

# Scaling of visual acuity with body size in mammals and birds

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## Summary

1. Kirschfeld (1976) suggested that visual acuity is directly proportional to body length across a wide range of animal species. A survey of eye size, visual acuity and body size of birds and mammals that is consistent with Kirschfeld's suggestion is reported. Hypoallometry (scaling factor  $< 1$ ) for eye size *vs* body size combines with hyperallometry (scaling factor  $> 1$ ) for acuity *vs* eye size to produce roughly linear scaling between acuity and body size.

2. Kirschfeld (1976) also suggested that the distance at which important objects are typically viewed is a linear function of body length. 'Subjective distance' (viewing distance/body length) was therefore thought to be independent of body size across species. However, for prey detection by mammalian and avian predators, it is doubtful that subjective visual distances are size independent because prey size and visual acuity both scale by factors  $> 0.5$  with predator body size; hence, detection distance should scale with size by a factor  $> 1$ . Scaling analyses also suggest that subjective visual distances for intraspecific social interactions are size dependent.

3. A positive association between body size and viewing distance has implications for the scaling of coat pattern features. In environments with fractal visual backgrounds (in which perceived sizes of background pattern elements do not change as distance from the background changes), larger animal species should have larger coat patches than smaller species if they are adapted to be cryptic at greater viewing distances than smaller species are.

*Key-words:* Allometry, animal coloration, predation, vision

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## Introduction

The literature on animal scaling (*sensu* Schmidt-Nielsen 1984) is vast and continues to be a source of much interest (e.g. Kozłowski & Weiner 1997; West, Brown & Enquist 1997). However, comparatively little has been published on the scaling of visual performance, perhaps because authorities such as Walls (1942), Thompson (1952) and Calder (1984) dismissed the subject. Kirschfeld (1976) presented the first quantitative cross-species summary of visual acuity in relation to body size, from which he argued that maximal visual acuity  $A$  (cycles per degree) tends to scale with body length  $L^1$ .  $A/L$ , which Kirschfeld called 'subjective resolution', was therefore thought to be roughly independent of  $L$  across species. Kirschfeld noted that size-independence of  $A/L$  would be expected if both  $A$  and  $L$  are directly proportional (isometric) to eye diameter.

Kirschfeld (1976) also defined 'subjective distance' as  $D/L$ , where  $D$  is the absolute distance at which an animal usually views objects in its environment. He suggested that  $A/L$  and  $D/L$  might be matched so

that the amount of visual detail typically perceived is independent of body size:

If two animals have the same subjective resolution, this means that for the same 'subjective distance' of an object the same number of points per object are scanned or resolved. For example, if we ( $[L] \approx 2$  m) look at a fly in a distance of 5 m, we resolve this fly into the same number of points as a fly ( $[L] \approx 2$  mm) looking at another fly from a distance of 5 mm.

Vogel (1988) offered a similar, if less specific, suggestion when he wondered 'why eyes of the same size will not suffice for all – perhaps bigger animals more commonly look at more distant things.'

Hughes (1977) disputed the idea that size-adjusted acuity is constant even within an order of magnitude for homeothermic vertebrates:

The need of large diffraction limited eyes for high resolution vision is predominantly centred on the detection and identification of either prey or predator at a distance adequate to, respectively, enable

certain escape or stealthy approach. The inherent properties of an environment set limits on these requirements which are fairly independent of the size of its denizens.

Hughes presented data suggesting that eye size does not scale isometrically across the full range of mammalian body sizes. However, these conclusions were not accompanied by statistical analyses.

My goal here is to reconsider Kirschfeld's ideas on visual scaling with reference to mammals and birds. In the following sections I consider the scaling of eye size *vs* body size, visual acuity *vs* eye size, and visual acuity *vs* body size. Implications for inter- and intraspecific visual interactions and for the scaling of coat patterns are then discussed.

## Methods

Scaling factors  $b$  were computed from the power equation  $y = ax^b$  as the slopes of straight lines fitted to bivariate relations after  $\log_{10}$ -transformation (e.g. Calder 1984). The effect of 'phylogenetic inertia' on independence of species-level data is a matter of concern when such computations are made (e.g. Harvey & Pagel 1991; Ricklefs & Starck 1996). Phylogenetic relationships for most of the species treated here are not known with certainty. Scaling factors computed from cross-species data (for comparison with previous studies that have used this method) as well as those determined by 'phylogenetically independent comparisons' (Harvey & Pagel 1991) are presented. After  $\log_{10}$ -transformation, these comparisons were generated by Purvis & Rambaut's (1995) computer program for comparative analysis by independent contrasts (CAIC). Taxonomy (following Sibley & Monroe 1990 and Wilson & Reeder 1993) stood in for phylogeny, branch lengths were assumed equal, and contrasts at the phylogenetic root were omitted in order to exclude 'grade' effects (Purvis & Rambaut 1995). Using simulations, Purvis, Gittleman & Luh (1994) showed that even when phylogenies were poorly resolved and branch lengths were incorrectly assumed equal, CAIC-based analyses provided more accurate results than those based directly on cross-species data.

