Feeding methods, visual fields and vigilance in dabbling ducks (Anatidae)

M. GUILLEMAIN*†, G. R. MARTIN‡ and H. FRITZ§

ONCFS, La Tour du Valat, Le Sambuc, 13200 Arles, France, Centre for Ecology and Hydrology, CEH-Dorset, Winfrith Technology Centre, Winfrith Newburgh, Dorchester, Dorset DT2 8ZD, UK, and Centre d'Etudes Biologiques de Chizé, CNRS UPR 1934, 79360 Beauvoir-sur-Niort, France; ‡School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK; and §Centre d'Etudes Biologiques de Chizé, CNRS UPR 1934, 79360 Beauvoir-sur-Niort, France

Summary

1. Visual fields were determined in two species of dabbling ducks (Anatini): Shoveler *Anas clypeata* L. (planktivore whose foraging is guided mainly by tactile cues) and Wigeon *A. penelope* L. (herbivore whose foraging is guided mainly by visual cues).

2. The binocular fields of Shoveler and Wigeon are of similar maximum width (20°), but they differ in their position and vertical extent. The bill of the Shoveler lies in the very periphery of its frontal binocular field, which extends through 220° thus providing comprehensive visual coverage about the head. In Wigeon the bill is positioned more centrally in the frontal binocular field, which extends through 150° and results in the birds having a narrow blind area behind the head.

3. The vigilance behaviour of Shoveler and Wigeon when foraging simultaneously was studied using a focal observation procedure at sites where the two species winter in sympatry. Focal Wigeon almost only fed by grazing. Only Shoveler feeding by dabbling (filtering the first centimetres of water) were used in the analyses. Wigeon spent significantly more time in head-up vigilance than Shoveler ($F_{1,75} = 14.70$, $P = 0.0003$).

4. It is proposed that this interspecific difference in the proportion of time spent in vigilance behaviour may be an adaptive response to differences in the visual field topography of these species, particularly with respect to the presence/absence of a blind area to the rear of the head.

5. The ability of foragers to combine part of their vigilance behaviour with head-down feeding has recently been recognized as influencing the trade-offs related to vigilance while foraging. This study shows that this ability may vary significantly between species, even within the same genus, and that these variations are likely to be due to contrasted visual fields, themselves related to the type of feeding techniques employed by the different duck species.

Key-words: *Anas clypeata*, *Anas penelope*, Anatidae

Functional Ecology (2002) **16**, 522–529

Introduction

Although it has long been considered that feeding and vigilance are mutually exclusive activities (e.g. Bertram 1980; Hart & Lendrem 1984; Lima & Dill 1990; McNamara & Houston 1992), there is a growing body of evidence that animals can sometimes maintain some level of vigilance while foraging, even with the head down (Arenz & Leger 1997; Lima & Bednekoff 1999;

†Correspondence: M. Guilleman, Office National de la Chasse et de la Faune Sauvage, CNERA Avifaune Migratrice, La Tour du Valat, Le Sambuc, 13200 Arles, France. E-mail: m.guillemain@oncfs.gouv.fr

Guillemain, Duncan & Fritz 2001). This ability to combine vigilance and foraging could be of crucial importance for species whose food type and/or energy requirements necessitate long daily foraging times. For example, individuals may be unable to compensate for the loss of feeding time if vigilance is achieved only through 'head-up' scans during which feeding is impossible.

This ability to combine feeding and head-down vigilance should be related to the visual fields of the individuals. Species with wider visual fields and more comprehensive vision above and to the rear of the head should thus be more likely to combine feeding and head-down vigilance. Conflicting with vision to the

rear is the necessity for frontal binocular vision. In many species of birds the bill is placed approximately centrally within a vertically long but narrow binocular field (Martin & Katzir 1999a). This visual field topography has been associated with the need for accurate visual control of bill position during foraging (Martin & Katzir 1999a). In all bird species examined to date the extent of the cyclopean visual field (the total visual field about the head) appears to be maximized (Martin 1999). However, the actual extent is constrained by the size of each monocular field and by the need for frontal binocular vision. A comprehensive visual field (without a blind sector above or to the rear of the head) is achieved only in those bird species in which foraging is primarily guided by tactile cues (Martin 1986b, 1999).

