
Volume 254
Issue 4
21 October 2008
ISSN 0022-5193
ELSEVIER
Journal of Theoretical Biology

Journal of Theoretical Biology 254 (2008) 756–767

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

"X-ray vision" and the evolution of forward-facing eyes

Mark A. Changizi [a,b,*], Shinsuke Shimojo [c]

[a] Sloan-Swartz Center for Theoretical Neurobiology, Caltech, Pasadena, CA 91124, USA
[b] Department of Cognitive Science, Rensselaer Polytechnic Institute, Troy, NY 12180, USA
[c] Division of Biology, MC 139-74, Caltech, Pasadena, CA 91125, USA

ARTICLE INFO

Article history:
Received 13 March 2008
Accepted 8 July 2008
Available online 15 July 2008

Keywords:
Convergence
Stereo
Binocularity
Evolution
Function
Optimality

ABSTRACT

Why do our eyes face forward, and why do many mammals have eyes facing sideways? Here, we describe results suggesting that the degree of binocular convergence is selected to maximize how much the mammal can see in its environment. Mammals in non-cluttered environments can see the most around them with panoramic, laterally directed eyes. Mammals in cluttered environments, however, can see best when their eyes face forward, for binocularity has the power of "seeing through" clutter out in the world. Evidence across mammals closely fits the predictions of this "X-ray" hypothesis.

1. Introduction

The most salient visual property of forests is that it is so difficult to see in them. Leaves (and other plant material) conspire to reduce viewing distances from hundreds of meters outside of forests to only several meters inside them. Here, we investigate whether our forward-facing eyes, and our consequently larger binocular visual field and absence of panoramic vision, have been selected for maximizing our ability to see in leafy environments like forests. (To see the forest through the trees.) More generally, we examine the hypothesis that binocular convergence (the degree to which the orbits face in the same direction, and which correlates highly with the binocular overlap ($R^2 = 0.7$; Heesy, 2004)) in mammals is selected so as to maximize what the mammal can see, given the level of clutter with which it must contend. Our main prediction will be that mammals outside of leafy habitats tend to have sideways-facing eyes, but that within leafy habitats, binocular convergence should increase with body size. As we will see, it is only the larger animals in leafy habitats—the "large and leafy"—where forward-facing eyes allows them to see more of what is around them.

2. The X-ray hypothesis

Most of us have noticed how when you hold up your finger vertically and fixate your eyes on something far beyond it, you perceive two copies of your finger, and both copies of your finger appear transparent. Because your finger width is less than your interpupillary distance, you have this ability to "see through" your finger … which is why we call our hypothesis below the "X-ray hypothesis." Fig. 1a and b demonstrate this: despite each eye seeing different parts of a photograph of Darwin, with both eyes we perceive all of him, and also perceive there to be (two copies of) transparent leaves in front. (See also Forte et al., 2002.) If instead only one eye was pointed toward Darwin, nearly half his face would be occluded, potentially preventing you from recognizing him at all. This is the key intuition we now flesh out, that in some circumstances more can be recognized in the binocular region, in which case it is advantageous to have a large binocular region—i.e., to have forward-facing eyes.

One of the keys to this X-ray benefit of binocular vision is that the probability for one eye seeing a target on the other side of an occlusion is independent of the probability for the other eye. When this is the case the probability that at least one eye sees the target is $p_{binoc} = 1-(1-p_{monoc})^2 = p_{monoc}(2-p_{monoc})$, where p_{monoc} is the probability of seeing the target for monocular vision. We call the ratio of these probabilities the "X-ray power" of binocular vision, which is $B = p_{binoc}/p_{monoc} = 2-p_{monoc}$. When the environment is clear of leaves and plant materials—i.e., "not leafy"—the probability of monocular vision seeing the target is high, say, $p_{monoc} \approx 1$, in which case the X-ray power is $B \approx 1$, so that two eyes have no advantage relative to one eye at seeing a target. (So, it is better to have a smaller binocular field.) When, however, the environment is highly leafy or forested, the probability of monocular vision seeing the target drops, and the X-ray power B rises, eventually toward 2 (e.g., see Fig. 1c). The benefits of binocular vision occur, then, when the probabilities of the eyes

---

[*] Corresponding author at: Department of Cognitive Science, Rensselaer Polytechnic Institute, Troy, NY 12180, USA. Tel.: +1 518 276 3788.

E-mail addresses: changizi@rpi.edu (M.A. Changizi), sshimojo@its.caltech.edu (S. Shimojo).

0022-5193/$ - see front matter © 2008 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jtbi.2008.07.011

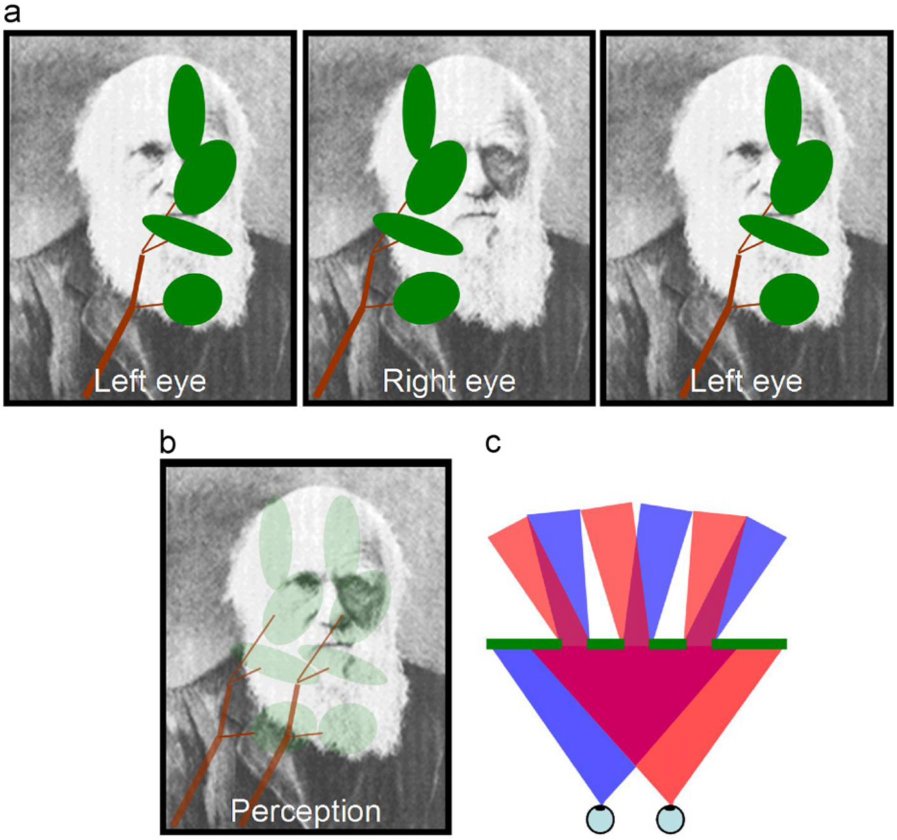

Fig. 1. (a) Stereogram illustrating our ability to see through clutter (the left two images are for uncrossed viewers, the right two for crossed viewing). (b) Illustration of what one sees when looking at Darwin through the clutter in (a). (c) The lines of sight behind a layer of "leaves" for binocular vision, indicating that (i) two eyes can see up to twice as well behind the clutter as one eye, and (ii) when this occurs there is little or no disparity information for stereopsis.

seeing the target through the leaves are independent, *and* when the environment is highly leafy.

To help characterize and quantify the environmental conditions under which binocular vision has a probabilistic advantage over monocular vision, we simulated walls of randomly placed leaves through which a simulated observer attempts to see a target. Fig. 2 shows that binocular vision's X-ray powers depend on two main features, the "leafiness" of the environment and the interpupillary distance of the observer relative to the sizes of the leaves. In Fig. 2a, the y-axis measures leafiness as the average gap between leaves, and in Fig. 2b the y-axis measures leafiness along a complementary dimension, the distance from the observer to the leaves. In each case, lower values on the y-axis mean a more leafy environment. The x-axis for each plot is the interpupillary distance (measured in units of maximum leaf size). One can see from the "monocular" and "binocular" plots that binocular vision has greater probabilities of seeing targets, that the advantage to binocular vision suddenly appears as the interpupillary distance passes a threshold (determined in part by the characteristic sizes of the leaves), and after this transition there is no benefit to further increasing interpupillary distance. From the "X-ray power" plots, one can see that binocular vision dominates monocular vision when the environment is leafy *and* the interpupillary distance is high, i.e., approximately to the lower right of these plots. When these conditions apply, we will call the environment "cluttered," and Fig. 2c summarizes these results. For example, then, a forest that is cluttered for a human may not be cluttered for a mouse because the mouse's eyes are so close together relative to the range of leaf sizes that nearly everything one eye sees the other does as well; from the mouse's point of view in the forest, most of the leaves are the size of cars and houses to us, and the mouse gets little or no X-ray power from binocular vision (and is thus better off with sideways-facing eyes).

