Visual fields in Blue Ducks *Hymenolaimus malacorhynchos* and Pink-eared Ducks *Malacorhynchus membranaceus*: visual and tactile foraging

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Blue Ducks *Hymenolaimus malacorhynchos* (Anatidae), an IUCN Red Listed Endangered species, reside in headwaters of New Zealand rivers and feed primarily on aquatic invertebrates. However, whether such food items are detected by tactile or visual cues is unknown. That Blue Ducks may use tactile cues when foraging is suggested by the presence of specialized flaps of thickened, keratinized epidermis containing Herbst’s corpuscles along the ventral margins of the upper mandibles near the bill tip. Similar bill flaps are found only in one other duck species, Pink-eared Ducks *Malacorhynchus membranaceus*, that surface filter-feed on a range of planktonic organisms. Using an ophthalmoscopic reflex technique we determined the visual fields of both species. In Blue Ducks the eyes are frontally placed resulting in a relatively wide binocular field into which the narrow tapering bill intrudes. There is a large blind area to the rear of the head. This visual field topography is similar to that of other visually guided foragers including those that take mobile prey from the water column, e.g. penguins (Spheniscidae). By contrast, Pink-eared Duck visual fields show features found in other tactile feeding ducks: a narrow frontal binocular field with the bill falling at the periphery, and comprehensive visual coverage of the celestial hemisphere. We conclude that although Blue Ducks may take prey from rock surfaces they are primarily visual feeders of the water column and we suggest therefore that their foraging may be significantly disrupted by changes in water clarity. This introduces a previously unconsidered factor into the selection of sites for population enhancement or re-introductions, a current conservation focus.

In birds, the position and extent of the region of binocular vision appear to be determined primarily by feeding ecology (Martin & Katzir 1999). Of prime importance is the degree to which vision is used for the precise control of bill position when pecking or lunging at prey, or when feeding chicks. In species that feed in this way the bill falls either centrally or just below the centre of the frontal binocular field (Martin et al. 2004, 2005). The interpretation of this arrangement is that the control of bill position by visual cues is thought to be primarily a result of the symmetrical optical flow-fields generated in each eye within the forward-facing binocular sector, as the head moves towards an object (Martin et al. 2005). Such flow fields specify directly the direction of travel and the time to contact a target, and this information is processed sufficiently fast by the brain to control rapid pecking or lunging at items. Stereoscopic cues that may be available from binocular vision are, however, too slow for the control of such rapid movements (Davies & Green 1994).

In birds that do not require such precise control of rapid bill movements (probe and filter feeders with precocial self-feeding chicks), the bill falls outside or at the periphery of the binocular field. In such
examples the binocular field extends above and behind the head, and so provides comprehensive visual coverage, but it is clear that vision cannot be used for the precise control of bill position (Martin 1994, Guillemain et al. 2002).

Knowledge of visual field characteristics in birds can therefore be used to determine the importance of visual and tactile cues in their foraging. We have employed this technique to determine whether Blue Ducks *Hymenolaimus malacorhynchos* (Anatidae) use visual and/or tactile cues to guide their foraging. For comparison we also determined visual fields in Pink-eared Ducks *Malacorhynchus membranaceus*, a species whose foraging is known to be primarily guided by tactile cues (Kear 2005).

New Zealand's Blue Ducks presently inhabit forested headwater catchments of rivers with medium to steep gradients (Kear & Burton 1971, Collier et al. 1993). Stomach analysis has shown that they feed on a wide variety of aquatic invertebrates (Collier 1991, Veltman et al. 1995) and occasionally on small amounts of plant material (Marchant & Higgins 1990). How these birds catch their prey is not known. Are these food items detected by tactile cues when 'blind searching' among rocks and stones of the riverbed, or are Blue Ducks detecting individual items by sight either on the substrates or in the water column? This is an important question; Blue Ducks are the subject of considerable conservation concern because of their ongoing population decline and range contraction. They are classified as an IUCN Red Listed Endangered species with an estimated world population of 2440 individuals (BirdLife International 2006). Population decline and range contraction were attributed initially to competition for aquatic insects with introduced fish, but more recent attention has focused upon the deforestation of river catchments causing a decrease in water clarity and silting leading to a reduction of invertebrate prey, and to introduced mammalian predators (Kear 2005). If Blue Ducks are primarily visual feeders their foraging may be significantly disrupted by changes to water clarity. This would introduce a previously unconsidered factor into the selection of sites for population enhancement or re-introductions, a current conservation focus (Collier 2004).