Guillemain *et al.* (2001) suggest that dabbling ducks (Anatidae, Anatini) (Carboneras 1992) are able to combine a part of their vigilance time with foraging, as long as the birds' eyes are above the water surface while foraging. However, this ability should also depend upon species-specific visual fields, which themselves should be related to the role of vision in foraging (Martin & Katzir 1999a). Although congeneric, Shoveler *Anas clypeata* L. and Wigeon *A. penelope* L. have very different food habits: Wigeon are mainly herbivorous and, when foraging in wet grassland or marsh areas, selectively peck at individual plant leaves (Jacobsen 1992). Shoveler are mainly planktivorous, and typically filter the upper centimetres of the water column to collect zooplankton (Dubowy 1996; Guillemain, Fritz & Guillon 2000). Both species have long daily foraging times. In Wigeon this is attributed to low digestive efficiency and, in Shoveler, it is attributed to the need to filter large volumes of water to collect sufficient plankton (Thomas 1982). Minimizing head-up vigilance time in order to maximize feeding time should thus be important in both species.

To date visual field topography has been determined and compared between bird species that differ markedly in their phylogeny and/or foraging ecology (Martin 1999). Comparisons have not been conducted in congeneric species. We show here that visual field topography in congeneric Shoveler and Wigeon differ significantly, that differences are consistent with contrasted feeding methods between the two species, and demonstrate a significant interspecific difference in head-up vigilance times that can be correlated with visual field differences. In addition, we investigated if the temporal structure of feeding (length of scan and feeding bouts) differs between the two species.

Methods

VISUAL FIELDS

Measurements of visual fields were made in alert birds, using an ophthalmoscopic reflex technique and procedures similar to those used previously with other bird species (Martin 1984, 1986a, 1986b, 1994; Martin &

Katzir 1994a, 1994b, 1995). Measurements were made in two adult Shoveler and two adult Wigeon. Birds were obtained from the collection held at the Wildfowl and Wetland Trust, Slimbridge, UK. After the measurements the birds were returned to the collection. Each bird was held in a foam rubber cradle with its head held in position at the centre of a visual perimeter by a specially manufactured bill holder. The eyes were examined using an ophthalmoscope mounted on the perimeter arm. For each eye, the visual projections of the following were determined as a function of elevation in the median sagittal plane of the bird's head (the vertical plane that bisects the head lengthways): (a) the limits of the *retinal visual field* (that portion of the optical field which is served by retina and hence in which vision is possible); and (b) the edges of the *pecten*, a unique structure of avian eyes. It is a heavily pigmented vascular structure projecting from the retina into the vitreous body at the point of exit of the optic nerve. Its primary function is the nutrition of the retina; it serves as conspicuous landmark in the retina (Martin 1985). The position of the visual projections of these features could be read to an accuracy of ±0·5° at any one elevation. Across a range of species these measures have been found to be highly repeatable within individuals, and to within a maximum of ±4° between individuals (Martin & Katzir 1994a, 1999b). Procedures that in other bird species (Common Starlings *Sturnus vulgaris*, Martin 1986a; Manx Shearwaters *Puffinus puffinus*, Martin & Brooke 1991; and herons, Ardeidae, Martin & Katzir 1994a) have readily elicited eye movements when birds are positioned in this apparatus (such as light tapping sounds and flashes of light in the periphery of the visual field) were employed. For a detailed description of the apparatus and methods see Martin & Katzir (1994a). The procedures used were performed under guidelines established by the United Kingdom, Animal (Scientific Procedures) Act, 1986.