On the basis of these results and the qualitative summary in Fig. 2c, our main prediction later (see Fig. 4a) will be that because cluttered conditions occur only when animals are large *and* environments are highly leafy, and because X-ray power is effective only in cluttered conditions, we expect the forward-facing eyed animals to be those that are large and in leafy environments. However, before discussing the prediction further, and setting out to provide preliminary tests of them, it is important to ask why the X-ray advantage to forward-facing eyes outweighs the complete loss of vision behind an animal's head, something animals with sideways-facing eyes have? That is, the binocular advantage is for two eyes looking in the same direction that *one* of the eyes of a sideways-eyed animal faces; but what about the sideways-eyed animal's other eye which may see in directions that neither eye of the forward-eyed animal can see? In short, how does seeing a factor of up to two better in front compensate for the infinitely worse vision behind?

In an attempt to begin to address this, let us consider the region around the animal that is under its visual surveillance, in the sense that if an object suddenly appeared in a spot within that region, the observer would see enough of the object that it is recognized. For starters, we will assume that the cluttered environment is such that a binocular viewer sees sufficiently well past the leaf wall that any object placed there will be recognizable, but that a monocular viewer (with up to half the probability of seeing any small target) will typically be unable to recognize the object. How large are their respective visually surveyable regions in these conditions? The answer will depend on the complex details of the leafy environment, but it is possible to get a rough

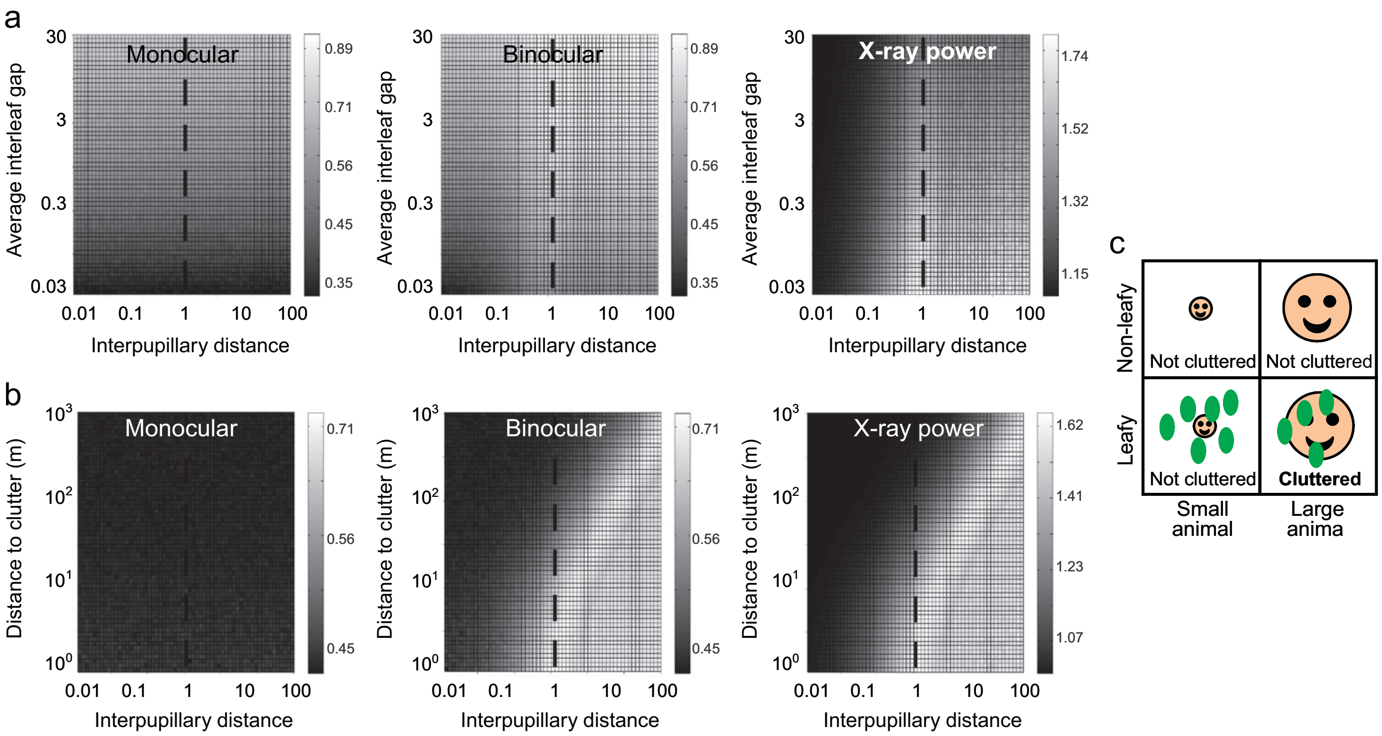

Fig. 2. (a) The probability of viewing a small target through a layer of leaves for monocular (left) and binocular (middle) viewers, and the binocular-to-monocular probability ratio (on the right, showing the "X-ray power," which ranges from 1 to 2, the former when binocular provides no benefit relative to monocular, the latter when binocular provides the maximal benefit relative to monocular vision). The y-axis is the average gap size between leaves (an inverse measure of leafiness), and the x-axis is the interpupillary distance; each axis is in units of maximum leaf size. The vertical line is at the value of the maximum leaf size, after which there is no further advantage to increasing interpupillary distance. The plots were a result of simulations where an observer is placed one meter in front of a "wall of leaves" with leaf widths ranging uniformly from 0 to 5 cm, and the target to be seen is five meters behind the clutter. For each bin in the plot, 500 random walls-of-leaves were created. (b) Similar plots as in (a), but the y-axis now is another measure of leafiness, namely the distance from the observer to the wall of leaves. Similar simulations were carried out, with the average leaf gap set to 5 cm (varying from 0 to 10 cm). [Note that for the two "X-ray power" plots (on the right) in (a) and (b), the probability of both eyes seeing the same target is the "negative", or inverse, of the plots shown, and so (disparity based) stereopsis breaks down exactly when X-ray functions well.] (c) Summary of the two contributors to clutteriness, where "X-ray power" becomes effective. Namely, clutteriness occurs when in leafy environments (i.e., lower in each of the "X-ray power" plots) *and* when the animal is large (i.e., to the right in each of the "X-ray power" plots).

idea. First, note that one of the reasons binocular vision can see so well beyond a wall of leaves is that each eye tends to see a different (and probabilistically independent) view behind the wall. In fact, if one relabels the z-axis of the "X-ray power" plots in Fig. 2 to range from 100% to 0% (rather than from approximately 1–2), then the plots as shown reflect the percentage of the view beyond the wall that is overlapping. When X-ray power approaches 2 (i.e., the whitish parts of the plot, on the bottom right) there is little or no binocular overlap beyond the wall, and when the X-ray power approaches 1 (the black parts) there is almost complete overlap. (Note that this entails that X-ray vision functions well exactly when disparity-based stereopsis fails, and vice versa.) Because in cluttered conditions binocular vision has only a monocular view of what is behind the wall of leaves, if there is another wall of leaves at some distance behind the first, the binocular viewer will no longer have any special advantage for seeing through it; informally, the X-ray power of binocular vision in cluttered environments can only accommodate one layer of clutter, not multiple ones. Therefore, given the assumptions we made above—that the binocular viewing probability is above threshold for object recognition, but that the monocular viewing probability is below threshold—the visually surveyable region around a monocular viewer will be the region between the viewer and the first layer of leaves (and in all directions from the observer), whereas for a binocular viewer the visually surveyable region will be the region between the viewer and the *second* layer of clutter, but only in front of the observer.

To get a more specific estimate of the relative sizes of the visually surveyable regions for binocular and monocular viewers, suppose that there is a typical inter-layer, or inter-wall, distance for leafy environments (e.g., the distance between leafy arbors of a tree, or the distance between trees), and suppose that a typical position for an animal is halfway between walls. Fig. 3 shows a hexagonal array of leaf walls in a leafy environment, with an animal at the center of one of the inter-wall regions (the lower middle hexagon). Clearly, the structure of most leafy environments, like forests, is radically more complex and varied than this, but this canonical model helps elucidate the basic point. Fig. 3a illustrates the visually accessible regions around an animal with low convergence, i.e., with nearly panoramic vision, and having only a thin binocular region. Most of the large visual field of this animal is monocular, and cannot see much beyond the first layer of leaves, as is indicated by the gray region filled within the hexagon. However, within the animal's small binocular region it is possible to see beyond one layer of leaves, and Fig. 3a shows that the animal can visually survey the region reaching out and stopping at the next layer of leaves. In the limit of full panoramic vision and no binocular region, this animal would be able to visually cover only one hexagon of area around it, namely its own hexagon. Fig. 3b is the same, but for an animal with high convergence. For this animal, there is little visual area covered behind it, but this is easily made up for by the fact that the large binocular region can see past a large swathe of clutter, allowing it to visually cover a large area in front of it. In the limit of an entirely forward-facing binocular field, this animal would be able to visually survey half its own hexagon, as well as the three hexagons in front of it, for a total visual coverage of 3.5 hexagons, or 3.5 times as much area around it as the totally panoramic, all-monocular-vision animal. This argument assumes

