*J. Zool., Lond.* (2001) **254**, 521–528  Printed in the United Kingdom

# Functional morphology of the pecten oculi in the nocturnal spotted eagle owl (*Bubo bubo africanus*), and the diurnal black kite (*Milvus migrans*) and domestic fowl (*Gallus gallus* var. *domesticus*): a comparative study

S. G. Kiama[1,2]*, J. N. Maina[3], J. Bhattacharjee[4] and K. D. Weyrauch[5]

[1] Institute of Anatomy, University of Bern, Bühlstrasse 26, CH-3000, Bern 9, Switzerland
[2] Department of Veterinary Anatomy, University of Nairobi, P.O. Box 30197, Nairobi, Kenya
[3] Department of Anatomical Sciences, The University of Witwatersrand, Johannesburg 2193, South Africa
[4] Department of Zoology, Egerton University, P.O. Box 536, Njoro, Kenya
[5] Institute of Veterinary Anatomy, Free University of Berlin, D-14195, Berlin, Germany

*(Accepted 5 October 2000)*

**Abstract**

The pecten oculi is a highly vascularized and pigmented organ that overlies the optic disc and projects into the vitreous body in the avian eye. First reported over 300 years ago, its function(s) remains a puzzle to ornithologists, ophthalmologists and anatomists. Morphometric study of this unique organ was undertaken in birds exhibiting apparently different visual acuities, namely two species of diurnal birds (the ground-dwelling domestic fowl *Gallus gallus* var. *domesticus* and a highly active predator bird, the black kite (*Milvus migrans*) and a nocturnal bird (the spotted-eagle owl *Bubo bubo africanus*). The volume of the owl's eye was 4.8 and 2.2 times larger than that of the fowl and the kite, respectively. However, the pecten of the fowl consisted of more pleats (16–18) compared to the kite (12–13) and the owl (5–6). The volume of the pecten of the kite was 1.4 and 2.7 times larger than that of the fowl and the owl, respectively ($P < 0.05$). Similarly, the surface area of the pecten of the kite was 2.6 and 4 times larger than that of the fowl and owl, respectively ($P < 0.05$). The volume density of blood vessels (lumen and wall) in the pecten of the kite, fowl and owl comprised 67.7%, 66.9% and 62.6%, respectively, the pigmented tissue constituting the rest. Both the volume density and the volume of the blood in the pecten were higher in the diurnal birds (kite, fowl) than the owl ($P < 0.05$). The surface area of the capillary luminal surface was 1.7 and 5.3 times higher in the kite than in the fowl and the owl, respectively ($P < 0.05$). These results suggest that the functional morphology of the pecten correlates with the life-style of the bird and with functional need, and lends further support to the nutritive role of the pecten.

**Key words**: pecten oculi, spotted eagle owl, black kite, domestic fowl

## INTRODUCTION

Birds are highly dependent on their eyes while flying, feeding and breeding (Campbell & Lack, 1985). Diurnal birds and in particular birds of prey exhibit high visual acuity while nocturnal birds exhibit high visual sensitivity (Hughes, 1977). Visual acuity and visual sensitivity require different construction in the optical apparatus and the retinal structure (Tansley, 1965; Hughes, 1977). A thorough description of the structure of the eye in nocturnal and diurnal birds can be found in Walls (1963) and Duke-Elder (1958). The retina of birds is generally thicker than that of most other vertebrates (Duke-Elder, 1958) and among birds, the diurnal birds of prey possess the thickest retina. For example, the retina is 630 μm thick in the diurnal birds of prey such as the snake eagle *Circaetus gallicus* but only 360 μm thick in nocturnal eagle owl *Bubo bubo* (Pearson, 1972). Despite its unusual thickness, the avian retina is devoid of blood vessels (De Schaepdriver *et al.*, 1989; Samuelson, 1991) and the source of nutrients, especially to its inner nuclear layer, is yet to be resolved. The retina of diurnal birds is dominated by cones, has a high concentration of bipolar cells and consequently has a relatively thick inner nuclear layer. Contrarily, in nocturnal birds where acute vision has been sacrificed for sensitivity, rods are predominant, and the outer nuclear layer is thicker than the inner nuclear layer (Silman, 1973).

The pecten oculi, a highly vascularized body unique to the avian eye has been suggested to play a major role in supplying nutrients to the avascular avian retina (Kiama *et al.*, 1998; Wolburg *et al.*, 1999). Many other functions have been ascribed to the pecten oculi. These

*All correspondence to: Dr S. G. Kiama, Department of Veterinary Anatomy, University of Nairobi, P.O. Box 30197, Nairobi, Kenya.

include, regulation of intraocular pressure (Seaman & Himelfarb, 1963), reduction of intraocular glare (Barlow & Ostwald, 1972), regulation of intraocular pH (Brach, 1975), and increasing sensory effect of moving objects (Crozier & Wolf, 1944).