Several line-fitting methods are available for determining slopes of the log-transformed scaling relations. Choice of the most appropriate technique depends on one's goal (description or prediction) and on how the  $y$  error variance compares to the  $x$  error variance (Harvey & Pagel 1991). This ratio is not known for the cases treated here, but error variances (which include measurement error and sampling error) are likely to be appreciable in both variates. The methods of ordinary least squares (OLS, for which  $x$  error variance is assumed to be 0) and reduced major axis (RMA, for which error variances are assumed proportionate to observed  $x$  and  $y$  variances) were used. The OLS technique was used in earlier studies of visual size

scaling and is most appropriate for making predictions, but the RMA method (OLS slope/correlation coefficient = standard deviation ( $y$ )/standard deviation ( $x$ )) provides the least biased estimate when error variances are unknown (Ricker 1973; Kendall & Stuart 1979; Rayner 1985; McArdle 1988). Standard errors and confidence limits of the slope calculated from the OLS analysis can be applied to the RMA estimates (Ricker 1973; Sokal & Rohlf 1995). Empirical scaling factors are reported to two decimal places, but my conclusions do not hinge on this level of precision. Except where noted, all scaling factors are significantly different from 0 ( $P < 0.05$ ).

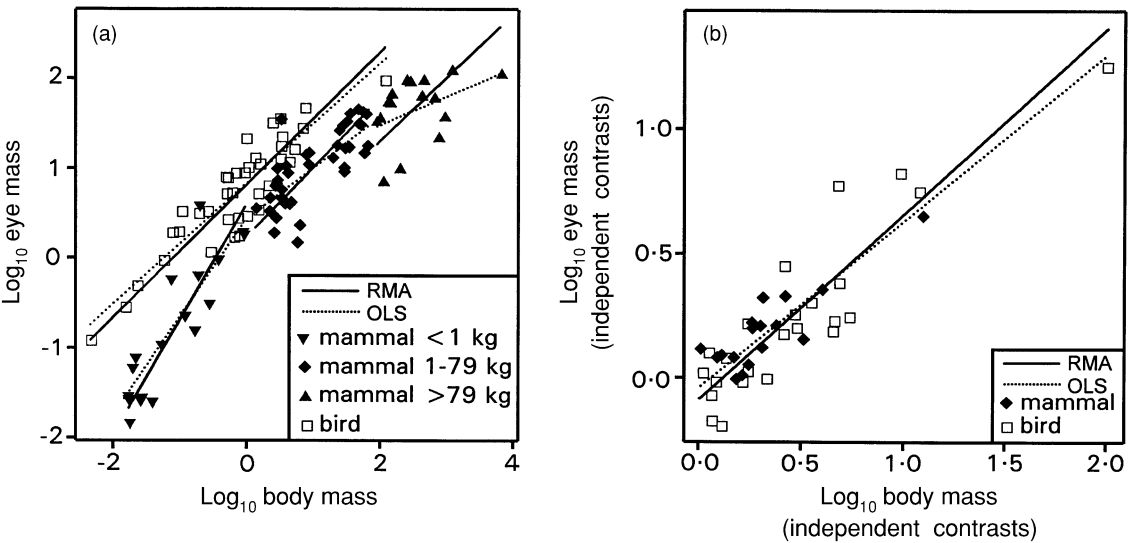
Purvis & Rambaut (1995) recommended forcing regressions from independent contrasts through the origin. That is proper when the contrasts are computed from data on arithmetic scales. However, when contrasts are computed from log-transformed data, forcing regressions through the origin is questionable. When contrasts are computed from log-transformed data, the point (0,0) represents two sets of contrasts whose differences are 0, which in turn corresponds to a 1/1 ratio with arithmetic scales; there is no reason to force the fitted functions through a point representing two ratios of equal contrasts. In any case,  $y$  intercepts reported here are close to 0 for lines fitted to independent contrasts from log-transformed data.

