Restricted range of ocular accommodation in barn owls (Aves: Tytonidae)

H.C. Howland*, M.J. Howland*, K. Schmid and J.D. Pettigrew**

Vision, Touch and Hearing Research Centre, Department of Physiology and Pharmacology, The University of Queensland, 4072, Queensland, Australia

Accepted November 28, 1990

Summary. In an examination of the focusing abilities of 15 species of owls, the North American barn owl, Tyto alba pratincola (Bonaparte 1838), was an outstanding accommodator, having a range of accommodation exceeding 10 diopters (Murphy and Howland 1983). Using comparable methods, we examined the accommodation of 4 specimens of the Australian barn owl, Tyto alba delicatula (Gould 1837). We failed to elicit accommodation greater than two diopters, and most stimuli failed to evoke any discernable accommodation at all. Furthermore, examination of other Australian tytonid owls, the grass owl, T. longimembris, the sooty owl, T. tenebricosa, and both the mainland and Tasmanian subspecies of the masked owl, T. novaehollandiae novaehollandiae and T. novaehollandiae castanops, also failed to reveal anything but very moderate accommodative ranges. We conclude that the outstanding accommodative ability of the American barn owl is truly an exception to the modest accommodative abilities of the tytonid owls generally.

Key words: Photorefraction – Accommodation – Tytonidae – Near vision

Introduction

The technique of photorefraction has enabled new kinds of observations to be made on both the magnitude and the dynamics of accommodation in unrestrained animals. The technique has been applied to a wide variety of different vertebrate eyes, including those of adult and infant humans (Howland and Sayles 1984), penguins (Sivak et al. 1987), flying foxes (Murphy et al. 1983), crocodiles (Fleishman et al. 1988), chickens (Schaeffel and Howland 1988) and owls (Murphy and Howland 1983). In their study of owl accommodation, Murphy and Howland (1983) found an interesting, general relation between the size of the owls and the degree of accommodation which was achieved. Small owls had a greater range of accommodation than larger owls, in keeping with the closer distances at which smaller owls might be expected to deal with prey items. In contravention of this inverse relation between body size and range of accommodation, a single species of moderate size stood apart in having a range of accommodation equal to, or exceeding, that of the smallest owls studied. This species, the North American barn owl, Tyto alba pratincola, from the family Tytonidae, was also distinguished by its separate phylogeny from the other owls studied, all of which were in the family Strigidae. The family Tytonidae is known for its highly specialised auditory system when compared to the more visual Strigidae (Konishi 1973; Volman and Konishi 1989).

Because the American barn owl was the only tytonid owl that Murphy and Howland (1983) investigated, the possibility remained that great accommodative ability was shared by all owls of the family Tytonidae. In the present study we sought to investigate the unexpected accommodative behaviour of Tyto alba pratincola in a comparative way by including other members of the family. Australia has 5 different species in the genus Tyto, covering a range of size and habits. We were able to use photorefraction to examine 4 species of Australian tytonid, plus one additional subspecies. All 4 Australian species of tytonid owl showed modest accommodative abilities, pointing to the exceptional nature of the American barn owl in this regard, and raising questions regarding singularity of the barn owl species, Tyto alba.

Materials and methods

Animals. We used captive animals kept in flight cages at the Veterinary Farm, University of Queensland and at the Featherdale Wild Animal Park in Doomsday, New South Wales. On the days of testing, Queensland birds were brought to the central campus in St. Lucia and examined in darkened rooms in the Ritchie building. In Queensland, birds were held by their legs by one of us while
the other operated the refractive equipment. After initially failing to find a range of accommodation like that found in the N. American barn owl we attempted to habituate these birds to a screen perch while their feet were tethered with leather thongs ('jesses'), as is the practice in falconry. Adaptation to the perch was facilitated by the administration of small (1 mg intramuscular) of the anesthetic, ketamine, which had a tranquilizing effect on the animals. We examined two Australian barn owls (Tyto alba delicatula), two grass owls (Tyto longimembris), and two greater sooty owls (Tyto tenebricosa) in our laboratory. Birds in Featherdale (two barn owls, Tyto alba delicatula, one mainland masked owl, Tyto novaehollandiae novaehollandiae and two Tasmanian masked owls, Tyto novaehollandiae castanops) were examined after dark, during feeding time, in their flight cages where they were unrestrained. Our greatest efforts went into attempting to find appropriate stimuli for accommodation.