From these data (corrected for viewing from an hypothetical viewing point placed at infinity) a topographical map of the complete visual field and its principal components was constructed. These features are: *monocular field*, the visual field of a single eye; *binocular field*, the area where monocular fields overlap; *cyclopean field*, the total visual field produced by the combination of both monocular fields. In both species visual fields were measured when the birds' heads had adopted natural postures that were similar to those typically observed under natural conditions in that species and also depicted in field guide illustrations. The position was quantified by the angle of a line joining the eye and bill tip with respect to the horizontal and calibrated from photographs of the birds held in the apparatus. These head positions are shown diagrammatically in Fig. 1. From these data the widths of the retinal visual fields of each eye and the extent to which they overlap to produce the binocular field were determined for each bird.
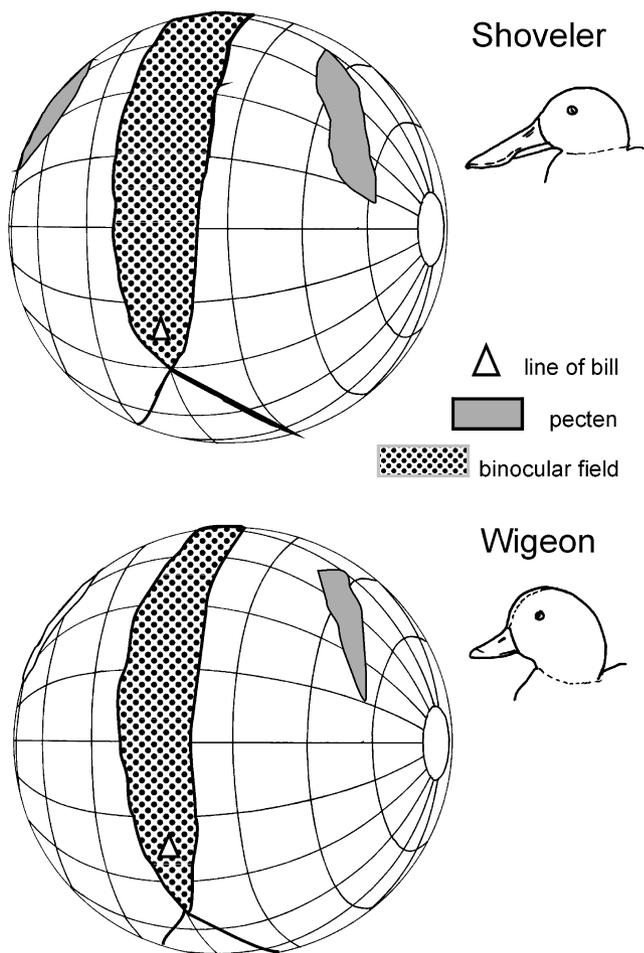
Fig. 1. Visual fields of Shoveler and Wigeon. Each diagram shows a perspective view of a projection of the retinal field boundaries, pectens and bill tip. The binocular portion of the field is highlighted. For co-ordinates the diagrams use the conventional latitude and longitude system but with the equator aligned vertically in the median sagittal plane of the head (grids are at 20° intervals). It should be imagined that the bird's head lies at the centre of a transparent sphere with the features of the visual field projected onto its surface. The bird's head is facing and looking to the left of the observer. It is shown in the sketch in the correct vertical orientation for the co-ordinate system which was also the head position employed when measurements were made.

STUDY SITES AND BEHAVIOURAL OBSERVATIONS IN THE FIELD

The behaviour of Wigeon and Shoveler was studied during the winters (September–March) 1995/96–1997/98 on two protected areas in the Marshes of Rochefort, Western France: the nature reserve of Yves and the nature reserve of Moëze. Ducks were observed on a 32-ha and 24-ha water body and surrounding wet grasslands at Moëze and Yves, respectively. Scan sampling of flock behaviour showed that ducks fed intensively at these sites, with no significant difference between the two reserves (bilateral Student's t-tests, $P > 0.40$): foraging represented 38·0% (±4·6 SE, $n = 25$ weekly data) and 48·0% (±4·6 SE, $n = 25$ weekly data) of diurnal activities of Wigeon and Shoveler, respectively. The two species used different foraging techniques at our study sites, as already reported in the literature (Carboneras 1992). Wigeon almost only fed by grazing (pecking individual leaves of grass plants), while Shoveler fed by dabbling (filtering the top few centimetres of water) or foraged deeper in the water column by dipping and up-ending (Table 1).

The observation protocol followed that of Guillemain *et al.* (2001). Focal observations (10 min, Altmann 1974) were conducted on feeding individuals chosen at chance; each change in behaviour was recorded on a portable computer that automatically incorporated time to the nearest 0·5 s. Observations took place at each site 1 day per week between 07.00 and 19.00, for a total of 30 study days. Data were recorded by the same observers throughout the study. Analyses were restricted to the temporal organization of behaviour during meals, i.e. successions of feeding bouts and interruptions, hereafter termed scans (standing, swimming or walking in an upright position). Meals were considered terminated by any activity other than feeding or short (i.e. ≤10 s) scans (Cézilly & Brun 1989). All meals of Wigeon consisted of a succession of pecks (i.e. grazing). In Shoveler, some meals related to focal birds foraging with the eyes underwater (i.e. dipping or up-ending). It is assumed that ducks foraging with the eyes underwater cannot visually monitor their environment. Those meals when Shoveler were dipping or up-ending were discarded from the analyses, as ducks using underwater methods have been shown to have different vigilance patterns (Guillemain *et al.* 2001). A total of 45 Wigeon and 32 Shoveler focal observations were used in the analyses. The mean length of feeding bouts and scans, and the proportion of time spent overtly vigilant, were calculated for each meal. For each focal bird the mean value of each behaviour over all meals was calculated, meals thus being weighted equally. The frequency of scan bouts was not considered in the analyses since it was closely related to feeding bout length ($Y = 0.53X^{-0.82}$, $R^2 = 0.88$, df = 75).