## Eye size and body size

Previous investigations of the scaling of eye size with body size have produced conflicting conclusions. Hughes (1977) plotted  $\log_{10}$  axial length of the eye *vs*  $\log_{10}$  body mass for a collection of 39 vertebrate species, mostly mammals and birds. Apparently judging the slopes visually, Hughes stated that the scaling factor relating axial eye length to body mass was about 1/3 for medium-size mammal species,  $> 1/3$  for small mammals, and  $< 1/3$  for large mammals. When converted to axes with the same dimensions, these slopes corresponded, respectively, to 1 (isometric),  $> 1$  ('hyperallometric' following Calder 1984 or 'positively allometric' following Huxley & Teissier 1936), and  $< 1$  ('hypoallometric' following Calder 1984 or 'negatively allometric' following Huxley & Teissier 1936). On average, birds clearly had larger eyes per unit body mass than mammals did, and the scaling factor for birds appeared to be between that for small and medium-size mammals. Hughes published neither the raw data nor confidence intervals for the scaling factors. In contrast, Calder (1984) reported an OLS scaling factor of 0.70 (hypoallometric) from Quiring's (1950) data for avian eye mass *vs* body mass. Brooke, Hanley & Laughlin (1999) also reported hypoallometry (0.68 OLS, 0.74 RMA) from their own data on avian eye size. For an unspecified collection of mammals, Vogel (1988) reported an OLS scaling factor of 1.80 for log-transformed eye mass *vs* body mass<sup>1/3</sup> (which corresponds to 0.60 when both

**Table 1.** Parameter estimates for regression of  $\log_{10}$  eye mass (g) vs  $\log_{10}$  body mass (kg). Data are from Quiring (1950). Slopes are scaling factors. For mammal species, the range of  $\log_{10}$  body mass was divided into three equal parts

| Sample units                                | OLS slope | RMA slope | $\pm 95\%$ CI (slope) | OLS intercept | RMA intercept | <i>r</i> | <i>N</i> |
|---------------------------------------------|-----------|-----------|-----------------------|---------------|---------------|----------|----------|
| Bird species                                | 0.67      | 0.74      | 0.10                  | 0.82          | 0.83          | 0.90     | 38       |
| Mammal species, smallest third              | 1.14      | 1.28      | 0.32                  | 0.45          | 0.60          | 0.89     | 18       |
| Mammal species, middle third                | 0.59      | 0.78      | 0.17                  | 0.43          | 0.24          | 0.76     | 39       |
| Mammal species, largest third               | 0.31      | 0.70      | 0.37                  | 0.89          | -0.08         | 0.44     | 16       |
| Birds and mammals,<br>independent contrasts | 0.67      | 0.74      | 0.11                  | -0.05         | -0.08         | 0.90     | 41       |



**Fig. 1.** (a)  $\log_{10}$  eye mass (g) vs  $\log_{10}$  body mass (kg) for bird and mammal species. Mammal subgroups correspond to equal thirds of the data range on a log scale. Fitted lines: RMA = reduced major axis, OLS = ordinary least squares. (b) Independent contrasts of  $\log_{10}$  eye mass (g) vs  $\log_{10}$  body mass (kg) for bird and mammal species.

axes have the same dimensions). Burton (1998) suggested that mammalian eye mass scales isometrically with body mass up to about 30 kg, and that eye mass and body mass are independent of one another at larger body sizes.