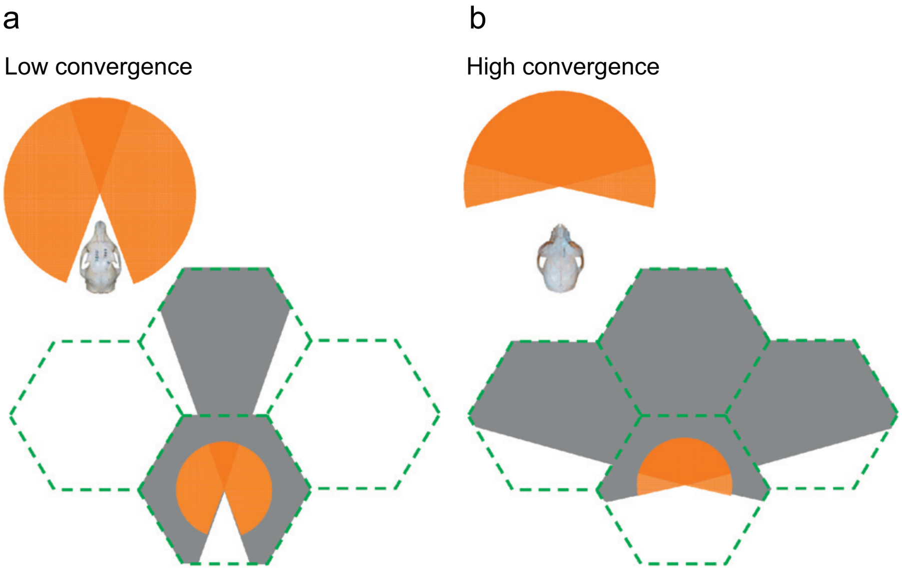

Fig. 3. A simple example of the visually surveyable regions around an animal in one canonical kind of cluttery environment, namely an environment consisting of layers of leaves with a characteristic inter-layer distance, leading to a hexagonal arrangement of leaf-layers. We say that a region is "visually surveyable" if it is the case that if an object suddenly appeared within it, then sufficiently much of it would be visible that the observer would recognize it. (a) For a sideways-facing eyed animal (with interpupillary distance greater than the leaf sizes), its monocular vision can survey objects up to the first layer of leaves, but will often see sufficiently little beyond the layer to recognize objects there. Only in its small binocular region (which can see a target beyond clutter with up to twice the probability as monocular vision) will it be able to survey regions beyond the first layer of clutter. Beyond the first layer of leaves, however, binocular vision becomes monocular, and so binocular vision typically will be unable to recognize objects beyond the second layer of leaves. The gray region indicates the regions visually surveyable to this animal under these conditions. (b) For a forward-facing eyed animal, most of its visual field is binocular, but it can see little behind it. However, the larger binocular field can potentially visually survey disproportionately large regions around the animal, as is illustrated here.

that it is the *area* around the animal that matters most, something that is true of most mammals (e.g., viewing directions are much more often along the two ground dimensions than along the third dimension). However, for many mammals the third dimension may significantly contribute, perhaps nearly equally to the other two dimensions, in which case it is the total viewed *volume* that should be calculated. The analogous model but extended to roughly spherical regions packed around the viewer's sphere would lead to 6.5 viewable spheres for the high convergence animal compared to just one sphere for the low convergence animal. We emphasize again that these estimates of the greater visually surveyable regions for forward-facing eyes are only illustrative estimates. The actual ratio can often be less than what we just described, if, for example, the next layer of leaves is only a short distance behind the first layer. Alternatively, the ratio can be much greater, if, for example, the second layer of clutter is very far behind the first layer of clutter, or there is no second layer of clutter at all.

This leads to a simple statement of our hypothesis, which is that "orbital convergence may have been selected to maximize the visually surveyable region around the animal." In non-cluttered environments—i.e., either the environment is non-leafy, or the interpupillary distance is small compared to leaf sizes, or both—binocular vision cannot see with any greater probability than monocular vision, and so the greatest surveyable region comes from having sideways-facing eyes. However, in cluttered environments—i.e., the environment is leafy *and* the animal's interpupillary distance is larger than the leaf sizes—binocular vision can see past leaf walls, and can visually survey a greater region around it than can monocular vision (with 3.5–6.5 being two rough upper estimates of such factors). In this light, we can make our main prediction.

3. Testing the X-ray hypothesis

For our main prediction, recall that animals outside of leafy environments do not have to deal with clutter no matter their interpupillary distance (Fig. 2c), and so there is never any X-ray advantage to forward-facing eyes. Animals not in leafy environments are therefore predicted to have low convergence no matter their size (Fig. 4a). For animals in leafy environments, however, whether the environment is cluttered depends on the animal's interpupillary distance (Fig. 2c), so that animals with small interpupillary distances experience a non-cluttered environment whereas larger animals live in progressively more cluttered environments. Accordingly, for animals in leafy environments the prediction is that small animals should have low convergence like that found for animals in non-leafy environments, but that larger animals should have progressively greater convergence (Fig. 4a).

We utilized orbital convergence data for 319 species across 17 mammalian orders from the dissertation of Heesy (2003). For each species, we determined its habitat categorization using Myers et al. (2006) and *Grzimek's Animal Life Encyclopedia*. A species was categorized as "non-forest" if the habitats were among deserts, dunes, plains, grasslands, savannas, mountains, and scrub, categorized as "forest" if the habitats were forests (including temperate rainforests, tropical rainforests, etc.), and categorized as "intermediate" if forests were mentioned as one of the main habitats along with non-forest habitats (see legend of Appendix Table A.1). Fig. 4b and c show how orbital convergence varies with body mass for these three categories of animal, and one can see that convergence increases with body size for forest species, but stays low and does not increase for the other two categories, consistent with the prediction in Fig. 4a.

In the analysis just above, we utilized "forest" versus "non-forest" as a proxy for leafiness. But leafy environments are not equivalent to forest environments. An animal outside of the forest who disproportionately inhabits bushes or tall grasses may effectively inhabit a leafy environment and will get the viewing benefits of forward-facing eyes. And, on the other hand, an animal in the forest but who favors clear areas on the ground may experience a non-leafy environment, and will get no benefit from

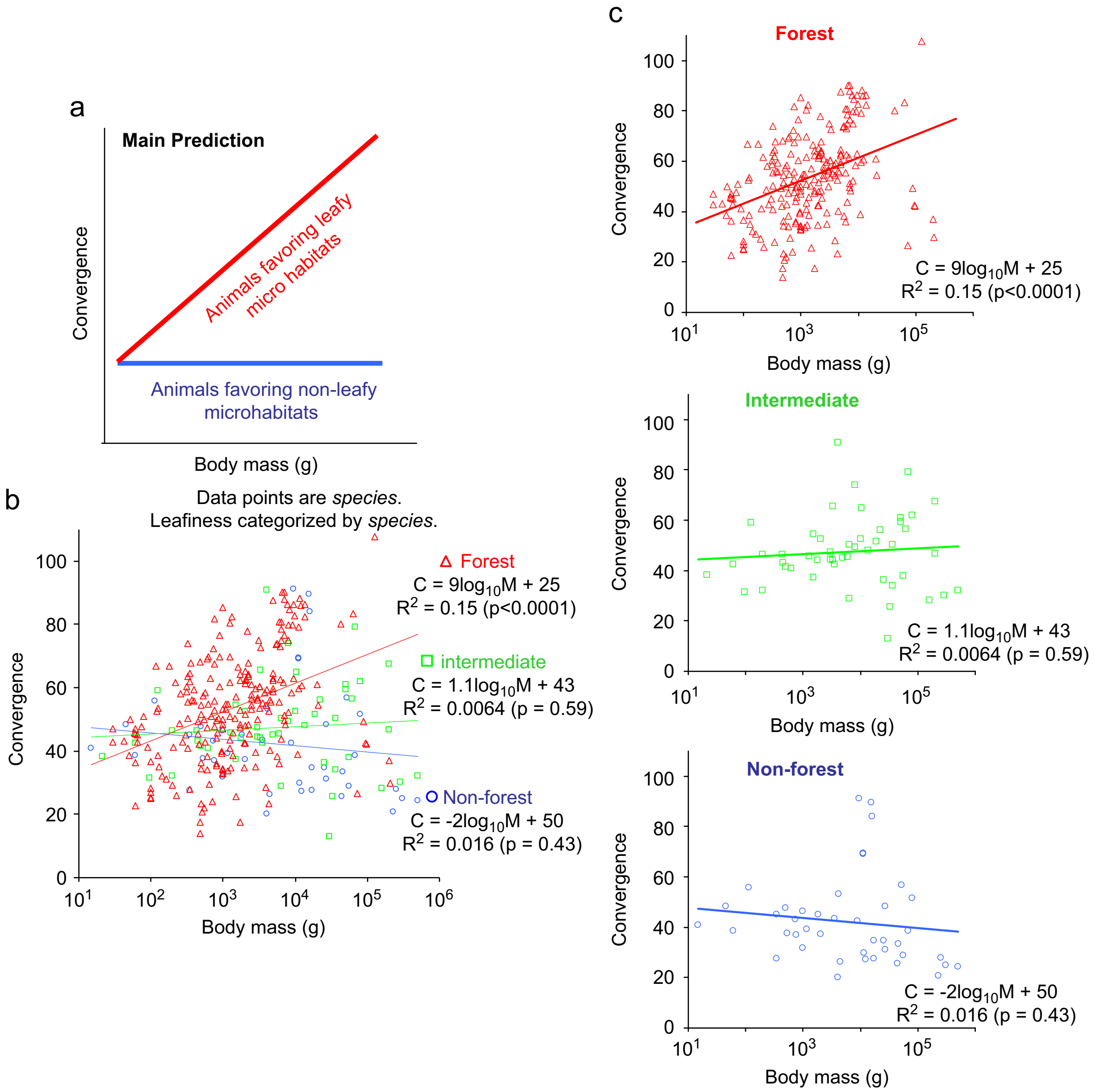

Fig. 4. (a) Predicted relationships for convergence versus body size, for mammals in leafy and non-leafy habitats. Non-leafy mammals are in non-cluttery environments no matter their size, and so convergence should be low and unchanging as a function of body size. Small mammals in leafy habitats do not tend to be in a cluttery environment, but the larger they are the more cluttery is their environment (Fig. 2). In leafy environments, then, convergence is predicted to be low for small animals, but to increase as a function of body size. (b) Convergence versus body mass for 319 species from Heesy (2003). The data are split into three groups based on whether the species was found primarily in forests, non-forests, or an intermediate categorization where one of the habitats is forest. One can see that, consistent with the prediction in (a), convergence increases as a function of body size for the species from forest habitats (top), and convergence stays low and does not increase for the species from non-forest and intermediate habitats (bottom and middle). [Least-squares equations and correlations are shown.] (c) The same three groups of data in (b), but plotted separately.