In all birds so far studied, the pecten is situated in the lower posterior temporal quadrant of the fundus (Thomson, 1929; Kiama *et al.*, 1998) and corresponds embryologically to the position of the choroid fissure (Uehara *et al.*, 1990) and morphologically to an elongated optic disc (Bhattacharjee, 1993). Three morphological types of pecten oculi are recognized: conical type, vaned type and pleated type (Meyer, 1977; Kiama *et al.*, 1994). The pleated pecten is the most common and arises from the linear optic disc as a single accordion folded lamina, which in most species is held together apically by a bridge of tissue (Braekevelt, 1998). It consists of an elaborate vasculature, pigmented tissue, and a superficial covering membrane (Meyer, 1977).

Although the structure of the pecten has received a lot of attention (Bawa & YashRoy, 1974; Bhattacharjee, 1993; Braekevelt, 1993; Kiama *et al.*, 1994) data on quantitative structural characteristics are scarce. Save for a preliminary morphometric study to determine the proportion of pectineal blood vessels in the cormorant *Phalacrocorax carbo* (Bhattacharjee & Maina, 1987), most other available data are based mainly if not exclusively on the number of pleats (Thomson, 1929; Meyer, 1977) and information concerning the precise size of the pectens is lacking.

In this study we asked whether pectineal sizes are related to the life-style of the birds. Therefore, we investigated morphometric parameters in the pecten oculi in birds inhabiting distinct niches and light regimes and therefore apparent differing levels of visual reliance as an attempt to relate pectineal morphology to function.

## MATERIALS AND METHODS

The pecten oculi of 2 species of diurnal birds, the relatively inactive, ground-dwelling domestic fowl *Gallus gallus* var. *domesticus* and the fairly agile bird of prey, black kite *Milvus migrans*, and 1 species of nocturnal bird of prey, spotted eagle owl *Bubo bubo africanus*, were investigated. A total of 5 kites, 4 owls and 5 fowls were used in the study. The birds were killed using pentobarbitone sodium injected into the brachial vein and the pecten gently perfused via the left and right internal carotid arteries with warm (35 °C) physiological saline until the eyes were completely blanched. This was followed by perfusion fixation with 2.5%, 0.2 M, phosphate buffered (pH 7.4) glutaraldehyde solution before which the right auricle was cut open for drainage. The eyes were enucleated, weighed and volume measured by weight displacement (Scherle, 1970) and then cut into anterior and posterior halves. Vitreous humour was washed with phosphate buffer and the posterior hemisphere of the eye was immersed briefly in the same fixative as above. The pecten oculi was carefully dissected out and immersed in the 2.5%, 0.2 M, phosphate buffered (pH 7.4) glutaraldehyde solution for 6 h.

### Determination of pecten volume

The volume of the pecten was determined by the weight displacement method of Scherle (1970). Briefly, a small jar containing a sufficient amount of physiological saline was placed on a sartorius balance that was subsequently set to zero. The pecten oculi was freely suspended by a fine thread from the arm of a small stand and completely immersed into the physiological saline. The weight gain registered was taken to be equivalent to the volume of the pecten oculi.

### Estimation of pectineal surface area

The pecten was severed from around its base and bridge, placed in a petri dish containing phosphate buffer, gently unfolded and flat mounted on a slide without stretching it. The pecten was projected on a television monitor connected to a light microscope at a final magnification of $\times 50$ and its surface area estimated using a 100-point quadratic lattice grid. The area ($A$) in real units was estimated from the product of the total number of points ($P$) falling on the pecten and the area equivalent of one test point (a/$P$). Thus

$$A = P.\ a/P \qquad (1)$$

### Structural hierarchy of the pecten oculi

The pecten consisted basically of an elaborate vascular system and extravascular pigmented tissue. The vascular component was divided into wall and lumen of blood vessels (Fig. 1). An estimate of the lumen of the blood vessels was taken to represent an estimate of the blood volume in the pecten. The extravascular component consisted of the pigmented cells and the vitreopectineal membrane.

### Tissue sampling protocol

The pecten was placed on a dissecting plate and divided into 4 parallel strips running from the base to the apex. Each of these strips was then cut perpendicular to their long axis into 3 pieces. Starting with a random sample, 6 pieces were selected by systematic random sampling from each pecten and embedded in epon for morphometric analysis. The pieces were washed in phosphate buffer, post-fixed in 1% osmium tetroxide followed by dehydration in a graded series of ethanol through propylene oxide and embedded in epoxy resin. One semi-thin and 1 ultra-thin section was cut from each block using an ultramicrotome. Semi-thin sections were stained with 0.5% toluidine blue for light microscopy

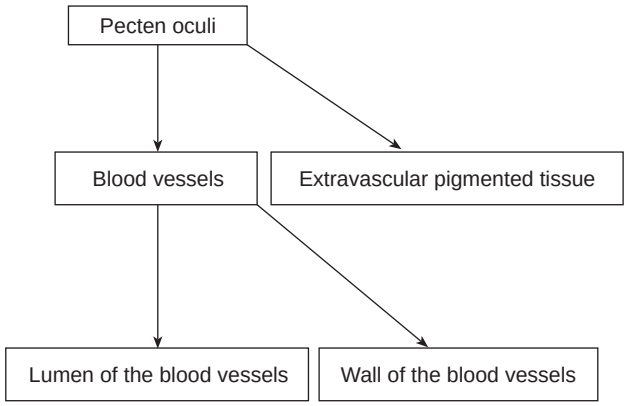


**Fig. 1**. Structural hierarchy of the pecten oculi.

while ultra-thin sections were stained with lead citrate and counter stained with uranyl acetate for transmission electron microscopy (TEM). The semi-thin sections were viewed under a light microscope connected to a television monitor at a final linear magnification of $\times 2200$ and analysis of the target parameters done on fields selected by systematic random sampling. TEM sections were viewed using Zeiss 10 CR transmission electron microscope connected to a television monitor at a final magnification of $\times 34\,800$.