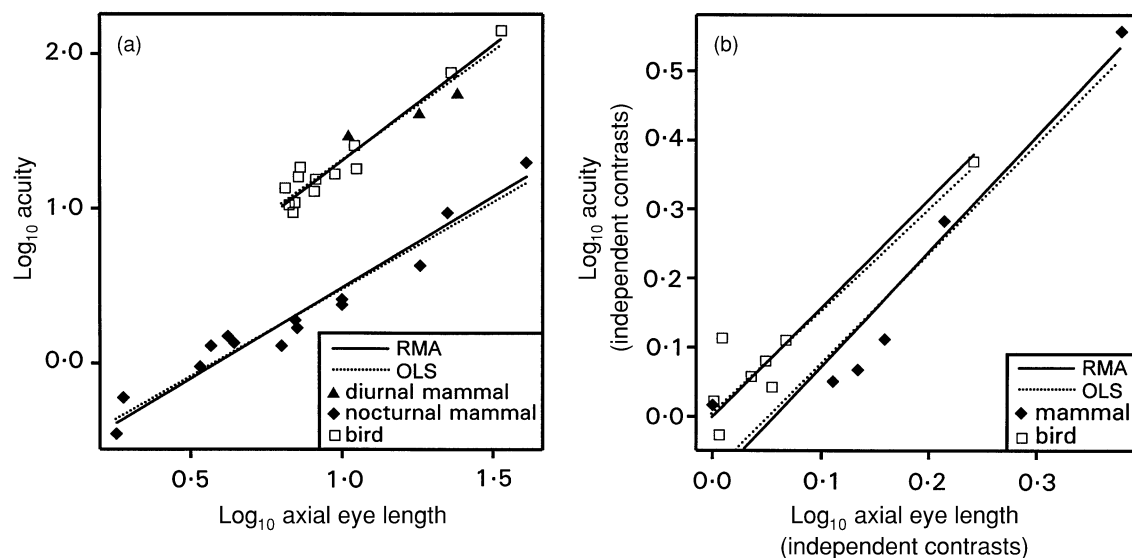
Scaling factors for eye mass vs body mass of birds and non-aquatic mammals were recalculated from Quiring's (1950) data (available from the author). For bird species, the scaling factor (0.67 OLS, 0.74 RMA; Table 1) was close to the estimates of Calder (1984) and Brooke *et al.* (1999). Overall, eyes of mammals scaled similarly (0.71 OLS, 0.76 RMA), but Hughes (1977) was correct that a simple linear model is not appropriate for mammals (Fig. 1a). Sequential (type 1) sums of squares (SAS Institute Inc. 1991) indicated that a quadratic polynomial fits the mammalian species-level data significantly better than a simple linear model. However, these data were fit as well by a piecewise linear regression with two arbitrary breakpoints at 33% and 67% of the mass range ( $R^2 = 0.92$  for both the polynomial and the piecewise regression, which was produced by the SAS TRANSREG procedure, SAS Institute Inc. 1989). The scaling factors suggested hyperallometry for small mammals, but hypoallometry for mid-size and large

mammals (Table 1). Analysis of covariance among birds, mid-size mammals, and large mammals indicated that their scaling factors did not differ significantly. The SAS GLM procedure (SAS Institute Inc. 1991) estimated the overall average scaling factor for birds, mid-size mammals and large mammals as 0.62 (OLS) and 0.76 (RMA)  $\pm$  0.09 (95% confidence interval).

The relationship between phylogenetically independent contrasts for eye mass and body mass did not differ significantly between mammals and birds (Fig. 1b). The OLS and RMA scaling factors calculated from the contrasts were identical to those determined across species for birds (Table 1).

Confidence intervals (Table 1) indicated that the scaling factors were significantly  $> 0$  in all cases except for large mammals by OLS. The scaling factors were significantly  $< 1$  in all cases except for small mammals by OLS and RMA and for large mammals by RMA.

It is worth noting that interspecific scaling factors for bird and mammal brains (Harvey & Krebs 1990) are similar to those above for eyes. Because the retina is an outgrowth of the brain, it is perhaps not surprising that eyes and brains scale similarly. However, the causes of hypoallometric brain scaling are not fully understood (e.g. see Calder 1984; Harvey & Krebs



**Fig. 2.** (a) Log<sub>10</sub> visual acuity (cycles/deg) vs log<sub>10</sub> axial eye length (mm) for bird and mammal species. Fitted lines: RMA = reduced major axis, OLS = ordinary least squares. (b) Independent contrasts of log<sub>10</sub> visual acuity (cycles/deg) vs log<sub>10</sub> axial eye length (mm) for bird and mammal species.

**Table 2.** Parameter estimates for the regression of visual acuity (cycles/deg) vs axial eye length (mm) of birds and mammals. Slopes are scaling factors

| Sample units                   | OLS slope | RMA slope | ± 95% CI (slope) | OLS intercept | RMA intercept | <i>r</i> | <i>N</i> |
|--------------------------------|-----------|-----------|------------------|---------------|---------------|----------|----------|
| Diurnal species                | 1.42      | 1.48      | 0.23             | -0.11         | -0.17         | 0.96     | 16       |
| Nocturnal species              | 1.12      | 1.15      | 0.17             | -0.64         | -0.66         | 0.97     | 14       |
| Birds, independent contrasts   | 1.43      | 1.54      | 0.54             | 0.01          | 0.01          | 0.93     | 8        |
| Mammals, independent contrasts | 1.56      | 1.64      | 0.72             | -0.08         | -0.09         | 0.95     | 6        |

1990; Kozłowski & Weiner 1997; West *et al.* 1997). Whether hypoallometric eye scaling can be viewed as a side-effect or as a partial cause of brain scaling remains to be determined (Brooke *et al.* 1999).