That Blue Ducks may use tactile cues when foraging is suggested by the presence of the flaps at their bill tips (Fig. 1). These flaps are relatively simple structures with a heavily keratinized epidermis containing a small number of Herbst's corpuscles (Gottschaldt 1985), mainly confined to the sections nearest the point of attachment to the upper jaw (Kear & Burton 1971). It is this structure that is referred to in the specific name. Among birds a similar structure is found only in one other duck species, Pink-eared Ducks that feed exclusively by filter-feeding to obtain a range of planktonic organisms (algae, microscopic seeds, crustaceans, molluscs, insects) in shallow, still and typically turbid waters (Kear 2005). The structure of these flaps has not been fully described but they appear to be well endowed with Herbst's corpuscles and are thought to have a role in the tactile feeding (Kear & Burton 1971). However, bill size and shape differ markedly in these two duck species (Fig. 1). The bill of Pink-eared Ducks is typical of many Anatidae in that it is expanded anteriorly. However, the bill of Blue Ducks is quite different, being narrow and tapering towards the tip, and with a straight culmen; these are a group of structural adaptations associated in other bird taxa with obtaining food items by pecking or lunging at individual items (Kear & Burton 1971).

Here we show marked differences between the visual fields of Blue Ducks and Pink-eared Ducks. Pink-eared Duck visual fields show clear characteristics of a tactile feeder whereas Blue Ducks have visual fields which suggest that they are primarily visually guided foragers.

**METHODS**

We determined visual fields in two adult Blue Ducks and two adult Pink-eared Ducks (sexes unknown) from the captive breeding collections held by the Wildfowl and Wetland Trust Centres at Slimbridge (Gloucestershire) and Arundel (West Sussex), England. Visual field parameters were determined using an ophthalmoscopic reflex technique, which has been used in a range of birds of different phylogeny, ecology and feeding techniques and which readily permits interspecific comparisons (Martin & Coetzee 2004, Martin et al. 2005). For a description of the apparatus and methods see the Appendix. The procedures used were performed under guidelines established by the United Kingdom, Animals (Scientific Procedures) Act, 1986.

**RESULTS**

The positions of the visual field margins in each of the birds were within 5° of each other at all elevations and hence we present mean data for each species. Maps of the frontal binocular fields are shown in
Figure 2. Horizontal sections through the visual fields in an approximately horizontal plane are shown in Figure 3, and the width of the binocular field as a function of elevation in the median sagittal plane in the Pink-eared Duck is shown in Figure 4. These results show that the visual fields of these two species of ducks differ markedly. These differences arise because the eyes of Blue Ducks are more frontally placed in the skull whereas those of Pink-eared Ducks are more lateral and higher in the skull (Fig. 1). In addition the visual field of each eye is narrower in Blue Ducks (173°) than in Pink-eared Ducks (190°) (Fig. 3).

The frontal binocular fields

The maximum width of the frontal binocular field in both species occurs approximately 20° above the bill. However, maximum binocularity in Blue Ducks (34°) is twice that in Pink-eared Ducks (17°). Moreover in Pink-eared Ducks the bill is positioned at the very periphery of the visual field whereas in Blue Ducks the bill intrudes into the binocular field and determines its limits, resulting in the ‘notch’ in the binocular field at the elevation of the bill (Fig. 2). This indicates that a Blue Duck can see its own bill tip while a Pink-eared Duck cannot.
To the rear of the head the visual fields of these two species also differ markedly. In Blue Ducks there is an extensive blind area behind the head (48° wide at the approximately horizontal plane) whereas in Pink-eared Ducks the visual fields of each eye overlap or coincide at all elevations behind the head (Figs 3 & 4). Thus, a Pink-eared Duck has comprehensive visual coverage of the hemisphere about its head, but a Blue Duck could only achieve similar visual coverage by the use of scanning head movements.