forward-facing eyes. What we would ideally like is, for any species, a measure of how leafy its microhabitats tend to be. In future work, the main author intends to acquire field measurements for varieties of microhabitats, measurements that will allow a more refined measure of which animals inhabit leafy microhabitats and which do not. In an effort to capture leafiness in a more refined manner, we carried out a second set of analyses to complement that in Fig. 4, this time where we categorized the level of "leafiness" at the level of the mammalian order, not at the level of species. Although, as discussed above, leafy environments are not equivalent to forest environments, there are almost certainly more leafy microhabitats within forests than in non-forests. A mammalian order with ranges of life styles better suited or specialized for leafy microhabitats might be expected to tend to have a greater percentage of its species in forest habitats. For this reason, we chose to measure the extent to which the species of an order inhabit forests, and use this as a proxy for the leafiness of the typical microhabitat for species of that mammalian order. So, for example, if most of the species in an order inhabit forests, then that suggests (in the absence of any other information to the contrary) that species in that order tend to be well suited for leafy microhabitats (even when their habitat is a non-forest one). If, on the other hand, few of the species in an order inhabit forests, then that suggests that species of this order tend to be well suited for non-leafy microhabitats (even when their habitat happens to be a forest one). Mammalian orders where, say, half the species inhabit forests would be an intermediate case. Appendix Table A.1 shows the habitats for each of the species, where 0 is for "non-forest," 1 for "intermediate," and 2 for "forest." For each mammalian order, these number codes were averaged to obtain a measure of the extent to which members of the order inhabit forest environments. From "forest" to "non-forest," the average habitat values for the 17 mammalian orders are shown along the right hand side of Fig. 5c. Seven orders have average habitat values of 2 or nearly 2—i.e., all or nearly all the species in each of these orders inhabit forests—and we categorized these as "leafy" orders (see upper right of Fig. 5c). Six mammalian orders have habitat values less than 1—i.e., each order is mostly non-forest—and we categorized these as "non-leafy" orders (see bottom right of Fig. 5c). The remaining four orders have habitat values of 1, 1.33, 1.4, and 1.5, in a similar direction as the seven "leafy" orders above, but because they do not appear to be part of the same cluster as the "leafy" seven (all seven which ranged from 1.87 to 2), we categorized them as an intermediate "semi-leafy" category (see middle right of Fig. 5c). In this way, we acquired a more refined measure of leafiness, but at the expense of less taxonomic resolution (i.e., categorizing leafiness at the order level rather than the species level).

Fig. 5b shows how orbital convergence varies as a function of body size for mammalian species in leafy, semi-leafy, and non-leafy orders. The results match the signature prediction in Fig. 5a, and are similar to the earlier results in Fig. 4b. The non-leafy orders have low convergence that does not vary with body size. For leafy orders, however, convergence is low for small body masses, but increases at larger body masses. Semi-leafy orders appear to be intermediary. In order to help communicate the contributions from the different orders, Fig. 5c shows the same data but with the data points coded by order. Note in the "leafy" plot of Fig. 5c that the four outliers at the bottom are sloths (although we do not currently have a hypothesis for why sloths would be outliers). In Fig. 6b each data point is now a family, rather than a species, and we find the same trend as before. (The two sloth families represented in the data now have an increased sway on the "leafy" plot, lowering the correlation, although it remains significant. Without the sloths included, the correlation rises to $R^2 = 0.44$, $p = 0.0003$.) Fig. 6c shows the same data as in Fig. 6b, but now with each point labeled by its family. One can see in Figs. 5c and 6c that for this data set each "leafiness" category is dominated by one mammalian order which is largely responsible for driving the overall trend, namely Primates for the "leafy" plot, Carnivora for the "semi-leafy" plot, and Artiodactyla for the "non-leafy" plot. This is one motivation for Fig. 7b, which is just like Fig. 6b, but confining the families to these three orders. One can again see the same signature effect. Fig. 7b is probably a more appropriate test of the prediction than that of Fig. 5b or Fig. 6b because although one expects leafy orders to have rising convergence (with body mass), the y-intercept and the slope of the rise may well differ from order to order (e.g., because of differences in the range of "leaf sizes," gaps between the leaves, distances to the leaf wall, extent to which the animal uses head

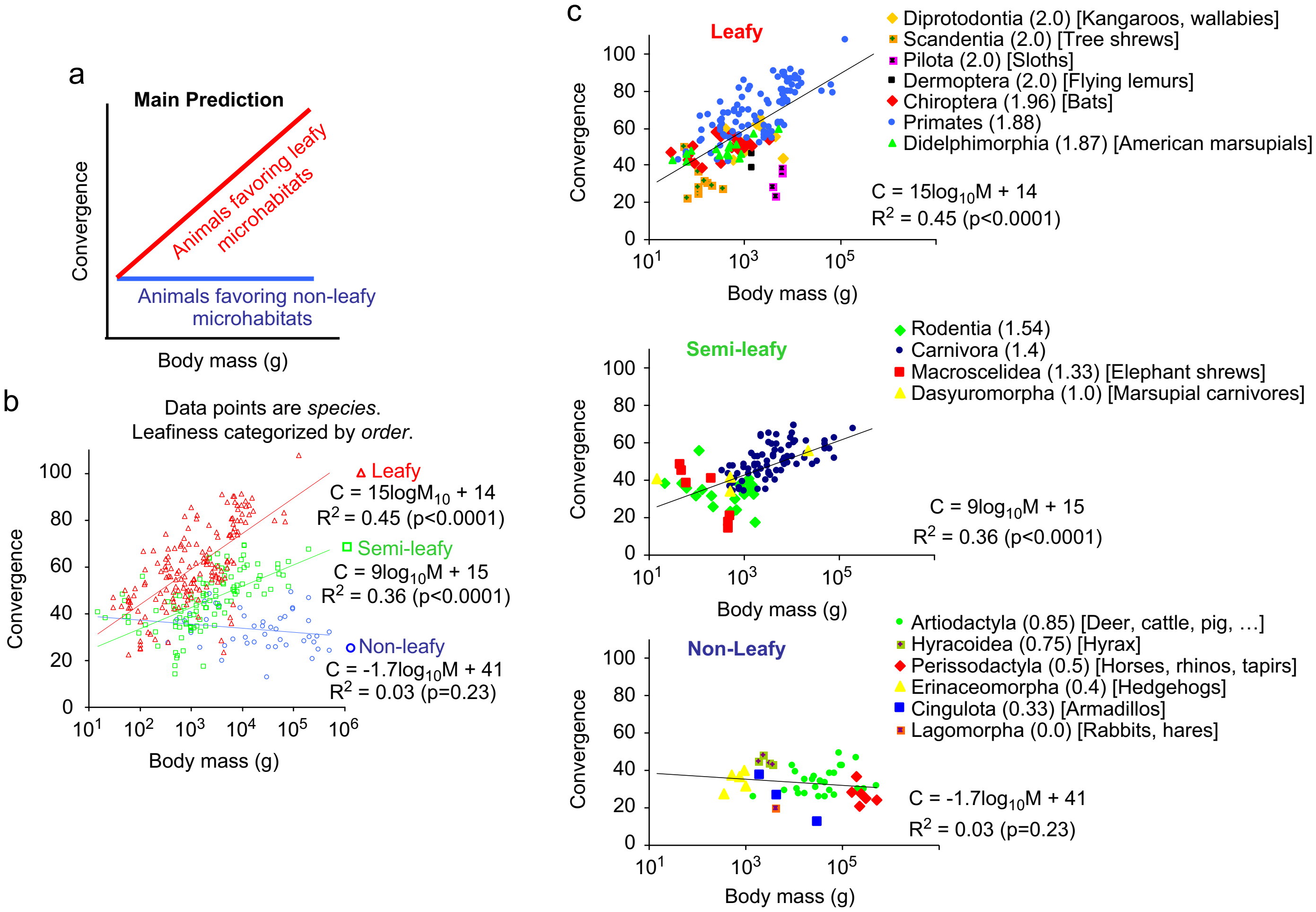

Fig. 5. (a) Main prediction (repeated from Fig. 4a). (b) Convergence versus body mass for 319 species from Heesy (2003), like in Fig. 4, but now where the data are split into three groups based on the degree to which each mammalian *order* tends to inhabit leafy environments. Again we see a fit to the prediction in (a), this time with the semi-leafy data being intermediate. (c) The same three groups in (b), but plotted separately and points labeled for the purpose of showing the taxonomic contributions. The parenthetic numbers in the legends indicate the degree to which each order tends to inhabit leafy environments, where 0 means non-leafy and 2 means leafy (see text, and Appendix Table A.1).