### Acuity and eye size

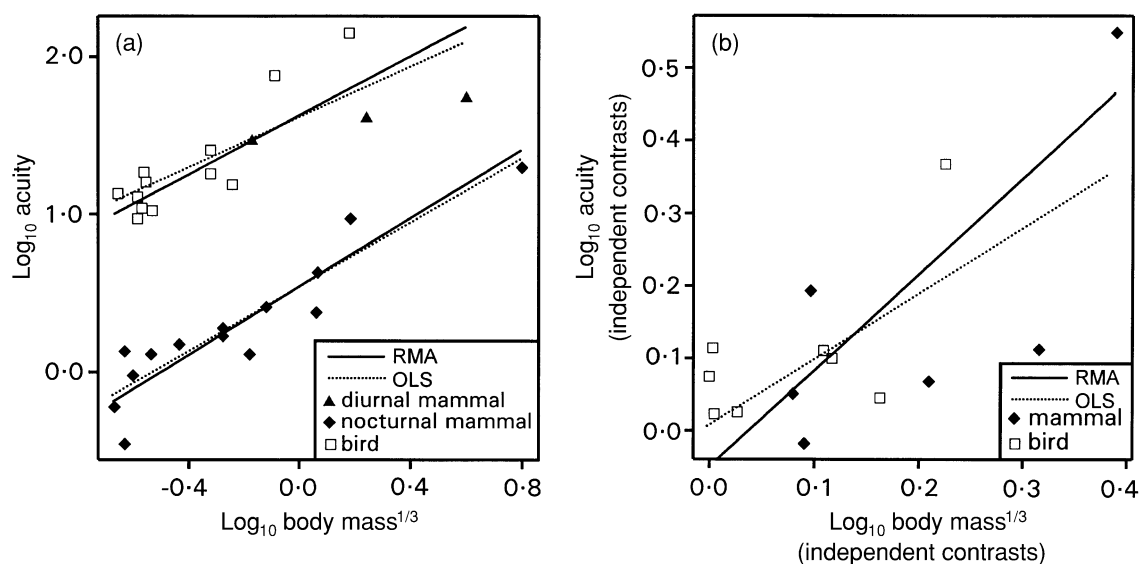
For the vertebrate eye, maximal visual acuity is proportional to  $1/\phi = f/s$ , where  $\phi$  is the angular separation of the individual receptors,  $f$  is the focal length (posterior nodal distance) and  $s$  is the linear separation between receptors (e.g. Goldsmith 1990). The diameter of an individual receptor, and therefore  $s$ , can be no smaller than about 1–2  $\mu\text{m}$  without impeding the receptor's function as a light waveguide (Kirschfeld 1976; Goldsmith 1990). Some vertebrate species approach this limit on photoreceptor size (Miller 1979; Raymond 1985, 1987; Snyder, Bossomaier & Hughes 1990), but not all do (Snyder, Bossomaier & Hughes 1986; J. K. Wetterer, unpublished manuscript).

Hughes (1977) suggested that mammalian focal length is approximately a constant fraction (0.60) of axial eye length, and that the retinal magnification factor (distance on retinal surface per degree visual angle) scales linearly with axial length. If that were true, and if photoreceptor size and packing did not

vary consistently with eye size, one would expect visual acuity to scale linearly with eye size, as Kirschfeld (1976) expected.

To test this suggestion, data from summaries for birds and mammals by Donner (1951) and Pettigrew, Dreher & Hopkins (1988), combined with data from some other sources, were used. These data (available from the author) included estimates of maximal acuity based entirely on anatomical analysis and estimates based on behavioural criteria through conditioning experiments. The behavioural measurements were fewer and were highly correlated with the anatomical estimates (Spearman  $R = 0.97$ ). Because results did not differ significantly between analyses based on behavioural and anatomical acuity estimates, only the latter are presented.

A cross-species plot (Fig. 2a) of acuity vs axial eye length suggested that the effect of diel activity pattern (diurnal vs nocturnal or acyclic) was greater than the effect of taxonomic affiliation, but the sample was too sparse for formal comparison of these effects. Scaling factors were determined separately for diurnal (birds and primates) and nocturnal species (other mammals) in the data set. The estimated scaling factors were hyperallometric in all cases, but the confidence band for nocturnal species included 1.0 (Table 2).