Refractive techniques. We used conventional slit retinoscopy with neutralizing lenses, orthogonal and isotropic photorefraction (Howland and Howland 1974; Howland et al. 1983), and (principally) infrared (IR) photorefractometry (Schaefeli et al. 1987) with and without neutralizing lenses. For video photorefraction and keratometry we employed a Panasonic CCTV camera Model WV-BL 200A, with IR filter removed. Most birds in the laboratory were examined at a distance of 1 m, while in flight cages the birds were manipulated at a distance of 3 m. Evaluation of photorefractive images when no neutralizing lenses were used was performed by replaying the videotapes in a frame by frame mode, and noting the eccentricity of the IR-emitting LEDs, as well as the pupil diameter and dark fraction of the pupil. Defocus relative to the camera was computed by the equation (Howland 1985):

\[ \text{Defocus in diopters} = \frac{E}{(P + A + D)} \]

where \( E \) is the distance of the LEDs from the edge of the camera aperture, \( P \) is the pupil diameter of the bird, \( A \) is the camera to subject distance and \( D \) is the fraction of the pupil diameter which remains unilluminated ('dark fraction') when measured orthogonally to the edge of the light reflex (see Fig. 1). With infrared photorefractometry birds were usually refracted in their vertical (90°) meridians as shown in Fig. 1.

In evaluating the data we replayed the videotapes and searched for those portions where the optical quality of the images was good for the birds' behavior was appropriate for measurement we desired to make. We measured the resting refractive state in relaxed animals who appeared to be viewing distant targets. Likewise accommodated was measured in animals who were attending to near targets, usually food items, though we also attempted to elicit accommodation by lunging at the animals, a strategy that Murphy and Howland (1983) had found effective. In computing resting refractive state and accommodative range we averaged several resting hyperopic measurements and several myopic measurements when the animals were accommodating, and then computed the difference between them.

Corneal curvature measurements

We constructed a ring of 8 IR light emitting diodes (diameter = 38 cm) which we placed around the 105 mm f/2.8 Micro-Nikkor lens attached to our IR sensitive video camera. The lens was focused at the closest possible distance (0.41 m). By measuring the size of the circle of lights reflected by the birds' cornea we could determine the radius of curvature of the cornea after the method outlined by Murphy and Howland (1983). Measurements were taken directly from the television monitor screen with a mm ruler or from a digitized image obtained from the video tape with a frame grabber. We calibrated our keratometer with reflections from steel ball bearings of known size. The principal measurement errors were due to the nonlinearity of the monitor screen and the parallax errors involved in the use of the ruler. With the ruler, the precision and accuracy of our measurements for large corneas (40 D) was approx. 0.5 D. The precision of our measurements for smaller corneas (70 D) was also approx. 0.5 D, but our measurements of the smaller ball bearing (71.03 D) showed a systematic error of +0.75 D. We corrected our keratometry readings for this error by assuming that it varied linearly from 0 to 0.75 D in the range 40 to 70 D, and by subtracting the appropriate value from our measurements. Both the precision and accuracy of the measurements were considerably improved when they were made with the frame grabber.

Results

Resting hyperopia

In the absence of an accommodative stimulus, all birds had a resting refractive state which was slightly hyperopic. The magnitude of the hyperopia varied from 1–2 diopters in different individuals and different species (Table 1). This hyperopia tended to be more pronounced in alarmed or angry birds (data not shown).
Accommodation

An appropriate near stimulus, such as a food item, usually resulted in a small accommodative change from the resting hyperopia in an emmetropic or myopic direction. This was visible as a partial reversal in the position of the infra-red reflex (Fig. 1). This change was most difficult to elicit from the grass owls, but was small in all individuals of all species studied (Table 1). The change of accommodative state, although small, was accomplished moderately rapidly (over 5–10 video frames corresponding to 10–20 diopters/s). This is a faster rate than occurs in mammals (Campbell and Westheimer 1960), but not as high as the speeds previously reported in some strigid owls (Murphy and Howland 1983).

