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When should faster-moving animals have better visual ability? A computational study of Leuckart's law

Shinsuke Satoi and Yoh Iwasa

Department of Biology, Kyushu University, Fukuoka, Japan

ABSTRACT

Background: Leuckart's law postulates that, among vertebrates, swifter animals should have larger eyes with better visual ability. It was supported for mammals but rejected for birds.

Question: We ask what are the conditions in which faster-moving animals evolve to have better visual ability?

Methods: Computer simulation studies of an animal moving on a plane containing many food items as well as obstacles. The animal moved at a constant speed but changed its directional angle when it recognized food items or obstacles. We examined the number of food items the animal consumed and the number of obstacles it collided with.

Results: We assume that visible distance is in proportion to eye size, and that it is accompanied by a small cost. We obtained the optimal visual distance, which depended on movement speed, and densities of foods and obstacles in the field.

Conclusions: The positive correlation between movement speed and optimal visual distance was stronger with more obstacles and fewer food items. In contrast, the correlation was weak (Leuckart's law does not hold) when food was abundant, obstacles were rare, and collision damage minimal.

Keywords: animal behaviour, eye size, Leuckart's law, locomotion, visual acuity.

INTRODUCTION

Animals obtain information regarding their physical and social environments through diverse sensory organs, receiving visual, auditory, tactile, and chemical signals. The size, position, and ability of sensory organs are likely to have evolved based on their costs and benefits to the animal (Walls, 1942; Hughes, 1977; Eisthen, 1997; Fay and Popper, 2000). Eyes are sensory organs for light, and almost all animals are equipped with eyes or organs with a similar function. The size of eyes is affected by many factors, including body size (Schultz, 1940; Kiltie, 2000; Howland *et al.*, 2004; Burton, 2008), activity pattern (Kay and Kirk, 2000; Garamszegi *et al.*, 2002; Kirk, 2006; Werner and Seifan, 2006; Hall and Ross, 2007; Hall, 2008), and diet (Garamszegi *et al.*, 2002; Lisney and Collin, 2007).

Leuckart (1876) proposed that swifter animals tend to have larger eyes than slower-moving species. Leuckart's law predicts a positive correlation between locomotive speed and eye size

Correspondence: Y. Iwasa, Department of Biology, Kyushu University, Fukuoka 812-8581, Japan. e-mail: yohiwasa@kyudai.jp

of animals if other aspects of their lives are equal (Leuckart, 1876; Walls, 1942; Hughes, 1977). Eyesight involves two features: sensitivity and resolution. Sensitivity is related to nocturnal vision, thus a high sensitivity allows animals to see surroundings under limited light conditions. In contrast, resolution refers to the precision of eyes, so animals with eyes capable of high resolution can see surroundings clearly and in fine detail. Both sensitivity and resolution are improved with larger eyes (Land and Nilsson, 2012).

Just as swift animals need to recognize surrounding objects while still far away from them, so they need eyes with high resolution to allow them to see distant objects clearly (Hughes, 1977; Heard-Booth and Kirk, 2012). As larger eyes ensure higher resolution, Leuckart's proposal of a positive correlation between locomotive speed and eye size is a plausible hypothesis. However, because of the difficulty of measuring the movement speed of animals, Leuckart's law has not been empirically examined since its proposal, more than 100 years ago. Brooke *et al.* (1999) studied the relationship between eye mass and flight speed predicted by fluid mechanics in 104 flying bird species and confirmed a positive correlation between the two variables. They also found that eye mass was smaller among flightless birds than among flying birds, after controlling for body mass. Kirk (2006) demonstrated that patas monkeys, which move quickly, have relatively large eyes for primates.

Hall and Heesy (2011), however, examined axial eye diameter and flight speed in 88 avian species, in the first test of Leuckart's law based on direct measurements of flight speed (earlier studies only estimated flight speed). They were unable to detect a correlation between eye size and movement speed in birds. Furthermore, they observed a negative correlation between relative eye size and movement speed, which is at odds with Leuckart's law (Hall and Heesy, 2011). They concluded that variation in the eye size of birds is driven mainly by factors other than movement speed. Heard-Booth and Kirk (2012) examined axial eye diameter and running speed in 50 species from ten mammalian orders. They found a significant positive correlation between absolute eye size and running speed, but no correlation between eye size and activity pattern (i.e. nocturnal/diurnal) in mammals. Moreover, the relationship between eye size and running speed was still significant when the effects of body mass and phylogeny were controlled for statistically (Heard-Booth and Kirk, 2012). Thus, these two comparative studies, conducted using different taxonomic groups, reached different conclusions.