## Morphometric methods

### *Volume density estimations*

The volume densities of main components of the pecten and those of the vascular system were estimated by point counting using an overlay coherent test system of points. Fields selected by systematic random sampling were overlaid with the test system and the number of points falling on the components of interest and those falling on the entire profile counted. The volume densities of the vascular system ($V_{v(bv,P)}$), extravascular pigmented tissue ($V_{v(ept,P)}$), wall of blood vessels, ($V_{v(w,\ bv)}$) and lumen of blood vessels ($V_{v(l,\ bv)}$) were estimated. These were estimated as the ratio of total points falling on the component of interest ($Pc$), say lumen of blood vessels, divided by the number of points falling on the entire pectineal profile ($Pt$). Thus the volume densities ($V_{v(c,P)}$) were determined from the formula (Weibel, 1979):

$$V_{v(c,P)} = Pc/Pt \tag{2}$$

The absolute volume of each component ($Vc$) was determined from the product of its volume density ($Vv_{(c,P)}$) and the absolute volume of the pecten oculi ($V$). Thus,

$$Vc = V_{v(c,P)} \times V \tag{3}$$

### *Surface area of the luminal surface of the capillaries*

In order to estimate the surface area of the luminal surface of the capillaries, the pecten was sampled at 2 levels of magnification. At level 1, the surface density of the luminal surface of the capillaries was estimated by superimposing a curvilinear test grid of Merz onto fields selected by systematic random sampling and counting the number of intersections ($I$) that the test system made with the luminal surface of the capillaries. Then the surface density ($S_v$) of the luminal surface of the capillaries was estimated using the formula (Weibel, 1979):

$$S_v = 2I.\ M/Lt \tag{4}$$

where, $M$ is the magnification and $Lt$ is the total length of the test system. $Lt$ was calculated using the formula:

$$Lt = Pt.((/2).d \tag{5}$$

where $Pt$ is the number of points in the test system and $d$ is the separation distance between the points in the test system used. The absolute surface area of the capillary luminal surface was calculated from the product of surface density and absolute volume of the pecten.

At the TEM level (level 2), we estimated the extent to which the endothelial plasmalemma infoldings amplified the luminal surface of the capillaries ($AF$). In order to achieve this, a Merz grid was superimposed on fields selected by systematic random sampling and the number of intersections between the test lines and the profiles of the microplicae ($Im$) and the endothelial surface ($Ie$) counted. The endothelial surface was defined as a line running at the base of the microfolds and across the apical plasmalemmal surface of the endothelial cells. Ten fields were selected by systematic random sampling from each section. The intersections were summed for each pecten and the amplification due to microplicae estimated as a ratio between the intersections of the test system with the microplicae and with the endothelial surface. Thus,

$$AF = I_m/I_e \tag{6}$$

## Statistical analysis

Student $t$-distribution was used to analyse for statistical significance.

# RESULTS

## Body masses, eye volumes and pectineal gross parameters

The mean mass of the domestic fowl *G. g*. var. *domesticus*, the black kite *M. migrans* and the spotted eagle owl *B. b. africanus* was $1369 \pm 153$g SD, $711 \pm 137$g (SD) and $633 \pm 65$g (SD), respectively (Table 1). In contrast, the volume of the eye per unit body weight was largest in the owl followed by the kite, while that of the fowl was the smallest ($P < 0.05$; Fig. 2). In all cases, the pecten projected as a dark brown mass from the linear optic disc into the vitreous body. The height of the

**Table 1**. Body masses, anteroposterior diameter of the eyes, pectineal pleat numbers height and length of the base of the pecten in the domestic fowl, black kite and the spotted eagle owl. Values represent mean + SD

| Species | Body mass (g) | Anteroposterior diameter of the eye (mm) | Height of pecten from base to apex (mm) | Length of pecten at the base (mm) |
|---|---|---|---|---|
| *Gallus gallus* var. *domesticus* domestic fowl | 1369 (153) | 13.9 (.72) | 4.38 (0.13) | 8.76 (0.35) |
| *Milvus migrans* black kite | 711 (137) | 21.9 (2.1) | 6.22 (0.35) | 9.4 (0.3) |
| *Bubo bubo africanus* spotted eagle owl | 633 (65) | 27.7 (1.4) | 6.02 (0.16) | 2.77 (0.09) |