Discussion

Large eyes of owls and the retinoscopy artefact

The corneal curvature is a good guide to the overall size of the eye. As can be seen from Table 1, tytonid corneal curvatures range from 35 D to 63 D, indicating eyeball sizes comparable to those of humans. In such large eyes, the artefact of retinoscopy (Glickstein and Millodot 1970) is negligible, and cannot account for the consistent resting hyperopia that we observed in all of our birds.

Resting hyperopia

A slight degree of hyperopia is a common finding in wild animals (Walls 1942). The hyperopia we observed in the resting state of all of our owls tends to conform with this observation. Apparently, hyperopia is a default position which at least ensures that distant targets, helpful for flight, will be in some degree of focus. Another role of resting hyperopia may be that it enables the ac-

Table 1. Corneal, refractive and accommodative data from 4 species, and one subspecies, of tytonid owls. N refers to the number of individual birds examined; n refers to the number of individual measurements that went into the computation of a particular measure. Corneal curvature is expressed in diopters, as is refraction and accommodative range. Astig. = astigmatism; RE = Right eye; LE = Left eye; M = male; F = female; None of the differences in corneal curvature between the two eyes of the same animal was significant.

<table>
<thead>
<tr>
<th>Owl species</th>
<th>N</th>
<th>Corneal curvature</th>
<th>Astig.</th>
<th>Wt  (g)</th>
<th>Refraction</th>
<th>Accommodation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>LE</td>
<td>n</td>
<td>RE</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Barn owl</td>
<td>4</td>
<td>47.2±1.4</td>
<td>5</td>
<td>47.7±0.1</td>
<td>5</td>
<td>none</td>
</tr>
<tr>
<td>Grass owl</td>
<td>2</td>
<td>63.3±1.4</td>
<td>8</td>
<td>61.8±1.8</td>
<td>10</td>
<td>none</td>
</tr>
<tr>
<td>Sooty owl F</td>
<td>1</td>
<td>34.7±0.1</td>
<td>8</td>
<td>34.4±0.1</td>
<td>8</td>
<td>none</td>
</tr>
<tr>
<td>Sooty owl M</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>none</td>
</tr>
<tr>
<td>Masked owl (Mainland)</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>none</td>
</tr>
<tr>
<td>Masked owl (Tasmanian)</td>
<td>1</td>
<td>44.2±0.2</td>
<td>6</td>
<td>44.2±0.3</td>
<td>6</td>
<td>none</td>
</tr>
</tbody>
</table>

* Orthogonal refractive measurement
commodative apparatus to operate with a single, unambiguous direction (toward myopia).

**Absence of large accommodative range**

Our results on 4 different species of Australian tytonid owl are in general confirmation of the results obtained from similar-sized strigid owls by Murphy and Howland (1983). The modest amount of accommodation we observed is comparable in magnitude to the small amounts of accommodation observed in medium-sized strigid owls. This tends to focus the discussion on the extraordinary accommodative powers of the North American barn owl.

**Australian barn owl not like the North American barn owl**

Perhaps the most puzzling finding of the present study was the dramatic difference observed between the accommodative behaviour of the Australian barn owl, *Tyto alba delicatula*, and the North American barn owl, *Tyto alba pratincola*. Whereas the Australian barn owl shows a highly-limited amount of accommodation (around 4 D), the North American barn owl has an extraordinary range of accommodation (>10 D) compared with strigid owls of the same size (Murphy and Howland 1983).

Since all 5 of the Australian representatives of the genus *Tyto* tend to conform, in their accommodative behaviour, to the pattern already described for other owls with the exception of the boreal barn owl, explanations must focus on the difference between the boreal and austral barn owls. Firstly, why should the boreal barn owl not fit the pattern shown by all other owls? Secondly, why should there be such a dramatic difference between members of the same species living in different hemispheres?