Here, we examine the conditions under which Leuckart's law holds, i.e. when the correlation between eye size and movement speed is strong. We conducted computer simulations of an animal moving on a plane containing many food items as well as obstacles. The animal moved at a constant speed but changed its directional angle when it recognized food items or obstacles. By considering the number of food items consumed, the number of obstacles with which the animal collided, as well as a small cost of visual acuity, we obtained the optimal visual acuity. We explored how the optimal visual acuity depends on visible distance, visible angle, turning ability, movement speed, and the densities of food and obstacles in the field. If the animal's visual acuity is close to the optimal value, and if visual distance is greater for large eye size, the positive correlation between movement speed and eye size will be greater when obstacles are more abundant, food items are rare, and there is marked damage due to collisions. In contrast, Leuckart's law may not hold in environments where food is abundant, obstacles are rare, and damage owing to collisions is limited.

MODEL

Using computer simulations, we considered an animal moving in a field, avoiding obstacles and foraging for food items, and examined how its performance depends on visual ability. Figure 1 illustrates a simulated field, in which many obstacles and food items are randomly distributed. The field is modelled as a $10{,}000 \times 10{,}000$ square lattice with periodic boundary conditions. A fan-shaped object on the plane indicates the area visible to a moving animal located at the pivot of the fan. Large and small circles represent obstacles and food items, respectively. The location of the focal animal, or the pivot of the fan, is specified by two coordinates, (x, y). The animal also has a direction to move in, which is given by the directional angle (θ). We assume that the animal moves at a constant speed v. These three variables specify the state of the animal.

The entire field contains a number of food items and obstacles that are not mobile and are distributed following Poisson point processes with constant densities. When the animal encounters a food item, it consumes it. In contrast, when the animal hits an obstacle, it incurs damage. The number of food items is f and the number of obstacles is r.

Movement and reorientation of the animal

The animal's ability to manoeuvre is characterized by four parameters: visible distance, R, is how far the animal can see, while visible angle, 2ω, represents over how wide an area the animal can see. The animal moves at a constant speed v. The spatial area the animal can see is in the shape of a fan (or a sector), the pivot of which is the animal's body. When the animal finds a food item or an obstacle, it may alter the direction of its locomotion to

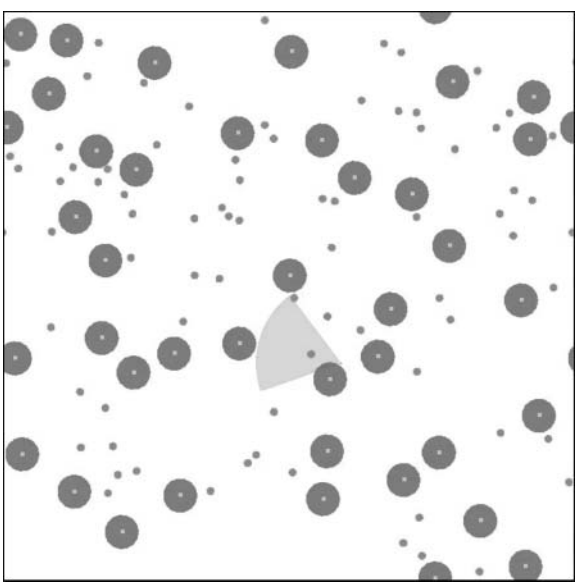

Fig. 1. Schematic representation of the model. The area in which the animal moves is modelled as a $10{,}000 \times 10{,}000$ square lattice with periodic boundary conditions. The fan-shaped object represents the area visible to the moving animal. Large and small circles represent obstacles and food items, respectively.

capture the food item or avoid the obstacle. The maximum speed of change in direction per step is specified by the animal's turning ability s. Thus, the simulation model consists of six parameters in total: four parameters that represent the animal's ability to manoeuvre, and two parameters that describe the environment (density of food items f and density of obstacles r).

The animal can see food items and obstacles that are within the visible area (the fan-shaped area with radius R and angle 2ω, with the pivot directly on the animal's body). If there are no obstacles to avoid within the visible area and if there is one or more food items, the animal will attempt to retrieve them. The animal first examines the reachability of each food item as well as the distance to it, based on its turning ability. Of the food items that are reachable, it attempts to reach the closest one first. After consuming it, the same procedure is again applied. In order to keep the number of food items constant, when a food item is consumed a new food item appears at a randomly chosen point.

In contrast, if there are one or more obstacles within the visible area, the animal attempts to avoid any collision, based on its turning ability. In calculating the path to follow, the animal starts to turn at the last possible moment that will allow it to avoid colliding with an obstacle. Avoiding colliding with an obstacle takes priority over food consumption. If there are multiple food items in the visible area, the animal first calculates the possible ways in which to reach each food item in turn, based on its own turning ability as well as the possibility of colliding with an obstacle on the way. If it is not possible to reach the food item without colliding with an obstacle, the animal excludes that food item from consideration. In other words, animals only approach food items that are retrievable without a collision.