Table 1. Foraging methods of Wigeon and Shoveler in the study area, expressed in percentage of total foraging time (mean ± SE). The number of data is the number of average weekly time-budgets over the winters 1995/96–1997/98. Sample size is lower in Wigeon because of weeks when Wigeon were not present

		Grazing	Dabbling	Deep foraging
Wigeon *A. penelope* ($n = 25$)		95·0 ± 2·9	4·4 ± 2·9	0·4 ± 0·3
Shoveler *A. clypeata* ($n = 28$)		0·3 ± 0·2	54·9 ± 6·8	44·8 ± 6·9
Student's t-test	$t =$	32·40	7·83	7·63
	$P <$	0·0001	0·0001	0·0001

Since ducks were not individually marked and we repeatedly observed them at the same foraging spots, some of them may have been sampled twice. However, the incidence of double sampling is likely to be low and thus should not cause an important problem for statistical analyses. Low incidence of double sampling is probably due to the following: (1) the turnover of individuals is typically rapid in wintering dabbling duck populations (Pradel *et al*. 1997), (2) the number of focal observations per species and site, relative to the number of individuals present, was low (mean flock sizes were more than 100, except Wigeon at Yves: 19 individuals), (3) the number of focal observations per species per day was small (1–6), and (4) the study lasted for three separated periods of 6 months.

Group size, distance to nearest neighbour and the frequency of predator appearance are likely to affect vigilance levels of individuals (Elgar 1989), thus confounding the comparison between species. Whenever possible the nearest neighbour distances (in duck-lengths) were recorded at the beginning and end of each session, as well as the feeding group size, i.e. the number of birds feeding together (<10 duck-lengths apart). Wigeon and Shoveler have similar body masses and body lengths, so that neighbour distances are expressed in comparable units in the two species. The frequency of fly-overs by large raptors (mostly Marsh Harriers *Circus aeruginosus*) was also monitored for each 3-h period of the day during which a focal observation was carried out. This was used as an index of predation risk (Fritz, Guillemain & Guérin 2000). Gulls (*Larus* spp.) and Grey Heron (*Ardea cinerea*) were not included, as the former very rarely threatened dabbling ducks at the study sites, and, as opposed to other Anseriformes (e.g. Brent Geese *Branta bernicla*, M. Guillemain *et al*., personal observation), *Anas* species were not observed to respond in any way to heron fly-overs.

Previous studies showed that the behaviour of dabbling ducks in western France may vary across hours during a day, and differ between early and late winter (Guillemain *et al*. 2000). Vigilance levels of dabbling ducks may also vary across winter because of changing energy requirements (Gauthier-Clerc, Tamisier & Cézilly 1998). These time variables were also included in the analyses.

Backwards stepwise general linear model procedures (GLM, SAS Institute 1990) were used to quantify the respective roles of Species (Wigeon or Shoveler), Site (Yves or Moëze), Time (i.e. before 1100; 1100–1459; after 1500) and Period (i.e. early [September–November] or late winter [December–15 March]) as factors, and group size, neighbour distance and the frequency of raptor fly-overs as covariates, in explaining vigilance patterns by foraging ducks (i.e. proportion of time spent in head-up vigilance, arcsine-transformed, length of foraging bouts and scans). Time classes were determined so as to be of comparable lengths.

The interaction between 'Species' and the other factors and covariates was also included in the analyses to test for differential effects on Wigeon and Shoveler. Multiple runs were performed, in which non-significant ($P > 0.05$) terms were gradually removed, starting with the interactions. If any interaction was significant, the procedure was stopped and only the variables not included in the interaction were then considered for further steps.

Results

VISUAL FIELDS

Data obtained for the two birds of each species were similar and are presented as means. The techniques employed failed to elicit eye movements of measurable amplitude. In other species such techniques readily elicit eye movements of large amplitude (see Methods). Thus, while it cannot be concluded with certainty that eye movements of large amplitude are non-existent in these ducks, it is likely that this is the case. The visual fields described are therefore unlikely to be changed significantly regardless of the head position adopted or the tasks performed by the birds.

BINOCULAR FIELD

In both species the region where binocular vision occurs is relatively long and narrow with a maximum width of approximately 20°, occurring at elevations between 20° above and 20° below the horizontal (Fig. 1). In Shoveler, the bill is placed about 10° above the lower edge of the frontal binocular field. In Wigeon the bill is placed more centrally (*c*. 20° above the lower edge of the binocular field), where the width of binocular vision is still at its maximum (Fig. 1). The vertical extent of the binocular field in the median sagittal plane differs between the two species (Fig. 2). In Wigeon the field extends through 150° resulting in a narrow (maximum width 10°) blind area extending from directly above the head to the horizontal. In Shoveler the area of binocular overlap extends through 220° to give the birds binocularity through the 180° arc extending between the horizontal in front and behind the head.