**Difference in willingness to accommodate?**

The first possibility is that the difference is one of willingness to accommodate rather than ability to accommodate. We have already drawn attention to the fact that alarmed or angry birds tend toward hyperopia that can be difficult to change, even with an attractive accommodative stimulus such as a food object presented close to the bird. If the Northern hemisphere barn owl had a more congenial disposition, one might argue that accommodation was easier to elicit in this species, rather than arguing that accommodation was fundamentally different. This possible explanation of the difference was uppermost in our minds when we sought out the most tame and tractable owls for our study. It was also for this reason that we developed a portable photorefractor so that we could study birds in their home cages during natural feeding activity. We consider that our birds had been given as much chance, if not more, to habituate to the conditions of measurement as the Northern barn owls in the previous study, which shared a coauthor with the present one (Murphy and Howland 1983). Moreover, many of our observations were carried out during normal feeding behaviour when it cannot be argued that the owls were not in an optimal emotional state to elicit accommodation. Given these considerations, we do not think that it is reasonable to argue that tytonids in general have poor accommodative ability because they are constitutionally more likely to be alarmed than the boreal barn owl. All of our subjects were calm and attentive to the accommodative stimulus which was clearly causing an alteration in accommodative state. They just could not summon the same accommodative output as a Northern barn owl.

**Northern barn owl and small prey**

Besides willingness to accommodate, another, more likely, possibility is that there exists a real difference in ability. This could have been brought about by the different selection pressures to which boreal barn owls may have been subjected, such as the rigors of Northern winters compared with the more gentle Australian climate. Boreal conditions may require an ability to survive on alternative, smaller, invertebrate prey when mammals are scarce. The proportion of such small prey taken by Northern hemisphere barn owls is known to increase.

<table>
<thead>
<tr>
<th>Table 2. Contrasts between the Australian (austral) barn owl, <em>Tyto alba delicatula</em>, and the North American, <em>T. alba pratincola</em> plus European, <em>T. alba guttata</em>, barn owls (boreal barn owl)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Boreal barn owl</td>
</tr>
<tr>
<td>Hunts in daylight</td>
</tr>
<tr>
<td>Invertebrates can become significant fraction of diet</td>
</tr>
<tr>
<td>Proportion of insects in diet increases with latitude</td>
</tr>
<tr>
<td>Continuous, ‘trilling’ or ‘ticking’ courtship song</td>
</tr>
<tr>
<td>Wide variety of nest sites, including burrows and ground scrapes</td>
</tr>
<tr>
<td>Size, up to 700 g</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td></td>
</tr>
</tbody>
</table>
with latitude (Herrera 1974) and there are a number of reports of Northern hemisphere barn owls for which beetles formed a significant, but temporary, part of the diet (Bunn et al. 1982). Smaller prey of this kind would require visual discriminations to take place at closer distances and require a correspondingly greater power of accommodation.

This explanation of the difference between boreal and austral barn owls is further supported by other differences in behavior (Table 2), such as the fact that boreal barn owls commonly hunt in daylight (Bunn et al. 1982), a behavior which has never been recorded for austral barn owls (Schodde and Mason 1981).

Sibling species of the barn owl?

The behavioral differences between boreal and austral barn owls raise the possibility that they may actually be separate species (‘sibling species’) which have been overlooked because classification was based on plumage characters rather than other features that might be more important for species recognition by these owls. Marshall (1978) has eloquently pointed out the pitfalls of using subtle visual characteristics, such as plumage pattern and coloration, to classify nocturnal birds. Species-specific behavior in such birds may be guided by less-visual signals that are more appropriate for species recognition at night, such as vocal and motor displays. Marshall (1978) describes cases where different colour phases of the same species had been classified as separate species, and converses cases where separate species, based on vocal and other aspects of behaviour, had been mistakenly placed within the same species because of similarity in plumage.

In the present case, one wonders whether the behavioral differences we have revealed between the North American barn owl and the Australian barn owl point to a deeper split than commonly recognised. We hesitate to suggest that photorefraction should be part of an ornithologist’s armamentarium, but perhaps molecular, genetic investigation would be more fruitful in revealing the true relationships of these two barn owls than the external characters, such as plumage, that have been used to date.

References

Herrera CM (1974) Trophic diversity of the barn owl Tyto alba in continental western Europe. Ornis Scandinavica 5: 181-191
Pettigrew JD, Little L, Stegenga T (1986) Incubation period of the Australian grass owl Tyto capensis longimembris. Emu 86: 117-118