Initial conditions

Before beginning the simulation, the 'radius for avoidance' is calculated to each obstacle. The radius for avoidance is defined as the radius of the circumference of a circle within which the moving animal can avoid certain obstacles if it engages in reorientation. This radius is determined when the radius of obstacles, movement speed, and turning ability are known.

The simulation was conducted based on the following steps. A set of parameter values (R, v, s, ω), the spatial distributions of obstacles and food items, and the initial position of the moving animal were defined. The distributions of obstacles and food items were determined to avoid overlap with other obstacles and food items. The initial position of the moving animal was also set to avoid overlap with obstacles and food items.

The distributions of food items and obstacles and the initial position of the animal were determined initially using random numbers. The animal then moved around in the simulated field for 10,000 steps. One movement step consists of reorientation, straight movement, and a judgement as to the possibility of a collision or the consumption of a food item. To remove the effect of our chosen initial conditions, the animal's first 100 movement steps were not recorded. We then began to record the number of collisions with obstacles and the number of food items consumed.

NUMBER OF ENCOUNTERS WITH FOOD ITEMS AND OBSTACLES

Figure 2a presents a contour plot of the results of simulations for the number of food items consumed. The horizontal axis is movement speed v, and the vertical axis is visible distance R. When movement speed is slow, the animal cannot increase the number of food items it

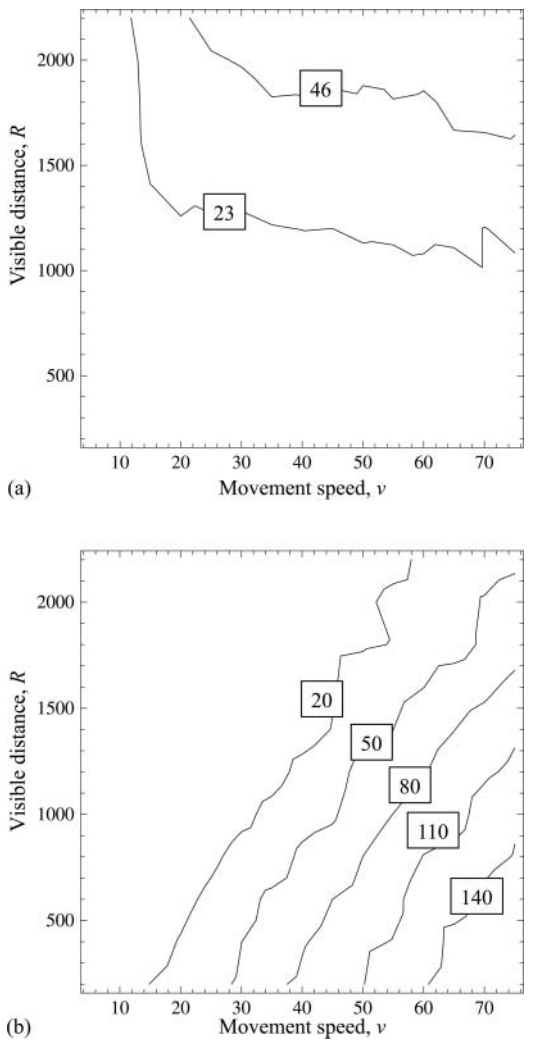

Fig. 2. Results of simulations shown as contour plots. (a) Number of food items consumed. More food items are consumed with a longer visual distance R and faster movement speed v. (b) Number of collisions. The risk of collision is higher with a short visual distance R and faster movement speed v. Parameters: $r = 30, f = 40$.

consumes even if it has a longer visible distance (Fig. 2a). In contrast, if the animal can move sufficiently quickly, an individual with a longer visible distance can consume significantly more food items than one with a shorter visible distance. Therefore, possessing a long visible distance is effective when movement speed is sufficiently fast.

Figure 2b provides a contour plot of the number of collisions with obstacles. If movement speed is slow, an animal will be able to avoid obstacles with a moderately long rather than long visible distance. In contrast, if movement speed is fast, an animal with a short visible distance will undergo many collisions; hence, a fast-moving animal requires a long visible distance.

COST OF VISION AND OPTIMAL VISIBLE DISTANCE

To explore the optimal visible distance for a given movement speed, we introduce the cost of vision. The cost of constructing and maintaining eyes is likely to be higher for elaborate eyes than for simple eyes, although there has been no clear experimental measurement of this cost. Here we assume that the fitness is:

$$\phi = (g - dh) \times \exp(-cR^2). \tag{1}$$

The number of food items consumed, g, and the number of collisions, d, can be calculated from computer simulations, as explained below. The constant h indicates the damage due to collision, relative to the benefit of food intake. We assume that the cost of eye size increases with visual ability in a quadratic manner. c is the coefficient of the cost of elaborating eyes.

