapfen der Retina. Archiv für mikroskopische anatomie und entwicklungsmechanik 3: 215-247.
- SHLAER, S. 1937. The relation between visual acuity and illumination. J. Gen. Physiol. 21: 165-188.
- SIVIAN, L.J. & WHITE, S.D. 1933. On minimal audible sound fields. J. Acoust. Soc. Am. 4: 288-321.
- SNYDER, A.W., LAUGHLIN, S.B. & STAVENGA, D.G. 1977. Information capacity of eyes. Vision Res. 17: 1163-1175.
- SOUTHERN, H.N. 1970 The natural control of a population of tawny owls (*Strix aluco*). J. Zool. Lond. 162: 197-285.
- SOUTHERN, H.N. & LOWE, V.P. 1968. The pattern and distribution of prey and predation in Tawny Owl territories. J. Anim. Ecol. 37: 75-97.
- SOUTHERN, H.N., VAUGHAN, R. & MUIR, R.C. 1954. The behaviour of young Tawny Owls after fledging. Bird Study 1: 101-110.
- TANSLEY, K. 1965. Vision in vertebrates. London: Chapman and Hall.
- VANDERPLANCK, F.L. 1934. The effect of infra-red waves on Tawny Owls (*Strix aluco*). Proc. Zool. Soc. Lond. 505-507.
- WALLS, G.L. 1942. The vertebrate eye and its adaptive radiation. Michigan: Cranbrook Institute of Science.
- WARDHOUGH, A.A. 1984. Wintering strategies of British Owls. Bird Study 31: 76-77.
- WILSON, E.O. 1975. Sociobiology. Cambridge, Mass: Harvard Univ. Press.
- Wood, C.A. 1917. The fundus oculi of birds. Chicago: Lakeside Press.
- WRIGHT, A.A. 1979. Color-vision psychophysics: a comparison of pigeon and human. In Granda, A.M. & Maxwell, J.H. (eds). Neural mechanisms of Behaviour in the Pigeon: 89-127. London: New York: Plenum.