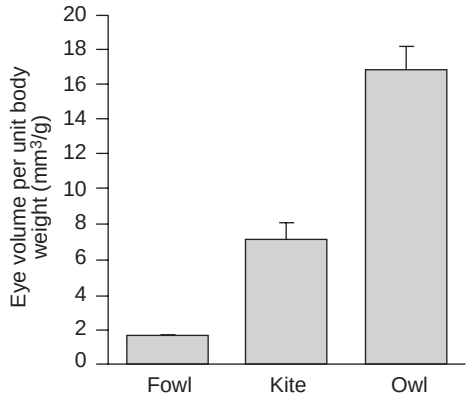


**Fig. 2**. Mean of eye volume per gram body weight ± SD in the domestic fowl, black kite and spotted eagle owl.

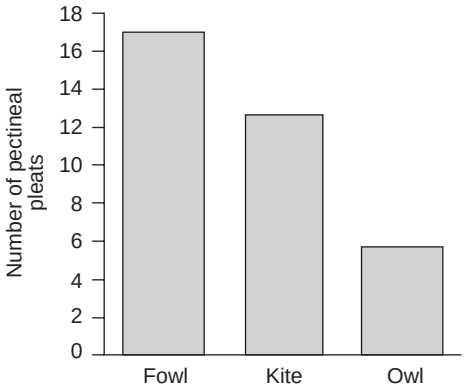


**Fig. 3**. Average number of pleats in the pecten oculi of the domestic fowl, black kite and spotted eagle owl.

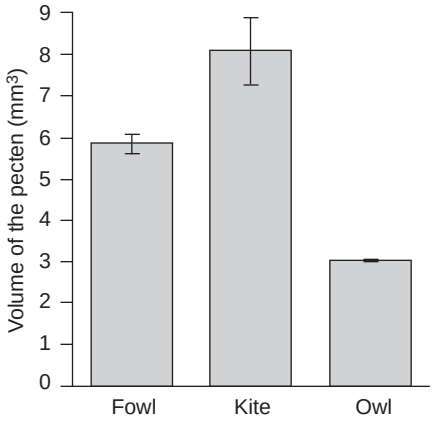


**Fig. 4**. Mean volume of the pecten ± SD in the domestic fowl, black kite and spotted eagle owl.

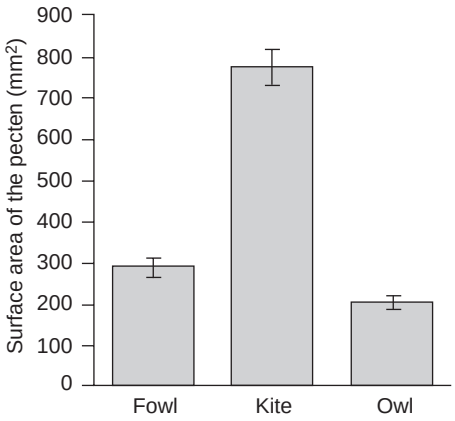


**Fig. 5**. Mean surface area of the pecten ± SD in the domestic fowl, black kite and spotted eagle owl.

pecten from the base to the highest point at the apex was similar between the owl and the kite. However, the length of the base of the pecten was 3.4 times longer in the kite than that in the owl ($P < 0.05$). The pecten of the fowl had a longer base but was shorter from base to apex than that of the owl ($P < 0.05$). In contrast, the pecten of the kite was higher from base to apex and longer at the base than that of the fowl ($P < 0.05$).

The pecten was in the form of a single sheet doubled back and forth to form several pleats. The pecten of the fowl consisted of more pleats (16–18) compared to the kite (12–13) and the owl (five to six) (Fig. 3). In contrast the pecten of the kite had a significantly larger volume compared to the fowl and the owl ($P < 0.05$; Fig. 4). Similarly the pecten of the kite had a significantly larger surface area than that of the fowl and the owl ($P < 0.05$; Fig. 5). The pecten of the fowl was significantly larger in volume (Fig. 3) and surface area (Fig. 4) compared to that of the owl ($P < 0.05$).

## Volumes of the vascular system and extravascular pigmented tissue

The pecten consisted of an elaborate vascular framework and scant extravascular pigmented tissue. The system of blood vessels (wall and lumen) in the pecten accounted for 67.7 ± 5.2% (SD), 66.9 ± 5% (SD) and 62.6 ± 6.2% (SD) in the kite, the fowl and the owl, respectively, pigmented tissue constituting the rest

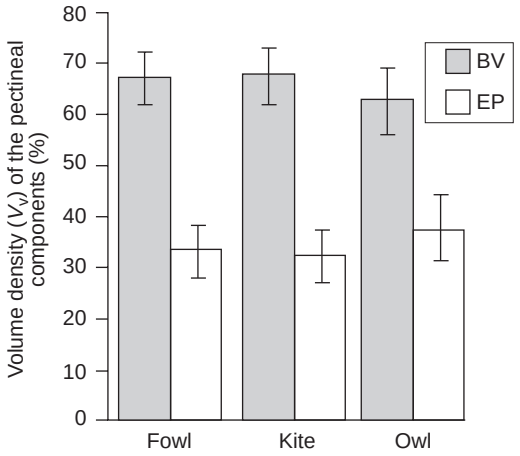


**Fig. 6**. Mean volume densities ± SD of the main components of the pecten oculi in the pecten oculi of the domestic fowl, black kite and spotted eagle owl. BV, blood vessels; EP, extravascular pigmented tissue.