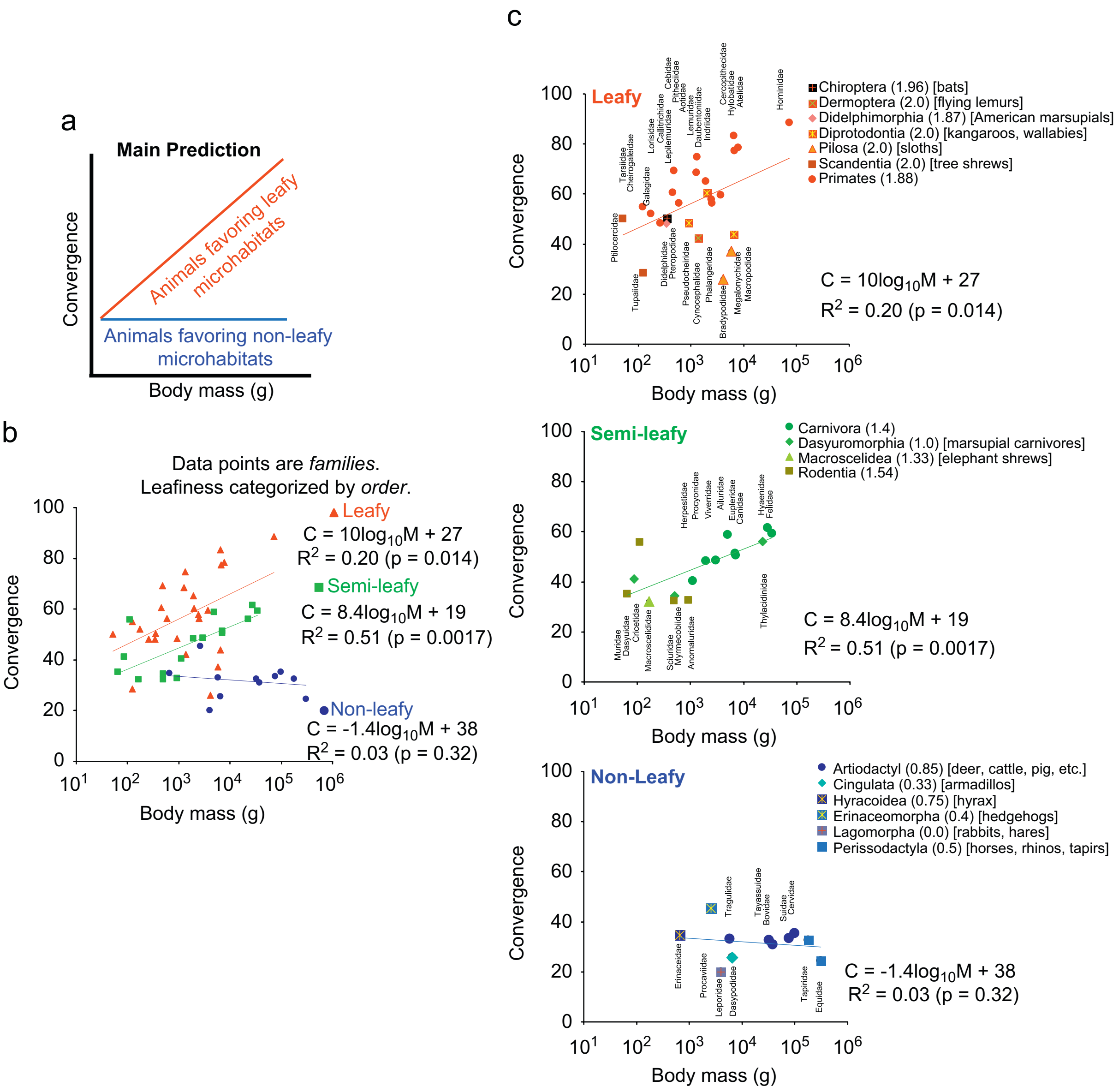

Fig. 6. (a) Main prediction (repeated from Fig. 4a). (b) Same data from Fig. 5 (i.e., "leafiness" categorized by order), but each data point now represents a family, rather than a species, helping to better appreciate the taxonomic variation. (c) Dame data as in (b), but separated by "clutter," and each order indicated by the data point type, and each family labeled.

parallax instead, etc.), in which case plotting them all together would tend to lower correlations. For example, perhaps the outlier sloths have increasing convergence, but just a lower *y*-intercept, and it is only because of the low range of sloth body sizes in the data set that we cannot detect the signature rise. As can be seen in Fig. 7b, the predicted signature of the X-ray hypothesis is now even more apparent, and the correlations for "leafy" and "semi-leafy" are much increased compared to before. Fig. 7c shows plots of the independent contrasts for these data, where the same effect is seen.

In addition to the main prediction just discussed (and tested in two distinct fashions, one fashion in Fig. 4, and the other in Figs. 5–7), there is a second prediction. As mentioned earlier, in cluttered environments binocular vision acquires a monocular view of what is beyond the clutter. That is, although the entire scene beyond the clutter may be visible, any given part of what is seen is only visible to one eye (e.g., see Fig. 1c). Building a coherent visual perception from such inputs creates special challenges for the visual system, including how to fuse the two non-overlapping views into the perception of a single scene, and how to perceive the depth relationships for objects seen behind clutter. If forward-facing eyes is for seeing better in cluttered environments as we hypothesize, then animals with forward-facing eyes should posses visual systems capable of solving these computational vision problems. Evidence has, in fact, accumulated over the last two decades that we do possess such mechanisms. Research has shown that a variety of ecological constraints on how clutter occludes and camouflages are "known" by our visual systems, so that we can see appropriate depth relationships in a single fused scene despite the lack of disparity in many parts of the stimulus (Nakayama et al., 1989; Nakayama and Shimojo, 1990; Shimojo and Nakayama, 1990a, b, 1994; Bacon and Mamassian, 2002). Shimojo et al. (1988) also showed that we veridically perceive motion through a slit behind clutter despite only one eye seeing the target at any one time, another perceptual capability expected for a creature of clutter but not for a mammal not having evolved in a cluttered environment. And, Arnold et al. (2007) showed that binocular rivalry is influenced by blur, so that perceptual

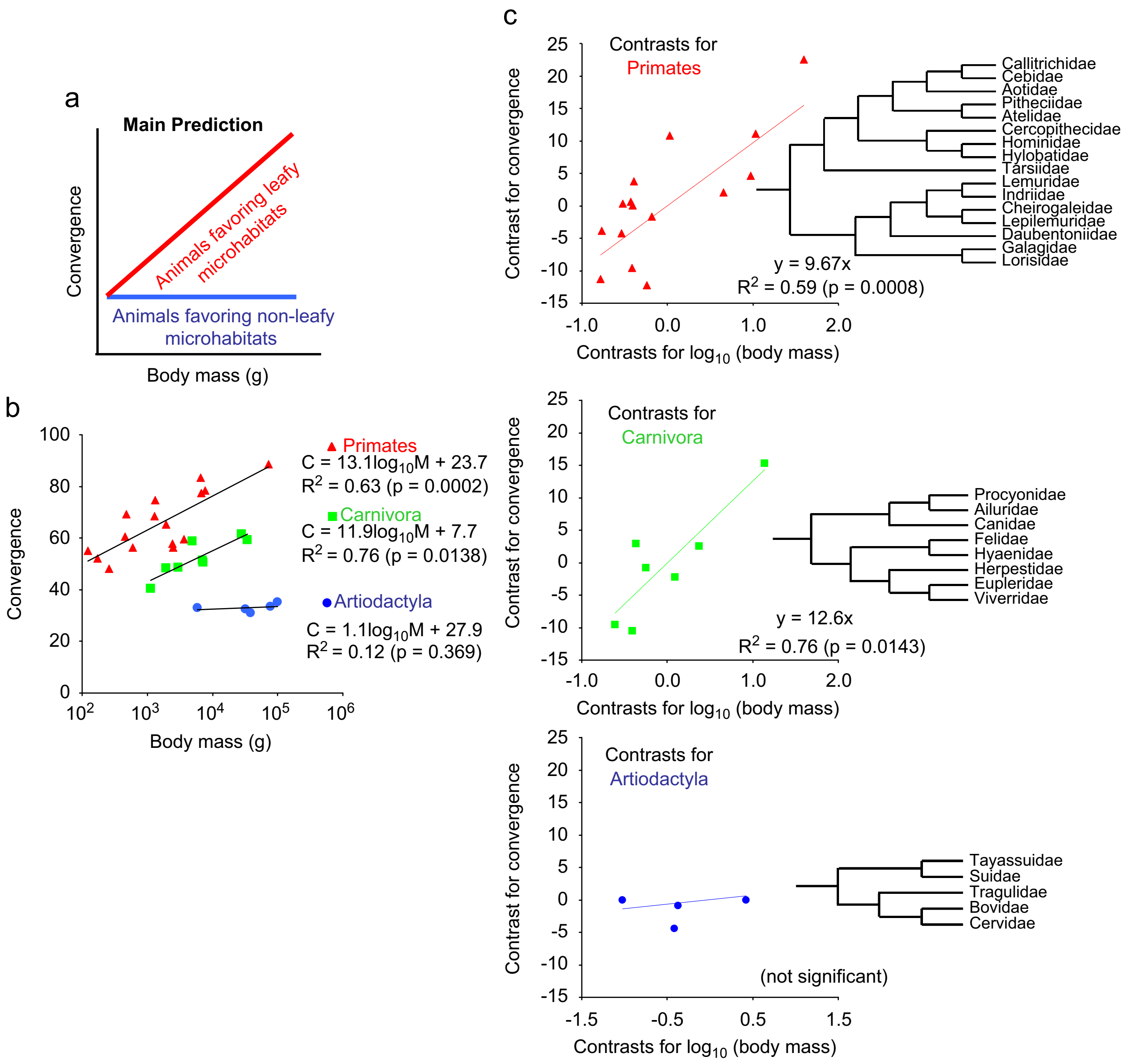

Fig. 7. (a) Main prediction (repeated from Fig. 4a). (b) Same kind of plot as that in Fig. 6b, but just for Primates, Carnivora and Artiodactyla, the three orders in each clutter-type that have the largest range at the family level, and account for most of the variation. (c) Independent contrasts (branch lengths ignored) for the families in these three orders, using the phylogenies shown (from Maddison and Schulz, 1996–2006).

dominance tends to track the in-focus image, consistent with what happens if you are gazing at an object through clutter, but the leaves (or you) are shifting so that the object is alternately visible to each eye.