**Fig. 3.** (a) Log<sub>10</sub> visual acuity (cycles/deg) vs log<sub>10</sub> body mass (kg<sup>1/3</sup>) for bird and mammal species. Fitted lines: RMA = reduced major axis, OLS = ordinary least squares. (b) Independent contrasts of log<sub>10</sub> visual acuity (cycles/deg) vs log<sub>10</sub> body mass (kg<sup>1/3</sup>) for bird and mammal species.

**Table 3.** Parameter estimates for the regression of log<sub>10</sub> visual acuity (cycles/deg) vs log<sub>10</sub> body mass (kg<sup>1/3</sup>) of birds and mammals. Slopes are scaling factors

| Sample units          | OLS slope | RMA slope | ± 95% CI (slope) | OLS intercept | RMA intercept | r    | N  |
|-----------------------|-----------|-----------|------------------|---------------|---------------|------|----|
| Diurnal species       | 0.76      | 0.93      | 0.32             | 1.58          | 1.62          | 0.93 | 15 |
| Nocturnal species     | 1.02      | 1.10      | 0.26             | 0.52          | 0.54          | 0.82 | 14 |
| Independent contrasts | 0.88      | 1.27      | 0.58             | 0.01          | -0.04         | 0.69 | 14 |

The overall scaling factors estimated by GLM were 1.21 (OLS) and 1.26 (RMA) ± 0.13 (95% CI).

For the relation between acuity and eye length by independent contrasts, analysis of covariance indicated similar scaling factors for birds and mammals, but there was a significantly greater y intercept for birds (Fig. 2b). The hyperallometric scaling factors computed from these independent contrasts were somewhat greater than the average scaling factors calculated across species (Table 2). The overall scaling factors estimated by GLM were 1.52 (OLS) and 1.62 (RMA) ± 0.35 (95% CI).

These results, suggesting hyperallometry rather than isometry in the scaling of visual acuity with eye size, were somewhat surprising. In part, this result may stem from the fact that the relationship between focal length and eye size in this data set was slightly hyperallometric (cross-species OLS slope = 1.10, RMA slope = 1.11, R = 0.99, 95% CI ± 0.06, N = 30) (cf. Hughes 1977; Pettigrew *et al.* 1988; Martin 1993; Brooke *et al.* 1999). Size-related trends in receptor packing also could be involved.

Acuity and body size

The relation between visual acuity and body size

was addressed in two ways. One method was to compare log<sub>10</sub> acuity and log<sub>10</sub> body mass<sup>1/3</sup>. The data for body mass were species averages from the literature (Dunning 1993; Silva 1995), not masses of the particular individuals used to estimate acuity; therefore some additional ‘noise’ in the data was expected. Differences between diurnal and nocturnal species were significant at the species level (Fig. 3a). The cross-species scaling factors estimated from these data ranged from 0.76 (OLS) to 1.10 (RMA), but none excluded 1 from the 95% confidence interval (Table 3). Residuals were not as uniformly distributed for these regressions (Fig. 3a) as for the relation between acuity and axial eye length (Fig. 2a). There was no suggestion that mammals < 1 kg scaled hyperallometrically and those > 1 kg hypoallometrically, as was the case for cross-species comparisons of eye size and body mass (Fig. 1a). The overall scaling factors estimated by GLM from species-level comparisons were 0.90 (OLS) and 1.02 (RMA) ± 0.20 (95% CI).

Independent contrasts produced no significant difference between birds and mammals in the scaling of acuity with body size (Fig. 3b). The correlation coefficient was lower for the independent contrasts than for the cross-species data (Table 3); hence, there was a greater difference between the OLS scaling

factor (0.88) and the RMA (1.27) estimate in this case. Confidence intervals for the relations computed from independent contrasts were broad and included 1.

As a second approach, the scaling factors (GLM averages) for eye mass *vs* body mass and for acuity *vs* eye length were multiplied to produce estimates of scaling factors for acuity as a function of body mass<sup>1/3</sup> (Welsh, Peterson & Altman 1988; cf. LaBarbera 1989). The resulting compound factors were 0.75 (cross-species OLS excluding small mammals), 0.96 (cross-species RMA excluding small mammals), 1.38 (cross-species OLS for small mammals), 1.61 (cross-species RMA for small mammals), 1.02 (independent contrasts OLS), and 1.20 (independent contrasts RMA). As products of two estimates that in turn have variance, the confidence intervals for these combined estimates must be large (Welsh *et al.* 1988). Because the cross-species estimates for small mammals differed more from those based on independent contrasts than was the case for birds and mammals > 1 kg, it appears that there was a greater phylogenetic influence in the data for small mammals.