CYCLOPEAN FIELD

The cyclopean retinal field describes the full extent of the volume of space around the head that at any one instant can provide visual information. Lateral placement of the eyes in the skull, coupled with the wide monocular fields and small binocular overlap, provides both Shoveler and Wigeon with visual fields that cover a substantial portion of the world surrounding the head. In Shoveler this cyclopean field provides the birds with total panoramic vision around and above the head (Fig. 2). In Wigeon, however, there is a blind sector to the rear that results
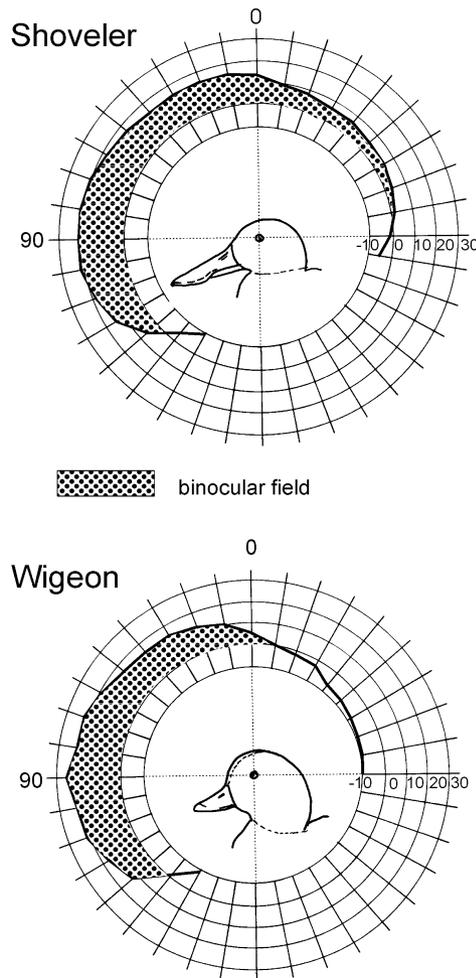
Shoveler

binocular field

Wigeon

Fig. 2. Binocular field width in Shoveler and Wigeon as a function of elevation in the median sagittal plane. Orientation of the bird's head as shown diagrammatically. All values are degrees and the grid is at 10° intervals.

in incomplete visual coverage of the volume surrounding the head.

FORAGING AND VIGILANCE BEHAVIOUR

Only 'Species' remained in the best fitting model of the backwards stepwise GLM of the percentage of time spent in head-up vigilance by foraging ducks: Wigeon spent significantly more time in head-up vigilance than Shoveler ($F_{1,75} = 14.70$, $P = 0.0003$; Fig. 3a). The vigilance levels of Wigeon were very stable across the day, ranging from 14·2% (±1·3 SE, $n = 26$) during midday to 15·1% (±2·6 SE, $n = 13$) in the afternoon. This percentage showed greater variation in Shoveler: although differences between periods of the winter were not significant, the range was 4·3% (±1·0 SE, $n = 4$) in the morning to 10·6% (±1·3 SE, $n = 14$) in midday. Across the season, Wigeon and Shoveler showed a similar (though non-significant) trend of higher vigilance in early winter (16·2% ± 1·6 SE, $n = 26$ and 10·1% ± 1·1 SE, $n = 22$, respectively) than in late winter (12·3% ± 1·1 SE, $n = 19$ and 6·0% ± 1·1 SE, $n = 10$, respectively).
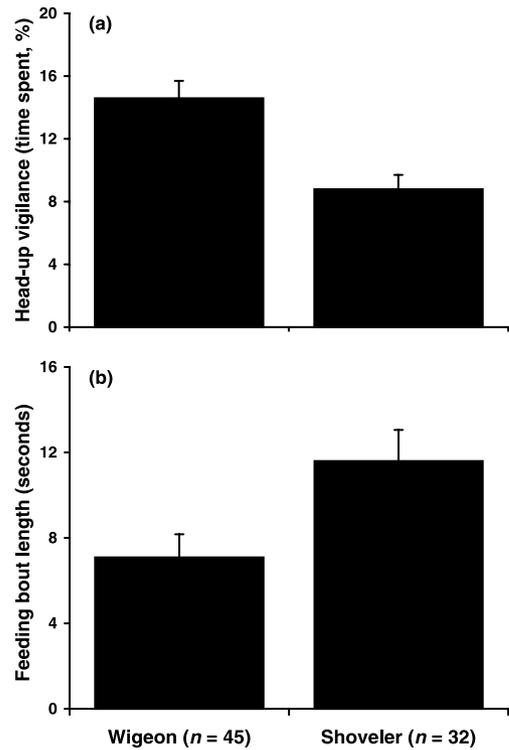

Fig. 3. Percentage of (a) time spent vigilant during meals and (b) length of scanning bouts by Wigeon and Shoveler. Columns are means + SE. Differences between species are significant in the two cases (see text).