4. Discussion

Other hypotheses for the function of forward-facing eyes have tended to assume, either explicitly or implicitly, that stereopsis is the key factor driving convergence, including the arboreal acrobatics hypothesis (Collins, 1921; Le Gros Clark, 1970), the visual predation hypothesis (Cartmill, 1972, 1997), and the angiosperm hypothesis (Sussman, 1991, 2004; Rasmussen, 1990). But in the cluttered environments where high convergence mammals tend to be found, for distances beyond the nearest leaves, the two eyes tend to have different views (Fig. 1c), and (disparity based) stereopsis degrades. Also, none of these stereopsis-based hypotheses (nor another by Pettigrew (1978) and Allman (1977) that forward-facing eyes are advantageous for reducing optical blurring during nocturnal predation) appears able to parsimoniously explain the empirical trends shown here. Finally, none of these hypotheses appear to have any theoretical justification for saying why their hypothesized function is more important than the costs of the loss of panoramic vision. For our X-ray hypothesis, however, there is a single currency: how much you can visually survey around yourself. You can see more in less cluttered environments with more sideways-facing eyes, but you can see more in more cluttered environments by facing both eyes more forwards, losing panoramic vision but gaining an increased view ahead that more than compensates for the loss of view behind (Fig. 3). Disparity-based stereo vision would still be important, especially for seeing uncluttered objects, but may not be key in understanding the evolution of forward-facing eyes.

Let's consider in more detail the most commonly accepted hypothesis for the function of forward-facing eyes, namely that the greater binocular field overlap widens the visual field capable of depth perception via stereopsis, which in turn is advantageous for visual predation (Cartmill, 1972, 1997). The results we have seen do not tend to support the conclusion that predators have the greatest convergence. First, as seen in Fig. 7b, Primates lie above Carnivora despite most primates—including likely ancestral primates (Sussman, 2004)—being much less faunivorous than most carnivores. Second, convergence is low for small predators but increases with body size, something the visual predation hypothesis cannot explain (without employing auxiliary hypotheses about supposed morphological constraints). If there is a link between predatorial behavior and forward-facing eyes, we speculate that it is because predators tend to prefer leafy cover in order to stalk prey, and that herbivores tend to keep away from leafy environments for safety.

We note that although the angiosperm hypothesis as originally discussed in Sussman (1991) appears to implicate stereopsis as the advantageous feature of forward-facing eyes for fruit and flower eating primates out in terminal branches (e.g., "… manipulating objects of very small size …, at very close range …"; Sussman, 1991, p. 219), Sussman would not appear to be committed to whether it is stereopsis or some other advantage (like X-ray). (Unlike arboreal acrobatics or visual predation, each which appears to have stereopsis as more central to the historical hypothesis.) This is because the central idea behind his angiosperm hypothesis is not stereopsis, but that there was "diffuse coevolutionary" interactions between flowering plants and animals (specifically primates, bats and plant-eating birds), so that as flowering plants evolved during the Eocene, some animals moved into terminal branch niches to access fruits and flowers. Our hypothesis fits well with Sussman's hypothesis for primate origins.

Finally, we conclude by speculating on whether these ideas could have implications for the evolution of interpupillary distance. Mammals in non-leafy environments with panoramic vision must have their eyes on the sides of their head in order to see behind them, and so interpupillary distance is expected to increase tightly as the 1/3 power of body mass (Fig. 8a). Fig. 8b shows interpupillary distance as a function of body mass, where the mammals are (as in Fig. 5b) split into "leafy," "semi-leafy," and "non-leafy" orders. One can see that, indeed, interpupillary distance increases tightly as about the 1/3 power of body mass for the non-leafy orders (Fig. 8b). In light of the X-ray hypothesis, there are four differences from this 1/3 power law for non-leafy orders that one might plausibly expect to find among leafy orders. These are "plausible expectations," not predictions that follow strictly from the X-ray hypothesis, because there could well be many other important selection pressures constraining interpupillary distance besides viewing considerations, selection pressures about which the X-ray hypothesis is silent. (1) First, for higher convergence mammals the eyes are not constrained to be on the sides of the head, and interpupillary distance can increase more slowly than the 1/3 power (Fig. 8a, lower slope of leafy line). This can be seen to be the case in Fig. 8b, where the leafy plot has a scaling exponent much lower than 1/3 (and the semi-leafy plot has an exponent in between). (2) Second, freed of the 1/3 geometrical scaling law, interpupillary distances for mammals in leafy environments can be driven by ecological factors such as leaf size and neuroanatomical costs to eye position, and the variation is accordingly expected to be much higher than for non-leafy mammals (Fig. 8a, leafy line is thick to indicate greater variation). It can be seen by a casual examination of Fig. 8b that the leafy data have substantially more variability for any given body mass than that for the non-leafy data (and that the semi-leafy data are in between). (3) Third, one might reasonably speculate (although it does not follow strictly from the X-ray hypothesis alone) that interpupillary distances of mammals in leafy environments might be constrained by the maximum leaf sizes found in leafy environments (Fig. 8a, gray region), because once interpupillary distances rise above the largest leaf sizes there is little or no further X-ray advantage to greater interpupillary distance (see Fig. 2). This is, in particular, true when the distance to the clutter is low (e.g., in Fig. 2b, lower than about 10 m, at which point the transition point along the interpupillary distance remains constant, and near the leaf size). For non-leafy mammals, this is not expected to be the case. Interpupillary distances of the leafy mammals in the data set do fall within the range of leaf sizes, which range from very small leaves (e.g., on small plants, conifer needles, and immature leaves) to the larger leaves found on many non-conifer trees (Fig. 8b). Only the largest leafy mammals have interpupillary distances the size of larger leaves, and as expected they do not tend to exceed the sizes of these larger leaves. In fact, one of the more salient properties in Fig. 8b is the extent to which the leafy mammals tend to cluster within the leaf regime, whereas non-leafy mammals do not show any clustering, and have interpupillary distances surpassing the larger

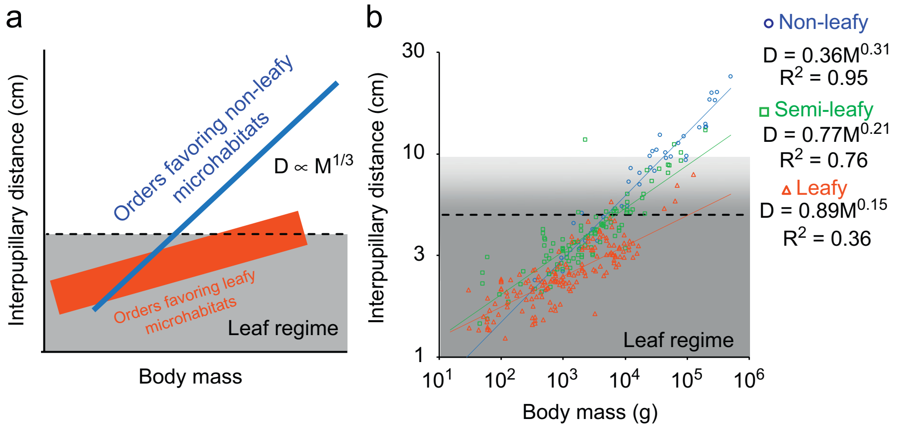

Fig. 8. (a) Speculated relationships for interpupillary distance versus body size, for leafy and non-leafy mammalian orders, motivated (but not strictly entailed) by the X-ray hypothesis. For non-leafy mammals, the relationship should be a low-variance (for any body mass) 1/3 power law that rises well above the ranges of leaf sizes of forests. For forest mammals, the relationship should be a (1) lower-than-1/3, (2) high-variance, power law that (3) does not rise much above the ranges of leaf sizes of forests, and (4) having a *y*-intercept greater than that for non-leafy mammalian orders. (b) Interpupillary distance versus body mass for the same species and categories as in Fig. 4. The upper limit to leaf sizes was estimated from White and More (2002) as the average non-conifer tree leaf size (the dotted line). Leaf sizes below it are shown in gray. Above this average is shown a decreasing gray scale for one standard deviation above the average, helping to represent the range of largest leaf sizes.

leaf sizes by nearly an order of magnitude (and semi-leafy mammals fall in between these two cases). (4) A final speculative interpupillary distance hypothesis motivated by the X-ray hypothesis is that, although large mammals in leafy habitats might be expected to have lower interpupillary distances than expected for their size (compared to mammals in non-leafy habitats), small mammals in leafy habitats might be expected to have greater interpupillary distance than expected for their size so that their binocular region can see through a greater range of leaf sizes. The *y*-intercepts (i.e., proportionality constants) of the best-fit lines in Fig. 8b are suggestively consistent with this, i.e., the proportionality constant for leafy mammals is more than twice that of the non-leafy mammals.