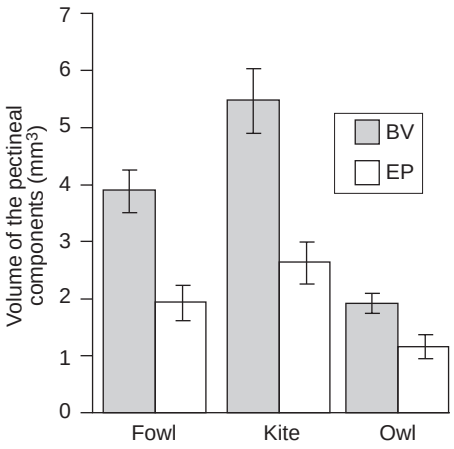


**Fig. 7** Mean volumes ± SD of the main components of the pecten oculi in the pecten oculi of the domestic fowl, black kite and spotted eagle owl. BV, blood vessels; EP, extravascular pigmented tissue.

(Fig. 6). There was no significant difference in the volume density of blood vessels and the pigmented tissue between the three species. However, the absolute volume of the vascular system was significantly higher in the kite than the fowl and the owl ($P < 0.05$; Fig. 6). Similarly, the owl had a significantly lower volume of the vascular system than the fowl ($P < 0.05$; Fig. 7).

The blood vessels of the pecten possessed a fairly thick wall. There was no significant difference in the volume density of the wall or lumen of blood vessels between the fowl and the kite (Fig. 8). However, there was a significant difference between the volume density of the wall and lumen of the blood vessels between the kite and the owl and also between the fowl and the owl $P < 0.05$ (Fig. 8). The absolute volumes of the lumen (volume of blood in the pecten) and wall of blood vessels were highest in the kite and lowest in the owl ($P < 0.05$; Fig. 9).

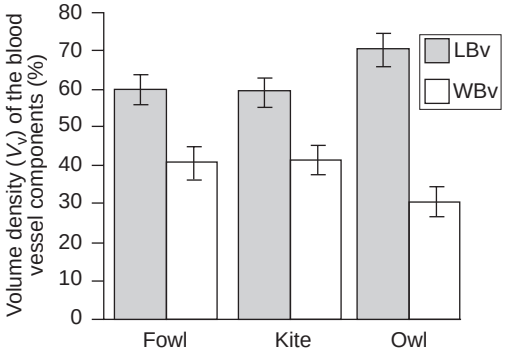


**Fig. 8**. Mean volume densities ± SD of the main components of blood vessels in the pecten oculi of the domestic fowl, black kite and spotted eagle owl. LBv, lumen of blood vessels; WBv, wall of blood vessels.

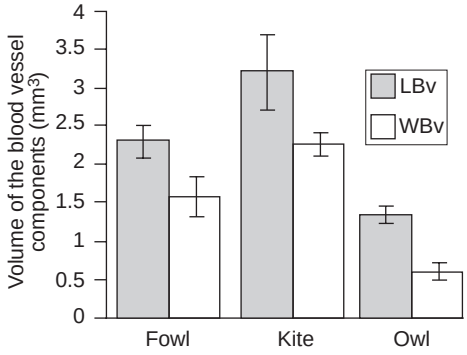


**Fig. 9**. Mean volume ± SD of the main components of blood vessels in the pecten oculi of the domestic fowl, black kite and spotted eagle owl. LBv, lumen of blood vessels; WBv, wall of blood vessels.

## Surface area of the capillary luminal surface

The surface densities of the capillary luminal surface in the pecten of the fowl, kite and owl were not significantly different (Table 2). However, after taking the volume of the entire pecten into account, the surface area of the capillary luminal surface was significantly higher in the kite than the fowl and the owl ($P < 0.05$). The surface area of the luminal surface of the capillaries in the pecten was also significantly larger in the fowl than that in the owl ($P < 0.05$; Table 2).

The plasmalemma of the endothelium was highly folded forming microplicae both on the basal and the luminal aspect of the capillaries. At the luminal surface of the capillaries, these microplicae amplified the capillary luminal surface area by a factor of 13.97 in the kite, 9.77 in the fowl and 6.72 in the owl (Table 2). The calculated total capillary luminal surface area after taking the amplification factors into account was two and five times higher in the kite than the fowl and the owl, respectively ($P < 0.05$; Fig. 10).