This difference between species arose from significantly shorter feeding bouts in Wigeon than in Shoveler, 'Species' being the only factor to remain in the best-fitting model of the backwards stepwise GLM of the length of feeding bouts ($F_{1,75} = 6.64$, $P = 0.0119$; Fig. 3b). Conversely, 'Species' did not explain a significant part of the variance in scan bout length: the best-fitting model of the backwards stepwise GLM for this behavioural parameter only included 'Site', with longer scan bouts in Moëze than in Yves (1·81 s ± 0·21 SE, $n = 44$ and 1·25 s ± 0·10 SE, $n = 33$, respectively, $F_{1,75} = 4.76$, $P = 0.0323$).

Discussion

VISUAL FIELDS AND FORAGING

In both Shoveler and Wigeon the maximum width of the frontal binocular field equals approximately 20° and is centred about the horizontal plane. This topography is very similar to that found in a wide range of bird species which differ in their ecology, phylogeny and eye size: such frontal binocular field topography has been proposed as a convergent feature which results from the limiting requirements for the extraction of information from the visual flow field of each eye as the head or body moves towards targets, whether in flight or in foraging (Martin & Katzir 1999b).

However, while there is apparent convergence of maximum frontal binocular field width in birds, two

main types of binocular field topography with respect to bill position within the binocular field have been described (Martin & Katzir 1999b). Thus, in species whose foraging involves visual guidance of bill position towards individual food items, as in pecking (e.g. Pigeon *Columba livia*, starling, Ostrich *Struthio camelus*), or strikes towards evasive prey (e.g. herons, Short-toed Eagle *Circaetus gallicus*), the bill is placed more centrally within the binocular field (Martin 1999). However, in species whose foraging can be mediated by tactile cues from the bill, and thus requires less precise visual control of bill position (e.g. Mallard *Anas platyrhynchos* and Woodcock *Scolopax rusticola*), the bill is placed in the periphery of the frontal binocular field (Martin 1986b, 1994). Bill position in Shoveler falls into the latter category. Foraging tactics used by Shoveler in our study area attested to the predominance of tactile cues and consisted of either filtering the upper centimetres of the water column or underwater foraging with the whole head submerged, as already observed in other studies (e.g. Dubowy 1996; Guillemain *et al.* 2000). In Wigeon, bill position is more centrally positioned in the frontal binocular field than in Shoveler, and the width of this field is slightly greater at the elevation of the bill. This can be interpreted as consistent with our observation that Wigeon almost only foraged by pecking at individual plant leaves in our study area, as they most generally do when foraging in grasslands (Jacobsen 1992). However, the fact that a considerable proportion of foraging by Wigeon can occur at night (e.g. Madsen 1988; Mayhew 1988), suggests that they may not rely exclusively on visual cues to collect their food, although light levels associated with this nocturnal foraging have not been recorded. Other evidence that Wigeon may not be exclusively visually guided foragers includes observations that in littoral areas Wigeon may feed on eelgrass (*Zostera* spp.), which is collected by dabbling in shallow water (e.g. Fox 1996), and in the Mediterranean region that the diet of Wigeon mostly consists of hydrophytes, which are collected by dipping or upending (Campredon 1982). Thus, it appears that the foraging of Wigeon may be guided by either tactile or visual cues, or by both cue types simultaneously, permitting foraging in a range of feeding situations. This is reflected in the more central position of the bill within the frontal binocular field and an incomplete visual field behind the head, possibly resulting from a slightly more forward placement of the eyes within the skull. On the other hand, Shoveler appear to be more exclusively reliant upon tactile cues and hence have a narrower choice of feeding situations. However, their eyes are placed more laterally permitting comprehensive visual coverage to the rear of the head.

VISUAL FIELDS AND VIGILANCE

Both Wigeon and Shoveler gain extensive visual coverage of the space about the head, but only in Shoveler is comprehensive visual coverage of the celestial hemisphere available. A Shoveler adopting the typical head position depicted in Fig. 2 can thus gather visual information from the whole volume about the head without the need for head movements. This should therefore allow foraging and other activities to be conducted more or less continuously while remaining alert to visual information from any direction about the head. In Wigeon, however, the cyclopean field is not comprehensive because of the small blind area that extends from above the head down to the horizontal behind. In addition, foraging Wigeon may not be able to maintain their attention in the lateral part of their visual field while pecking, but rather focus to the front of their head as they select food item visually. Thus, gathering visual information from the total volume about the head will require small movements of the head and it would be predicted that this would prohibit the continuous conduct of foraging behaviour. Although Garland & Adolph (1994) highlighted the caution with which one should infer adaptation from two-species comparative studies, it is very likely that the differences in vigilance behaviour between Shoveler and Wigeon is an adaptive response to differences in visual fields rather than just a proximate side-effect.