Kirschfeld's (1976) suggestion that acuity scales isometrically with body size therefore remains tenable at least for mammals > 1 kg and for birds. The reason for this result is not that isometry prevails throughout, as Kirschfeld suggested, but instead that hypoallometry of eye size *vs* body size is roughly compensated by hyperallometry of acuity *vs* eye size.

### **D/L: Interspecific visual interactions**

Direct information on distances at which animals typically view objects in their environment are not available to test Kirschfeld's conjecture that subjective distance ( $D/L$ ) shows no consistent variation across animal body sizes. However, further scaling arguments may allow indirect tests of the hypothesis with respect to interspecific predator-prey interactions and intraspecific social interactions. For predatory species,  $D$  could represent the distance at which prey is typically detected. Scaling of  $D$  could then be predicted from scaling of predator visual acuity *vs* predator body size and from scaling of prey size *vs* predator size.

Many studies have reported body-size relations between particular sets of vertebrate predators and prey. Vézina (1985) gathered data from such studies and provided a summary analysis for 294 'prey-weight distributions' (site- and species-specific samples). Double logarithmic OLS regressions between average prey mass and predator mass were calculated for 124 insectivore samples (passerines, amphibians, and reptiles), 13 piscivores (seabirds) and 157 'carnivores' (mostly mammals and birds that prey on other vertebrates). Vézina concluded that the scaling factor relating prey mass to predator mass was significantly less than one (0.86) for insectivores, not significantly different from one (0.87) for piscivores, and significantly greater

than one (1.18) for carnivores. However, the RMA estimates that I computed from Vézina's results were 1.21 for insectivores, 1.06 for piscivores and 1.39 for carnivores. (Reanalysis by independent contrasts also would have been of interest, but the raw data needed to do so were not available.) Vézina suggested that insectivores and carnivores may conform to a single trend relating predator size to prey size if one assumes that the difference documented between the two groups is an artefact of the absence of data for predators whose prey weigh 0.5–5 g. Vézina did not present the scaling factor after merging insectivore and carnivore data sets, but this clearly would have produced a higher estimate (steeper slope) (see Fig. 1 in Vézina 1985), more like those resulting from the RMA approach than like those produced by the OLS method.

Suppose that active visual predators detect prey at distances whose averages are directly proportional to the maximum distances at which prey are detected, so that the distinction between the two distances does not matter. In an environment with a plain background and plain, visually contrasting prey, the distance at which prey just become visually detectable ('critical detection distance') should be a positive function of both the prey's size  $l$  and the predator's acuity  $A$ . If critical detection distance  $D$  is proportional to  $l \times A$ , then the lowest OLS expectation for the scaling relationship between  $D$  and  $L$  is  $0.75 + 0.86 = 1.61$ . The lowest estimate by RMA is  $0.96 + 1.06 = 2.02$ . These and all other combinations of the estimated scaling factors produced above are inconsistent with the suggestion that  $D$  is proportional to  $L^1$ . The discrepancy between Kirschfeld's suggestion and the calculated scaling of detection distance with predator size would be greater if this distance were linearly related to surface area of the prey's body rather than to its length (e.g. Treisman 1975), and greater still if this area scaled by elastic or static stress criteria (Calder 1984).

Reaction distances have been widely studied in freshwater fish, but the emphasis has been on intra-specific ontogenetic effects, perhaps because indeterminate growth complicates interspecific comparisons. Such studies have produced results varying from isometry (Wanzenböck & Schiemer 1989) to hypoallometry ( $D \propto L^{0.48}$ ; Breck & Gitter 1983; see also Emerson, Greene & Charnov 1994) when reaction distance is compared to predator size, and prey size is constant. Breck & Gitter's (1983) hypoallometric result was attributed to increased receptor spacing in the eyes of larger sunfish (*Lepomis macrochirus*) in the study. Linear relations have generally been found in ontogenetic studies of fish prey size and reaction distances when predator size is constant (e.g. Aksnes & Giske 1993). If prey size is proportionate to predator size when both sizes vary,  $D$  would be expected to be approximately proportionate to  $L^{1.5}$  to  $L^2$ . Thus intraspecific variation in fish also appears to be incompatible with a prediction that visual

detection distances should scale in direct proportion to predator body size.