Our main theoretical contribution here was to put forth a new, heretofore-unnoticed function of forward-facing eyes (and binocular vision); namely, that forward-facing eyes can see better in cluttered environments (Fig. 1). (Forthcoming work describes how this x-ray function of binocularity allows, even more fundamentally, visuo-motor feedback from reaching appendages — such as a muzzle — without occluding the view beyond (Changizi, 2009)). In particular, when an animal is in a leafy environment like a forest and has an interpupillary distance above the sizes of the leaves, binocular vision can see much better past a layer of clutter (Fig. 2), which we termed "X-ray vision." In this light, we hypothesized that orbital convergence has been selected to maximize the visually surveyable region around an animal (Fig. 3). From this, we made our central prediction (Fig. 4a), which is that animals in non-leafy environments should have low convergence that does not vary with body mass, but that animals in leafy environments should have convergence that increases with body mass (and at small body masses the convergence becomes as low as that for animals in non-leafy environments). We found conformance to this prediction (via two tests, one summarized in Fig. 4, and the other analyzed in Figs. 5–7). We also discussed how at least humans possess the kinds of visual mechanisms needed for X-ray vision.

Acknowledgment

Support for this research was given by 5F32EY015370-02, NIH (to M.A.C.), and JST.ERATO, Japan (to S.S.).

Appendix

The habitats for each of the species are given in Table A1.

Table A1

Habitat species type						
Artiodactyla (avg = 0.85)	**Carnivora (contd!)**	**Chiroptera (avg = 1.96)**	**Diprotodontia (avg = 2.0)**	**Primates (avg = 1.88)**	**Primates (contd!)**	**Rodentia (avg = 1.54)**
1: *Bos taurus*	2: *Galidia elegans*	2: *Cynopterus brachyotis*	2: *Dactylonax palpator*	2: *Alouatta belzebul*	2: *Lemur catta*	2: *Aeretes melanopterus*
0: *Capra hircus*	2: *Galidictis fasciata*	2: *Dobsonia minor*	2: *Macropus eugenii*	2: *Alouatta caraya*	2: *Lemur macaco*	1: *Ammospemophilus leucurus*
1: *Cervus elaphus (canadensis)*	1: *Genetta angolensis*	2: *Eidolon dupreanum*	2: *Petauroides volans*	2: *Aotus nigriceps*	2: *Leontopithecus rosalia*	2: *Anomalurus beecrofti*
2: *Hyemoschus aquaticus*	2: *Genetta genetta*	2: *Eonycteris major*	2: *Petaurus australis*	2: *Aotus trivirgatus*	2: *Lepilemur dorsalis*	2: *Anomalurus derbianus*
0: *Litocranius walleri*	2: *Genetta maculata*	1: *Eonycteris robusta*	2: *Phalanger carmelitae*	2: *Arctocebus calabarensis*	2: *Lepilemur leucopus*	2: *Anomalurus fraseri*
0: *Mazama gouazoubira*	2: *Genetta servalina*	2: *Eonycteris spelaea*	2: *Phalanger lullulae*	2: *Ateles belzebuth*	2: *Lepilemur ruficaudatus*	2: *Anomalurus peli*
2: *Odocoileus virginianus*	1: *Genetta tigrina*	2: *Hypsignathus monstrosus*	2: *Phalanger orientalis*	2: *Ateles geoffroyi*	2: *Lophocebus albigena*	2: *Anomalurus pusillus*
0: *Oreotragus oreotragus*	1: *Genetta victoriae*	2: *Nyctimene celaeno*	2: *Phalanger sericeus*	2: *Ateles paniscus*	2: *Loris tardigradus*	0: *Cynomys ludovicianus*
0: *Ourebi ourebi*	1: *Helogale hirtula*	2: *Nyctimene major*	2: *Phalanger vestitus*	2: *Avahi laniger*	1: *Macaca mulatta*	0: *Mesocricetus auratus*
0: *Pelea capreolus*	2: *Hemigalus derbyanus*	2: *Pteropus admiralitatum*	2: *Pseudocheirus caroli*	2: *Brachyteles arachnoids*	2: *Microcebus murinus*	2: *Microsciurus isthmius*
0: *Procapra gutturosa*	*2: Herpestes ichneumon cafer*	2: *Pteropus alecto*	2: *Pseudocheirus forbesi*	2: *Callicebus caligatus*	2: *Microcebus rufus*	1: *Mus musculus*
0: *Pudu mephistophiles*	2: *Herpestes ichneumon funestus*	2: *Pteropus conspicillatus*	2: *Trichosurus arnhemensis*	2: *Callicebus moloch*	2: *Miopithecus talapoin*	1: *Petaurista cineraceus*
0: *Raphicerus campestris*	1: *Herpestes sanguineus*	2: *Pteropus giganteus*	2: *Trichosurus caninus*	2: *Callicebus personatus*	2: *Mirza coquereli*	2: *Petaurista elegans*
0: *Redunca redunca*	2: *Herpestes semitorquatus*	2: *Pteropus hypomelanus*	2: *Trichosurus vulpecula*	2: *Callicebus torquatus*	2: *Nasalis concolor*	2: *Petaurista leucogenys*
2: *Tragulus javanicus*	0: *Hyaena hyaena*	2: *Pteropus lylei*	**Erinaceomorpha (avg = 0.4)**	2: *Callimico goeldi*	2: *Nycticebus coucang*	2: *Petaurista petaurista*
1: *Tragulus napu*	1: *Ichneumia albicauda*	2: *Pteropus neohibernicus*	0: *Atelerix albiventris*	2: *Callithrix argentata*	2: *Nycticebus pygmaeus*	2: *Petinomys crinitis*
2: *Babyrousa babyrussa*	0: *Lycaon pictus*	2: *Pteropus poliocephalus*	2: *Echinosorex gymnura*	2: *Callithrix humeralifer*	2: *Otolemur crassicaudatus*	2: *Protoxerus strangeri*
1: *Catagonus wagneri*	2: *Lynx canadensis*	2: *Pteropus rayneri*	0: *Erinaceus europaeus*	2: *Callithrix jacchus*	2: *Pan troglodytes*	1: *Rattus rattus*
2: *Hylochoerus meinertzhageni*	1: *Lynx rufus floridanus*	2: *Pteropus rodricensis*	0: *Hemiechinus albulus/collaris*	2: *Cebuella pygmaea*	0: *Papio hamadryas*	2: *Ratufa bicolor*
2: *Potamochoerus porcus*	1: *Mungos mungo*	2: *Pteropus rufus*	0: *Paraechinus hypomelas*	2: *Cebus albifrons*	2: *Perodicticus potto*	2: *Sciurus carolinensis*
2: *Sus barbatus*	2: *Mustela putorius (furo)*	2: *Pteropus scapulatus*	**Hyracoidea (avg = 0.75)**	2: *Cebus apella*	2: *Phaner furcifer*	2: *Sciurus griseus*

Table A1 (*continued*)

Habitat species type

1: *Sus celebensis*
1: *Sus scrofa*
1: *Tayassu pecari*
1: *Tayassu tajacu*
0: *Ovis aries/Canadensis*

Carnivora (avg = 1.4)

0: *Acinonyx jubatus*
2: *Ailurus fulgens*
0: *Alopex lagopus*
2: *Arctictis binturong*
2: *Arctogalidia trivirgata*
1: *Atilax paludinosus*
2: *Bassaricyon alleni*
2: *Bassaricyon gabbi*
0: *Bassariscus astutus*
2: *Bdeogale jacksoni*
2: *Bdeogale nigripes*
1: *Canis lupus*
1: *Cerdocyon thous*
1: *Civettictis civetta*
1: *Crocuta crocuta*
2: *Crossarchus alexandri*
2: *Cryptoprocta ferox*
1: *Cuon alpinus*
0: *Cynictis penicillata*
1: *Cynictis selousi*
2: *Cynogale bennetti*
0: *Dologale dybowskii*
2: *Felis aurata*
2: *Felis bengalensis*
1: *Felis catus*
1: *Felis concolor*
2: *Felis pardalis*
2: *Felis planiceps*
0: *Felis serval*
2: *Felis tigrina*
2: *Felis viverrina*
2: *Felis wiedii*
2: *Nandinia binotata*
2: *Nasua nasua*
2: *Neofelis nebulosa*
2: *Nyctereutes procyonoides*
0: *Otocyon megalotis*
2: *Paguma larvata*
1: *Panthera leo*
1: *Panthera onca*
1: *Panthera uncia*
2: *Paradoxurus hermaphroditus*
2: *Poiana richardsoni*
2: *Potos flavus*
2: *Prionodon pardicolor*
2: *Procyon lotor*
0: *Proteles cristatus*
2: *Salanoia concolor*
1: *Speothos venaticus*
0: *Suricata suricatta*
2: *Urocyon cinereoargenteus*
2: *Viverra megaspila*
2: *Viverra tangalunga*
1: *Viverra zibetha*
1: *Viverricula indica*
1: *Vulpes vulpes fulva*
2: *Pteropus seychellensis*
2: *Pteropus vampyrus*
2: *Rousettus aegyptiacus*