**DISCUSSION**

**Visual fields and foraging**

As in other tactile and filter-feeding ducks (Mallards *Anas platyrhynchos* and Northern Shovelers *A. clypeata*)
Pink-eared Ducks have Type 2 visual fields (Martin & Coetzee 2004), which give them comprehensive vision of the hemisphere that surrounds their heads (Fig. 4). As also found in Mallards and Shovelers, maximum binocular overlap (17°) occurs in the frontal field close to the horizontal, with the bill tip falling at the very lower periphery of the visual field.

The visual fields of Blue Ducks, however, exhibit the four principal characteristics of Type 1 visual fields (Martin & Coetzee 2004) that are associated with visually guided pecking or lunging at prey: (1) the bill tip projection falls either centrally or within the lower half of the binocular area, (2) the binocular field is relatively long and narrow with maximum binocularity of approximately 30°, (3) maximum binocularity occurs 20–40° above the projection of the bill tip and (4) there is a large blind area to the rear of the head. Furthermore, in Blue Ducks the bill intrudes into the binocular field implying that a bird

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Figure 3. Horizontal sections through the visual fields of Blue Ducks and Pink-eared Ducks in a plane containing the frontal binocular field at its maximum width. This plane is indicated by the line through the eye in each of the drawings of the birds to the right of each visual field diagram.
can see its own bill tip and thus see items between the mandibles when they are opened. These features are found in a wide range of species which differ in their ecology and phylogeny but have in common precision pecking or lunging at prey. For example, similar visual field topographies are found in ground-hornbills and hornbills (Bucorvidae and Bucerotidae), which take individual items in the tips of their elongated down-curved bill by precision pecking (Martin & Coetzee 2004), and in penguins (Spheniscidae), which take aquatic prey directly in their bill in rapid pursuit movements (Martin 1999).

**The function of binocularity in birds**

An explanatory framework for such an interpretation of visual field topography is provided by the hypothesis that, in lateral-eyed vertebrates, binocularity is not associated with stereopsis (the perception of relative depth at close quarters that results from the simultaneous combination of information from the two eyes) but is the result of having part of each eye’s monocular field extending across the sagittal plane to ensure that a section of each eye’s visual field looks in the direction of travel (Martin & Katzir 1999). This arrangement provides a radially symmetrical portion of the optic flow-field in each eye. From this, information can be extracted that accurately specifies both direction of travel and time to contact the surface to which an animal’s head is moving (Davies & Green 1994, Lee 1994).

Forward placement of the eyes to provide such symmetrical optic flow-fields in each eye is, however, at the expense of comprehensive vision. This is because the monocular field of a vertebrate eye is rarely more than 180° in diameter (Martin 1994).
and therefore any forward placement of the eyes inevitably results in a blind area to the rear of the head. Thus, the topography of the complete visual field is likely to be the result of selective pressures that have ensured sufficient binocularity for the control of movement towards targets while at the same time preserving more comprehensive visual coverage above and to the rear of the head. The latter is clearly beneficial for the detection of predators or for the observation of others in a social group (Martin 1984, Guillemain et al. 2002). It seems likely therefore that the forward placement of the eyes in a bird’s skull, which results in a broad binocular field surrounding the bill, indicates that bill position can be brought under visual control during foraging.

Frontal binocular field width and foraging underwater

A particular similarity between the binocular fields of Blue Ducks and penguins lies in the large absolute width of their binocular fields. In bird species that forage in air using visual cues to control pecking or lunging movements towards individual items, the maximum width of the binocular field is between 20° and 30° (Martin & Coetzee 2004). However, in amphibious forms binocular field width is broader than in terrestrial forms and this probably results from the fact that upon immersion the widths of the monocular and binocular fields are reduced due to the loss of refraction by the cornea (Martin & Young 1984, Martin 1999). Thus, a broader binocular field in air becomes narrower upon immersion. This may explain why the binocular field of Blue Ducks (as measured in air) is broader than in the majority of terrestrial precision-pecking and lunging birds that have been investigated to date (Martin & Coetzee 2004).