**Table 2**. Surface density, surface area and amplification factor due to microplicae in the blood capillaries of the domestic fowl, black kite and spotted eagle owl. Values represent mean + SD

| Species | Surface density of the luminal surface of the blood capillaries ($mm^{-1}$) | Surface area of the luminal surface of the blood capillaries ($mm^2$) | Surface amplification factor due to microplicae |
|---|---|---|---|
| *Gallus gallus* var. *domesticus* domestic fowl | 50.31 (4.8) | 292.96 (27.9) | 9.77 (1.36) |
| *Milvus migrans* black kite | 45.64 (3.39) | 364.68 (43.05) | 13.97 (1.29) |
| *Bubo bubo africanus* spotted eagle owl | 48.25 (4.79) | 144.25 (13.88) | 6.72 (1.05) |

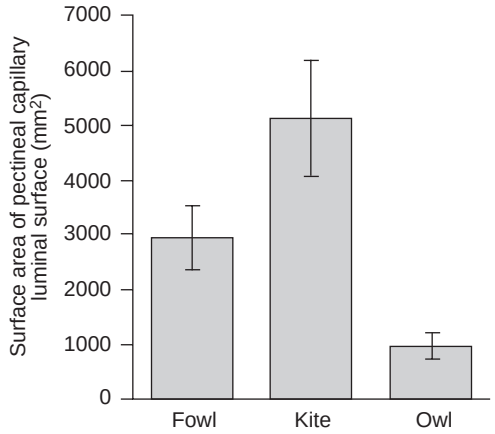


**Fig. 10** Mean surface area ± SD of the capillary luminal surface in the pecten oculi of the domestic fowl, black kite and spotted eagle owl.

## DISCUSSION

In birds where the retina is avascular, the presence of the pecten oculi, a highly vascularized intraocular organ with sparse pigmented tissue, strongly suggests a nutritive role (Meyer, 1977). A trophic role calls for an expansive surface area and high blood supply. This must, however, be achieved after obviating a certain constraint: the pecten must not be too large as to interfere with the optical function of the eye. Our results show that the avian pecten oculi has been designed to meet this demand, which probably differs in nocturnal and diurnal birds and with the life-style of the bird. Out of the three avian species studied, the pecten of the black kite *M. migrans* had the largest volume and surface area coupled with the most expansive surface area of the capillary luminal endothelium. In contrast, the spotted eagle owl *B. b. africanus* had the smallest pecten in volume, surface area as well as in respect to surface area of the capillary luminal endothelium. The fairly inactive, ground dwelling domestic fowl *G. g*. var. *domesticus* possessed a pecten that was intermediate in size, smaller than that in kite but larger than that in the owl. These results are consistent with the observation of Duke-Elder (1958) that diurnal birds have more elaborate pecten than nocturnal birds and Thomson's (1929) conjecture that suppression of flight is a determining factor in the size of pecten, the relatively large and more specialized forms being found in volant birds. The black kite is a diurnal bird of prey exhibiting an ubiquitous distribution (Brown, 1976). It is extremely agile at catching prey, aided by buoyant flight and high manoeuvrability imparted by the forked tail (Fry, Keuth & Urban, 1982). On the other hand, the spotted eagle owl is a nocturnal bird of prey that emerges from the roost at dusk to search for prey (Fry, Keuth & Urban, 1988). Although, no data are available regarding the visual capacity of the black kite and the eagle owl, diurnal birds, and in particular those of prey, are thought to exhibit high visual acuity while nocturnal birds exhibit high visual sensitivity (Hughes, 1977).

Our previous structural studies on the pecten (Kiama *et al*., 1994) demonstrated how the pleated pecten consists of a system of blood vessels effectively arranged into a thin lamina and reinforced by a large contingent of melanosomes. The present results show that the system of blood vessels in the pecten of the kite, fowl and owl account for 67.7%, 66.9% and 62.6%, respectively, of the entire pecten while the pigmented tissue constitutes the rest. Although there are no significant differences in the volume densities of blood vessels between the three species, such a value is remarkably high. Moreover, since the disparity in the volume of the pecten in the fowl, kite and owl is large, the absolute volume of the system of blood vessels is significantly different. Therefore this similarity in volume density may just reflect the developmental constraints of the pecten within the optical system where an increase in any one component is matched by the commensurate development of the others. The differences in overall size of the pecten could therefore be looked upon as crucial determinants in affording need-based nutritive function of the pecten, which is brought about by the diverse food-gathering practices evident in birds. The role of pigmented tissue in the pecten oculi has been debated for a long time. The suggested roles include raising the metabolism of the pecten by increasing its temperature through light absorption (Bawa & YashRoy, 1974), providing structural support (Braekevelt, 1993), and protecting the pectineal capillaries from the harmful effects of ultraviolet radiation (Kiama *et al*., 1994). Although the pigmented tissue could be performing any or all of these roles, the present data suggest that there is an optimum fraction of the pigment component the pecten has to concede with, without its nutritive role being compromised.