Cingulata (avg = 0.33)

0: *Chaetophractus villosus*
0: *Euphractus sexcinctus*
1: *Priodontes giganteus*

Dasyuromorphia (avg = 1.0)

1: *Dasyurus hallucatus*
2: *Myrmecobius fasciatus*
1: *Thylacinus cynocephalus*
0: *Sminthopsis crassicaudata*

Dermoptera (avg = 2.0)

2: *Cynocephalus variegates*
2: *Cynocephalus volans*

Didelphimorphia (avg = 1.87)

2: *Caluromys derbianus*
2: *Caluromys lanatus*
2: *Caluromys philander*
2: *Chironectes minimus*
2: *Didelphis albiventris*
2: *Didelphis marsupialis*
2: *Didelphis virginiana*
1: *Lutreolina crassicaudatus*
2: *Marmosa murina*
1: *Marmosa robinsoni*
2: *Metachirus nudicaudatus*
2: *Monodelphis Americana*
2: *Monodelphis brevicaudata*
2: *Philander andersoni*
2: *Philander opossum*
2: *Dendrohyrax arboreus*
1: *Dendrohyrax dorsalis*
0: *Heterohyrax brucei*
0: *Procavia capensis*

Lagomorpha (avg = 0)

0: *Lepus*

Macroscelidea (avg = 1.33)

0: *Elephantulus myurus*
0: *Macroscelides proboscideus*
2: *Petrodromus tetradactylus*
2: *Rhynchocyon chrysopygus*
2: *Rhynchocyon cirnei*
2: *Rhynchocyon petersi*

Perissodactyla (avg = 0.5)

0: *Equus caballus*
0: *Equus hemionus*
0: *Equus przewalskii*
0: *Equus zebra*
1: *Tapirus pinchaque*
2: *Tapirus terrestris*

Pilosa (avg = 2.0)

2: *Bradypus tridactylus*
2: *Bradypus variegates*
2: *Choloepus didactylus*
2: *Choloepus hoffmanni*
2: *Cebus capucinus*
2: *Cercocebus agilis*
2: *Cheirogaleus major*
2: *Cheirogaleus medius*
1: *Chlorocebus aethiops*
2: *Colobus guereza*
2: *Daubentonia madagascariensis*
0: *Erythrocebus patas*
2: *Eulemur coronatus*
2: *Eulemur fulvus*
2: *Eulemur mongoz*
2: *Eulemur rubriventer*
2: *Euoticus elegantulus*
2: *Galago alleni*
1: *Galago senegalensis*
2: *Galagoides demidoff*
2: *Gorilla gorilla*
2: *Hapalemur griseus*
2: *Hapalemur simus*
1: *Homo sapiens*
2: *Hylobates agilis*
2: *Hylobates hoolock*
2: *Hylobates lar*
2: *Hylobates moloch*
2: *Indri indri*
2: *Kasi Johnii*
2: *Lagothrix flavicauda*
2: *Lagothrix lagotricha*
2: *Pithecia monachus*
2: *Pithecia pithecia*
2: *Pongo pygmaeus*
2: *Presbytis melalophos*
2: *Procolobus badius*
2: *Propithecus diadema*
2: *Propithecus tattersalli*
2: *Propithecus verreauxi*
2: *Pygathrix nemaeus*
2: *Pygathrix nigripes*
2: *Rhinopithecus roxellanae*
2: *Saguinus fuscicollis*
2: *Saguinus nigricollis*
2: *Saguinus Oedipus*
2: *Saimiri boliviensis*
2: *Saimiri oerstedi*
2: *Saimiri sciureus*
2: *Semnopithecus entellus*
2: *Tarsius bancanus*
1: *Tarsius spectrum*
2: *Tarsius syrichta*
0: *Theropithecus gelada*
2: *Trachypithecus cristatus*
2: *Varecia variegata*
2: *Varecia variegata rubra*
0: *Spermophilus parryii*
2: *Tamiasciurus douglasii*
2: *Tamias striatus*

Scandentia (avg = 2.0)

2: *Anathana ellioti*
2: *Ptilocercus lowii*
2: *Tupaia glis*
2: *Tupaia berlangeri*
2: *Tupaia dorsalis*
2: *Tupaia gracilis*
2: *Tupaia javanica*
2: *Urogale everetti*
2: *Tupaia minor*
2: *Tupaia palawanensis*
2: *Tupaia tana*

Habitat categorizations:
0: desert, dune, arid plains, desert/savanna, mountains, short-grass grassland, scrub, savanna/scrub, open country, savanna/grassland, grassland, tundra.
1: burrows/forest/grassland, rocky forest, dense marsh, open spaces in forests, open forests, desert/savanna/forest/mountain, forest/plain/tundra, savanna/forests, forests/savanna, forests/grassland, forests/semi-deserts/mountains, forests/mountains, open scrub/forests.
2: semi-arboreal, dense cover, thick vegetation, forest, forest canopy, dense forest, forests/rainforests, rainforest, tropical forests, tropical rainforests.

References

Allman, J., 1977. Evolution of the visual system in the early primates. In: Sprague, J., Epsteins, A. (Eds.), Progress in Physiological Psychology, vol. 7. Academic Press, pp. 1–53.

Arnold, D.H., Grove, P.M., Wallis, T.S.A., 2007. Staying focused: a functional account of perceptual suppression during binocular rivalry. J. Vision 7, 1–8.

Bacon, B.A., Mamassian, P., 2002. Amodal completion and the perception of depth without binocular correspondence. Perception 31, 1037–1045.

Cartmill, M., 1972. Arboreal adaptations and the origin of the order Primates. In: Tuttle, R.H. (Ed.), The Functional and Evolutionary Biology of Primates. Aldine-Atherton, Chicago, pp. 97–122.

Cartmill, M., 1997. Explaining primate origins. In: Ember, C.R., Ember, M. (Eds.), Research Frontiers in Anthropology. Prentice-Hall, Englewood Cliffs, NJ, pp. 31–46.

Changizi, M.A., 2009. The Vision Revolution. Benbella Books.

Collins, E.T., 1921. Changes in the visual organs correlated with the adoption of arboreal life and with the assumption of the erect posure. Trans. Ophthalmol. Soc. UK 41, 10–90.

Forte, J., Peirce, J.W., Lennie, P., 2002. Binocular integration of partially occluded surfaces. Vision Res. 42, 1225–1235.

Grzimek's Animal Life Encyclopedia. The Gale Group, Inc., 2005.

Heesy, C.P., 2003. The evolution of orbit orientation in mammals and the function of the primate postorbital bar. Ph.D. Dissertation, Stony Brook, Stony Brook University, New York.

Heesy, C.P., 2004. On the relationship between orbit orientation and binocular visual field overlap in mammals. Anat. Rec. Part A 281A, 1104–1110.

Le Gros Clark, W.E., 1970. History of the Primates. British Museum, London.

Maddison, D.R., Schulz, K.-S. (Eds.), 1996–2006. The Tree of Life Web Project. 〈http://tolweb.org〉.

Myers, P., Espinosa, R., Parr, C.S., Jones, T., Hammond, G.S., Dewey, T.A., 2006. The Animal Diversity Web.

Nakayama, K., Shimojo, S., 1990. Da Vinci stereopsis: depth and subjective occluding contours from unpaired image points. Vision Res. 30, 1811–1825.

Nakayama, K., Shimojo, S., Silverman, G.H., 1989. Stereoscopic Depth: Its Relation to Image Segmentation, Grouping, and the Recognition of Occluded Objects.

Pettigrew, J.D., 1978. Comparison of the retinotopic organization of the visual wulst in nocturnal and diurnal raptors, with a note on the evolution of frontal vision. In: Cool, S.J., Smith, E.L. (Eds.), Frontiers of Visual Science. Springer, New York, pp. 328–335.

Rasmussen, D.T., 1990. Primate origins: lessons from a neotropical marsupial. Am. J. Primatol. 22, 263–277.

Shimojo, S., Nakayama, K., 1990a. Real world occlusion constraints and binocular rivalry. Vision Res. 30, 69–80.

Shimojo, S., Nakayama, K., 1990b. Amodal representation of occluded surfaces: role of invisible stimuli in apparent motion correspondence. Perception 19, 285–299.

Shimojo, S., Nakayama, K., 1994. Interocularly unpaired zones escape local binocular matching. Vision Res. 34, 1875–1881.

Shimojo, S., Silverman, G.H., Nakayama, K., 1988. An occlusion-related mechanism of depth perception based on motion and interocular sequence. Nature 333, 265–268.

Sussman, R.W., 1991. Primate origins and the evolution of angiosperms. Am. J. Primatol. 23, 209–223.

Sussman, R.W., 2004. Flowering plants and the origins of primates. In: Bekoff, M. (Ed.), Encyclopedia of Animal Behavior. Greenwood Press, Westport, CT.

White, J., More, D., 2002. The Illustrated Encyclopedia of Trees. Timber Press.