Behavioural observations are in accordance with this prediction: Wigeon did indeed spend more time vigilant during meals than Shoveler, owing to shorter feeding bouts. The difference in vigilance patterns cannot be related to the need for Wigeon to interrupt their feeding to swallow their food, since in other situations (mixed-species foraging groups where Wigeon were apparently relying on early warning by Brent Geese) these birds were capable of continuous feeding for more than 30 s (R. Caldow & M. Guillemain, unpublished data). It is also unlikely that Wigeon suffer a greater predation risk than Shoveler: the two species have comparable body masses (i.e. 680 g and 620 g, respectively, Madge & Burn 1987), and should thus share the same type of predators on their wintering grounds (Marsh Harrier are a threat to dabbling ducks in the study area, Fritz *et al*. 2000). It could be argued that, given that Wigeon feed on terrestrial ground while Shoveler feed in open water, Wigeon would be more exposed to predation risk and would consequently spend more time in vigilance (Jacobsen & Ugelvik 1994). However, Wigeon fed on small islets (*c*. 100 m^2) at Yves, and never more than a few metres away from water at Moëze, so predation risk is most unlikely to differ between the two species.

Conversely, different levels of predator disturbance may explain the longer scan bouts observed in Wigeon and Shoveler at Moëze compared to Yves, as the frequency of fly-overs by raptors during the period of this study has been reported to be much higher at the former site (Fritz *et al*. 2000). The fact that Shoveler had longer scans in the most disturbed area suggests that only some basal level of vigilance can be ensured by dabbling ducks when they have their head down,

even with a total panoramic vision. As already suggested in another study (Guillemain *et al.* 2001), head-up scans would be necessary to spot threats directly or to get precise information from the behaviour of congeners.

Aknowledgements

References

Altmann, J. (1974) Observational study of behaviour: sampling methods. *Behaviour* **49**, 227–267.

Arenz, C.L. & Leger, D.W. (1997) Artificial visual obstruction, antipredator vigilance, and predator detection in the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*). *Behaviour* **134**, 1101–1114.

Bertram, B.C.R. (1980) Vigilance and group size in ostriches. *Animal Behavior* **28**, 278–286.

Campredon, P. (1982) *Demographie et Ecologie du Canard siffleur* Anas penelope. *L. Pendant Son Hivernage En France*. PhD Thesis, Université des Sciences et Techniques du Languedoc, Montpellier.

Carboneras, C. (1992) *Family Anatidae (Ducks, Geese and Swans)*. Handbook of the Birds of the World, Vol. 1. *Ostrich to Ducks* (eds J. del Hoyo, A. Elliot & J. Sargatal), pp. 536–628. Lynx Edicions, Barcelona.

Cézilly, F. & Brun, B. (1989) Surveillance et picorage chez la tourterelle rieuse, *Streptopelia risoria*: effets de la présence d'un congénère et de la dispersion des graines. *Behaviour* **110**, 146–160.

Dubowy, P.J. (1996) Northern Shoveler (*Anas clypeata*). *The Birds of North America* (eds A. Poole & F. Gill). The Academy of Natural Sciences of Philadelphia and the American Ornithologists' Union, Washington, DC.

Elgar, M.A. (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Reviews* **64**, 13–33.

Fox, A.D. (1996) Zostera exploitation by brent geese and wigeon on the Exe estuary, southern England. *Bird Study* **43**, 257–268.

Fritz, H., Guillemain, M. & Guérin, S. (2000) Changes in the frequency of prospecting fly-overs by Marsh harriers *Circus aeruginosus* in relation to short-term fluctuations in dabbling ducks abundance. *Ardea* **88**, 9–16.

Garland, T. Jr & Adolph, S.C. (1994) Why not to do two-species comparative studies: limitations on inferring adaptation. *Physiological Zoology* **67**, 797–828.

Gauthier-Clerc, M., Tamisier, A. & Cézilly, F. (1998) Sleep-vigilance trade-off in green-winged teals (*Anas crecca crecca*). *Canadian Journal of Zoology* **76**, 2214–2218.

Guillemain, M., Duncan, P. & Fritz, H. (2001) Switching to a feeding method which obstructs vision increases head-up vigilance in dabbling ducks. *Journal of Avian Biology* **32**, 345–350.