The most striking characteristic of the pecten oculi is the unique morphology of the capillary endothelium. In our previous studies, we showed how the luminal surface of the capillary endothelium of the pecten oculi of the chicken (Kiama *et al*., 1997) and kite (Kiama *et al*., 1998) is endowed with microplicae that highly amplify the surface. This amplification seems to decline from the kite, to fowl, to owl. The low amplification of the luminal surface of the capillaries in the nocturnal owl as opposed to the high amplification of the same in the active diurnal kite probably reflects the lower demand placed on the pecten for nutrient delivery in the retina of the owl. This may be explained by the unique retina cytoarchitecture in diurnal and nocturnal birds. The retina of diurnal birds is dominated by cones, has a high concentration of bipolar cells and consequently has a relatively thick inner nuclear layer, while in nocturnal birds where acute vision has been sacrificed for sensitivity, the outer nuclear layer is thicker than the inner nuclear layer (Silman, 1973). In vertebrates where the retina circulation is present, it maintains the neural layers while the photoreceptors are maintained by the choroid circulation (Samuelson, 1991). The cells of the inner layers of the retina in birds fuels their energy metabolism mainly through glycolysis since mitochondria are minimal or lacking (Ruggiero & Sheffield, 1998) and therefore it is feasible that a higher cell density of the inner layers would result in a higher glucose demand from the pecten. Variations in the endothelial specialization of the pectineal blood vessels have been shown to exist, being relatively sparse in the owl, more abundant in the kestrel, and highly developed in the sparrow (Meyer, 1977).

Although our results are consistent with the widely held view that the pecten of diurnal birds possess more pleats than that of nocturnal birds, the data also suggest that the number of pleats may not reveal the true size of the pecten. Despite the pecten of the fowl possessing more pleats (16–18) as compared to the kite (12–13), the latter is larger in volume, surface area and in all other dimensions measured such as height from base to apex and the length of the base. This suggests that in addition to the pleat number serving the role of increasing the pecten size, other yet to be identified functions could be more important. As cited by Pumphrey (1948), Menner (1938) examined several birds and concluded that the pleats cast shadows on the functional part of the retina and that the extent of the pleats, and consequently of the shadow, is directly related to life-style. He thus inferred that the significance of the avian pecten might be to increase the sensory effect of small moving images through creation of a flicker response. This suggestion was later supported by Crozier & Wolf (1944). However, Barlow & Ostwald (1972) carried out experiments that showed that the pecten is placed in such a way as to cast its shadow on its own base and not on the sensory retina. Later, Tucker (1975) proposed that the folds of the pecten occur in the form of ribs that are specifically attached at the base and the bridge. He interpreted this to suggest that the pleats are present to impact mechanical stability and to aid in the ability of the pecten to withstand stress, which is necessary in aiding the pecten in its role of stabilizing the vitreous humour. Although it is difficult to understand how such small structure like the pecten would stabilize the vitreous, it is feasible that formation of the thin pectineal lamina into pleats would impart physical stability to the pecten. This would not only be because of the enlarged base of the pecten resulting from the apparent pyramidal shape it acquires, but also because of the pleats themselves. Physical stability in the pecten would be advantageous in preventing a lateral bend and hence avoid narrowing or occlusion of the blood vessels, which would be deleterious to the normal functioning of the pecten and the vitreous body.

Although this study gives important morphometric findings regarding the pecten oculi of diurnal and nocturnal birds, data which support the suggestion that the primary role of the pecten is that of a nutritive organ, further studies on more species of birds leading diverse life-styles are necessary in order to identify and comprehensively integrate all the primary factors that determine the design of the pecten. Experimental manipulations such as *in vivo* obliteration or surgical excision of the pecten followed by a study of subsequent changes in the vitreous body, retinal morphology, and the overall visual acuity may be most helpful in resolving the basis of functional design of the avian pecten.

**Acknowledgements**

We wish to thank Mrs Hindorf from the Institute of Anatomy, Free University of Berlin, Germany, Messrs J. Gacoka, S. Ochieng and P. Odhiambo of the Department of Veterinary Anatomy, University of Nairobi, Kenya and the late Joseph Kwambai of the National Museums of Kenya for their excellent technical assistance. This work was funded by the German Academic exchange program (DAAD).

## REFERENCES

Barlow, H. B. & Ostwald, T. S. (1972). Pecten of the pigeon's eye as an intraocular eye shade. *Nature (Lond.)* **236**: 88–90.

Bawa, S. R. & YashRoy, R. C. (1974). Effect of dark and light adaptation on the retina and pecten of chicken. *Exp. Eye Res.* **13**: 92–97.

Bhattacharjee, J. (1993). A presumably astroglial cell in the retinopectineal junction in *Gallus domesticus*, demonstrated by non-specific esterase staining. *Eur. J. Morphol.* **31**: 169–173.

Bhattacharjee, J. & Maina, J. N. (1987). Morphometric estimation of pectineal blood volume in the cormorant (*Pharacrocorax carbo*): a preliminary study. *Acta Anat*. **130**: 11A.

Brach, V. (1975). The effect of intraocular ablation of the pecten oculi of the chicken. *Invest. Ophthalmol*. **14**: 166–168.

Braekevelt, C. R. (1993). Fine structure of the pecten oculi in the great horned owl (*Bubo virginianus*). *Histol. Histopathol*. **8**: 9–15.