Foraging and its sensory bases in Blue Ducks

Studies of Blue Duck foraging behaviour and diet demonstrate that foraging occurs within specific microhabitats and that invertebrate prey have heterogeneous spatial and temporal distributions within the foraging areas (Veltman & Williams 1990, Collier 1991, Veltman et al. 1995, Collier 2004). The pronounced temporal variations in the compositions of benthic invertebrate communities (which are mostly a consequence of flood events and subsequent patterns of invertebrate recolonization) are reflected in changes in relative species composition in the diet. We hypothesize that it is these temporal and spatial heterogeneities of prey availability that have resulted in the evolution in Blue Ducks of behavioural, anatomical and physiological adaptations that enable the exploitation of a relatively wide range of invertebrate prey types. However, this broad invertebrate diet would seem to require at least two different feeding techniques that are controlled by different sensory cues. Thus, Blue Ducks may switch both temporally and spatially between different primary sense cues depending upon prey type availability. When exploiting the small sessile chironomid and cased caddis fly larvae, which can be scraped from rock surfaces, tactile cues from the bill are likely to be the primary cue used to guide behaviour. Hence, the birds can ‘forage blindly’ on, between and beneath rocks for these prey types. However, visually guided foraging is required when Blue Ducks are exploiting the larger and more nutritious prey (swimming mayfly and active stonefly larvae) that are highly mobile within the water column. We suggest that the enhanced binocularity of Blue Ducks, with the visual projection of the bill falling within the binocular field, coupled with their narrow tapering bill, functions to provide the precise visual control of bill position necessary for the capture of such prey. However, this visually guided foraging by Blue Ducks implies that decreased water clarity is likely to reduce foraging success, particularly for these larger mobile prey. Thus, rivers that experience changes in water clarity are likely to be poor locations in which to concentrate conservation management of this species as any mobile prey that are available will be increasingly difficult to catch. Such rivers are those prone to frequent and/or prolonged floods, perturbations due to volcanic activity, or those that drain catchments where land use increases siltation.

The function of bill tip skin flaps

We compared the vision of Blue Ducks and Pink-eared Ducks because they have in common an anatomical feature not found in other Anatidae: flexible flaps of skin that hang from the edges of the upper jaw and overlap the lower jaw near the bill tip. The presence of Herbst’s corpuscles in these flaps suggests a sensory function (Gottschaldt 1985) but further detailed work on their number and distribution is required before their possible tactile function in the foraging of either species can be understood in detail. © 2006 The Authors
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However, if they have a tactile function such flaps could serve to increase the sensory area on either side of the bill tip within which food items can be detected. This may be particularly important in Blue Ducks as their bill is both narrow and tapered.

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REFERENCES


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APPENDIX

Procedure

Each bird was restrained with the body immobilized and the head position fixed by holding the bill. In both species the bill was held in a specially built metal holder coated with cured silicone sealant to produce a non-slip surface and the bill held in position by tape (Micropore®). The body was held in a cradle of foam rubber and secured by straps (Velcro®). The bill holder was mounted on an adjustable mechanism and the head positioned so that the midpoint of a line joining the corneal vertices was at the approximate centre of a visual perimeter apparatus. The perimeter’s coordinate system followed conventional latitude and longitude with the equator aligned vertically in the birds’ median sagittal plane and this coordinate system is used for the presentation of the visual field data (Fig. 2). Each bird’s head was positioned with the plane through the eyes and bill tip pointing at an angle of approximately 25° below the horizontal. This head position approximated that which the birds adopted spontaneously when held in the hand. Heads in this position are depicted in Figure 2. The projection of the bill tip when measurements were made was determined accurately from photographs and the visual field data corrected for this.

The eyes were examined using an ophthalmoscope mounted on the perimeter arm. The visual projections of the limits of the frontal retinal visual field of each eye were determined as a function of elevation (10° intervals) in the median sagittal plane. To the rear of the head the limits of the retinal visual field were determined at all elevations down to the horizontal in the Pink-eared Ducks. However, because we did not wish to extend the period that the Blue Ducks were held the limits of the visual
fields at only one elevation close to the horizontal were determined. From these data (corrected for viewing from a hypothetical viewing point placed at infinity) topographical maps of the frontal visual fields and horizontal sections through the visual fields were constructed. The visual projections of the pectens were also determined. These provide significant landmarks within the visual field. The pecten is a highly pigmented structure within the anterior chamber of the eye that provides nutrition to the retina. It is situated above the point where the optic nerve exits. It is highly vascularized and does not contain photoreceptors and hence is a blind area within the visual field of each eye.