### ***D/L*: Intraspecific visual interactions**

The arguments above can be applied to intraspecific visual interactions if the scaling factor for predator–prey allometry is replaced by 1 (because in intraspecific interactions the viewer and visual target scale identically). Distance  $D$  for detecting conspecifics then would also be expected to scale hyperallometrically among species, and  $D/L$  should show a positive trend *vs*  $L$ .

A reviewer has suggested another way to investigate size-dependence of intraspecific visual distance from the scaling of population density or home range area. Published estimates of avian and mammalian scaling factors for body mass *vs* home range area or population density<sup>-1</sup> have covered about the same range of values as reported here for the scaling of visual acuity (Peters 1983; Calder 1984; LaBarbera 1989; Brown 1995). It is debatable whether these scaling relations imply greater average distance among individuals as body size increases (cf. Peters 1983; Calder 1984; Brown 1995), but if so then a functional link between intraspecific social spacing and visual acuity is suggested. In this light, it is intriguing that diurnal birds have maximal densities about one tenth those of mammals of the same size (Brown 1995, p. 133) while averaging about 10 times the visual acuity of nocturnal mammals of the same size (Fig. 3a, Table 3). However, as long as the scaling factor between individual area and body mass is  $> 0.67$ , then the scaling factor for  $D$  *vs*  $L$  should be  $> 1$  (assuming that home range  $\propto D^2$  and mass  $\propto L^3$ ). Kirschfeld's prediction on the scaling of  $D/L$  therefore appears not to be upheld for intraspecific or interspecific interactions.

### **Further tests: coat patterns and fractal visual environments**

Results presented here are consistent with size independence for subjective resolution ( $A/L$ ) but not for subjective distance ( $D/L$ ). Kirschfeld's (1976) rationale for predicting similarity of spatial visual experience among species of differing size is thus not supported. Scaling arguments led Brooke *et al.* (1999) to a comparable conclusion that larger birds resolve objects at a longer time to contact than smaller birds.

It is worth noting that the converse of Kirschfeld's argument has recently received attention in the psychophysical literature on visual processing. It has been suggested that natural scenes tend to be fractal ('self-similar'; Field 1987, 1989, 1993; Ruderman & Bialek 1994; Párraga *et al.* 1998; Ziegaus & Lang 1998) and that vertebrate visual systems are adapted to deal economically with such images (Swindale 1990; Van Essen, Anderson & Felleman 1992; Virsu & Hari 1996). When images are fractal, visual detail

does not change appreciably with viewing distance (Mandelbrot 1983).

Studies on spatial properties of cryptic animal coats (e.g. Kiltie, Fan & Laine 1995) might provide additional insights on these matters. From Kirschfeld's perspective, all species that are adapted for crypsis in a particular habitat would have coat patterns whose spatial elements are similar in size. This prediction follows from Kirschfeld's suggestion that all viewers (regardless of size) should perceive about the same amount of visual detail because of correlated variation in  $A/L$  and  $D/L$ .

On the other hand, if viewing distance increases disproportionately with body size, as my analyses suggest, then size-dependent variation in coat patterns could result (see also Murray 1989). In fractal visual environments, perceived sizes of background pattern elements would not change as the position of the viewer changes. However, the perceived sizes of coat pattern elements would decline with distance from the viewer at least until the viewer's ability to resolve such features was exceeded. Larger prey species would therefore need larger coat patches than smaller species if larger species were adapted to be cryptic at greater viewing distances than smaller species. Similar expectations would apply to coats of predators adapted for cryptic appearance to prey because size of predators (now treated as the visual targets) and acuity of prey (now treated as the viewers) increase with prey size. Kiltie & Edwards's (1998) observation that patchier coats tend to be associated with larger body size among squirrel species is consistent with this hypothesis, but more work on the scaling of cryptic coat patterns is needed.

Scaling analyses reported here also suggest that distances of intraspecific visual interactions are hyperallometric with body size. Intraspecific visual interactions typically would be expected to emphasize conspicuousness rather than crypsis. When viewing distances for social interactions differ appreciably from those for predator–prey interactions, it is possible for a single coat pattern to be conspicuous to conspecifics and cryptic to larger predators or smaller prey (e.g. Endler 1978, 1991). Otherwise, natural selection would be expected to resolve conflict between the two effects according to their comparative effects on fitness. When conspicuousness is paramount, it is difficult to predict how spatial patterns on coats should scale because there are many ways to stand out from a particular background pattern. Comparison of coat pattern scaling in males and females of sexually dimorphic species might shed light on this problem.

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