Braekevelt, C. R. (1998). Fine structure of the pecten oculi of the emu *(Dromaius novaehollandiae)*. *Tissue Cell* **30**: 157–165.

Brown, L. (1976). *Birds of prey, their biology and ecology*. London: Hamlyn.

Campbell, B. & Lack, E. (1985). *Dictionary of birds*. Calton: T & A. D. Poyser.

Crozier, W. J. & Wolf, E. (1944). Flicker response contours for the sparrow and the theory of the avian pecten. *J. gen. Physiol.* **27**: 315–324.

De Schaepdriver, L., Simoens, P., Lauwers, H. & De Geest, J. P. (1989). Retinal vascular patterns in domestic animals. *Res. Vet. Sci*. **47**: 34–42.

Duke-Elder, S. (1958). *System of ophthalmology*. London: Henry Kimpton.

Fry, C. H., Keuth, S. & Urban, E. K. (1982). *The birds of Africa* **I**. London: Academic Press.

Fry, C. H., Keuth, S. & Urban, E. K. (1988). *The birds of Africa* **III**. London: Academic Press.

Hughes, A. (1977). The topography of vision in mammals of contrasting life styles: comparative optics and retinal organisation. In *Handbook of sensory physiology* **VII/5**. *The visual system of vertebrates*: 613–756. Crescentelli, F. (Ed.). Berlin: Springer Verlag.

Kiama, S. G., Bhattacharjee, J., Maina, J. N. & Weyrauch, K. D. (1994). Scanning electron microscope study of the pecten oculi of the black kite (*Milvus migrans*): possible involvement of the melanosomes in protecting the pecten against damage by ultraviolet light. *J. Anat*. **185**: 637–642.

Kiama, S. G., Bhattacharjee, J., Maina, J. N. & Weyrauch, K. D. (1997). Surface specialisation of the capillary endothelium in the pecten oculi of the chicken, and their overt roles in pectineal haemodynamics and nutrient transfer to the inner neural retina. *Acta Biol. Hung*. **48**: 473– 483.

Kiama, S. G., Bhattacharjee, J., Maina, J. N., Weyrauch, K. D. & Gehr, P. (1998) A scanning electron microscope study of the luminal surface specialisations in the blood vessels of the pecten oculi in a diurnal bird, the black kite (*Milvus migrans*). *Ann. Anat*. **180**: 455–460.

Menner, E. (1938). Die bedevtung des pecten Im Auge des Vogel für die wahrnehmung von bevegungen, nebst bemerkungen uberseine ontogeine und histologie zool. *Jahrb. Abt. Aug. Zool. Physiol. Tiere* **58**: 481–538.

Meyer, D. B. (1977). The avian eye. In *Handbook of sensory physiology* **VII/5**. *The visual system of vertebrates*: 549–612. Crescentelli, F. (Ed.). Berlin: Springer Verlag.

Pearson, R. (1972). *The avian brain*. London: Academic Press

Pumphrey, R. J. (1948). The sense organs of birds. *Ibis* **90**: 171–199.

Ruggiero, F. P. & Sheffield, J. B. (1998). The use of avidin as a probe for the distribution of mitochondrial carboxylases in developing chick retina. *J. Histochem. Cytochem*. **46**: 177–183.

Samuelson, D. A. (1991). Ophthalmic embryology and anatomy. In *Veterinary ophthalmology*: 356–372. 2nd edn. Moses, R. A. & Hart, W. M. (Eds). St Louis: C. V. Mosby.

Scherle, W. (1970). A simple method for volumetry of organs in quantitative stereology. *Mikroscopie* **26**: 557–560.

Seaman, A. R. & Himelfarb, T. M. (1963). Correlated ultrafine structural changes of the avian pecten oculi and ciliary body of *Gallus domesticus*. Preliminary observations on the physiology. I. Effect of decreased intraocular pressure induced by intravenous injection of acetazolamide (diamox). *Am. J. Ophthalmol*. **56**: 278–296.

Silman, A. J. (1973). Avian Vision. In *Avian biology* **2**: 349–387. Farner, D. S., King, J. R. & Parker, K. C. (Eds). New York: Academic Press.

Tansley, K. (1965). *Vision in vertebrates*. London: Chapman & Hall.

Thomson, A. (1929). The pecten considered from an environmental point of view. *Ibis* **12**: 608–639.

Tucker, R. (1975). The surface of the pecten oculi of the pigeon. *Cell Tissue Res*. **157**: 457–465.

Uehara, M., Oomori, S., Kitagawa, H. & Ueshima, T. (1990). The development of the pecten oculi in the chick. *Jpn J. Vet Sci*. **52**: 503–512.

Walls, G. L. (1963). *The vertebrates eye and its adaptive radiation*. Bloomfield Hills: Crankbrook Institute of Science.

Weibel, E. R. (1979). *Stereological methods. Practical methods for biological morphometry*. London: Academic Press.

Wolburg, H., Libner, S., Reichenbach, A. & Gerhardt, H. (1999). The pecten oculi of the chicken: a model system for vascular differentiation and barrier maturation. *Int. Rev. Cytol*. **187**: 111–159.