Guillemain, M., Fritz, H. & Guillon, N. (2000) Foraging behavior and habitat choice of wintering Northern shoveler in a major wintering quarter in France. *Waterbirds* **23**, 35–363.

Hart, A. & Lendrem, D.W. (1984) Vigilance and scanning patterns in birds. *Animal Behavior* **32**, 1216–1224.

Jacobsen, O.W. (1992) Factors affecting selection of nitrogen-fertilized grassland areas by breeding wigeon *Anas penelope*. *Ornis Scandinavica* **23**, 121–131.

Jacobsen, O.W. & Ugelvik, M. (1994) Grazing and vigilance behaviour of breeding Eurasian wigeon in relation to distance from water. *Wildfowl* **45**, 119–123.

Lima, S.L. & Bednekoff, P.A. (1999) Back to the basics of antipredatory vigilance: can non-vigilant animals detect attack? *Animal Behavior* **58**, 537–543.

Lima, S.L. & Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**, 619–640.

Madge, S. & Burn, H. (1987) *Wildfowl, an Identification Guide to the Ducks, Geese and Swans of the World*. Christopher Helm, London.

Madsen, J. (1988) Autumn feeding ecology of herbivorous wildfowl in the Danish Wadden Sea, and impact of food supplies and shooting on movements. *Danish Review of Game Biology* **13**, 1–32.

Martin, G.R. (1984) The visual fields of the tawny owl, *Strix aluco* L. *Vision Research* **24**, 1739–1751.

Martin, G.R. (1985) Eye. *Form and Function in Birds*, Vol. 3 (eds A. S. King & J. McLelland), pp. 311–373. Academic Press, London.

Martin, G.R. (1986a) The eye of a passeriform bird, the European starling (*Sturnus vulgaris*): eye movement amplitude, visual fields and schematic optics. *Journal of Comparative Physiology A* **159**, 545–557.

Martin, G.R. (1986b) Total panoramic vision in the mallard duck, *Anas platyrhynchos*. *Vision Research* **26**, 1303–1306.

Martin, G.R. (1994) Visual fields in woodcocks *Scolopax rusticola* (Scolopacidae; Charadriiformes). *Journal of Comparative Physiology A* **174**, 787–793.

Martin, G.R. (1999) Optical structure and visual fields in birds: their relationship with foraging behaviour and ecology. *Adaptive Mechanisms in the Ecology of Vision* (eds S. N. Archer, M. B. A. Djamgoz, E. Loew, J. C. Partridge & S. Vallerga), pp. 485–507. Kluwer, Dordrecht.

Martin, G.R. & Brooke, M.D.L. (1991) The eye of a procellariiform seabird, the Manx shearwater, *Puffinus puffinus*: visual fields and optical structure. *Brain, Behaviour and Evolution* **37**, 65–78.

Martin, G.R. & Katzir, G. (1994a) Visual fields and eye movements in herons (Ardeidae). *Brain, Behaviour and Evolution* **44**, 74–85.

Martin, G.R. & Katzir, G. (1994b) Visual fields in the stone curlew *Burhinus oedicnemus*. *Ibis* **136**, 448–453.

Martin, G.R. & Katzir, G. (1995) Visual fields in ostriches. *Nature* **374**, 19–20.

Martin, G.R. & Katzir, G. (1999a) Visual fields, foraging and binocularity in birds. *Proceedings of the 22nd International Ornithological Congress, Durban* (eds N. Adams & R. Slowtow), pp. 2711–2728. Birdlife, Johannesburg.

Martin, G.R. & Katzir, G. (1999b) Visual field in short-toed eagles *Circaetus gallicus* and the function of binocularity in birds. *Brain, Behaviour and Evolution* **53**, 55–66.

Mayhew, P.W. (1988) The daily energy intake of European wigeon in winter. *Ornis Scandinavica* **19**, 217–223.

McNamara, J.M. & Houston, A.I. (1992) Evolutionary stable levels of vigilance as a function of group size. *Animal Behavior* **43**, 641–658.

Pradel, R., Rioux, N., Tamisier, A. & Lebreton, J.D. (1997) Individual turnover among wintering teal in Camargue: a mark–recapture study. *Journal of Wildlife Management* **61**, 816–821.

SAS Institute (1990) SAS/STAT User's Guide, *Version 6* 4th edn EDZ, Vol. 2. SAS Institute Inc., Cary.

Thomas, G.J. (1982) Autumn and winter feeding ecology of waterfowl at the Ouse Washes, England. *Journal of Zoology (London)* **197**, 131–172.