We can obtain the optimal visible distance, R_{opt}, as the value that maximizes fitness ϕ for a given movement speed v. An optimal eye size exists and depends on the cost of eye size, as illustrated in Fig. 3.

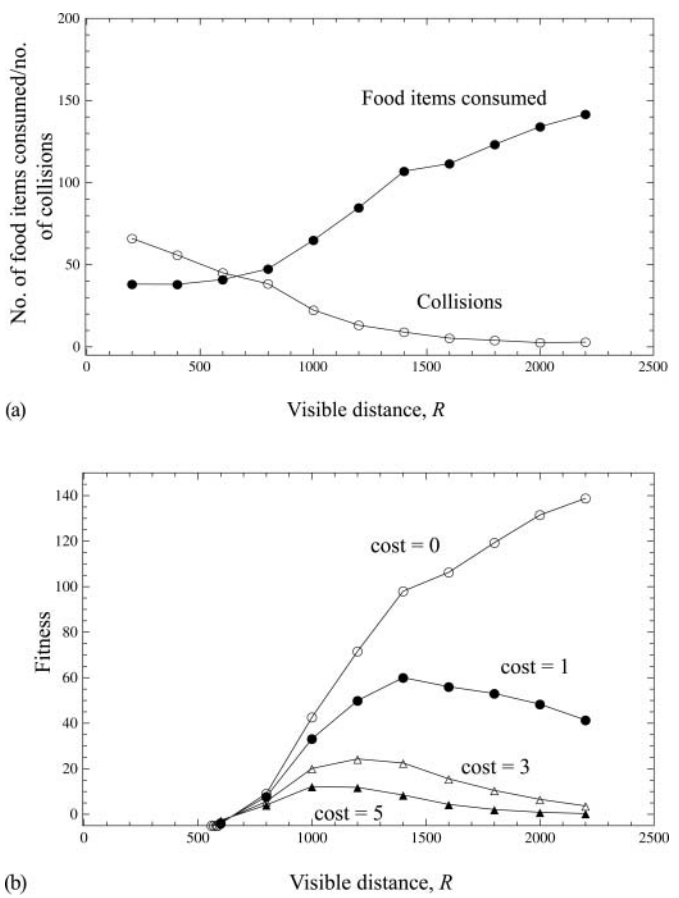

Fig. 3. Optimal eye size. (a) Number of food items consumed and number of collisions versus visible distance R. (b) Fitness calculated using equation (1) versus visible distance R. Parameters: $r = 20$, $f = 40$, $v = 20$.

Optimal visible distance increases with movement speed

We generated a number of simulation runs with different visible distances R and obtained the optimal visible distance R_{opt}. We then compared this value for different movement speeds v. Leuckart's law postulates that R_{opt} and v should be positively correlated.

Figure 4 shows that the optimal visible distance is longer for faster-moving animals than for slower-moving ones. This finding supports Leuckart's law, i.e. movement speed and visual ability are positively correlated if we consider a positive correlation between eye size and visible distance (Land and Nilsson, 2012). Figure 4 shows a linear relationship between $\ln R_{opt}$ and $\ln v$. Let us consider the linear regression of the logarithmic value of optimal visible distance and the logarithmic value of movement speed, $\ln v$: $\ln R_{opt} = \alpha \ln v + \beta$. From a number of simulation results with different v, we can estimate the speed sensitivity, α, as follows:

$$\alpha = \mathrm{cov}(\ln R_{opt}, \ln v)/\mathrm{var}(\ln v), \tag{2}$$

which indicates the strength of the dependence of R_{opt} on v. It is a quantity that has no dimension, and is called 'elasticity'. In population biology, elasticity has been used to analyse proportional sensitivity (de Kroon *et al.*, 1986; Caswell, 2000).

We obtained the value of α (equation 2), which was always positive. Hence, Leuckart's law holds in our model. However, the magnitude of α varied with parameter sets. Next we examined the dependence of α on different parameters.

Figure 5 illustrates how α depends on four parameters in the model, namely r, f, d, and c. We first chose a standard set of parameter values and then examined how α changed when one of the parameters, for example k, increased after being multiplied by factors of 1.3, 1.6, 1.9, 2.1, 2.4, and 2.7, while all other parameters were kept at their standard values. Speed sensitivity α increased or decreased almost linearly with $\ln(k/k_0)$, where k_0 is the standard value of parameter k. The slope indicates the dependence of α on the parameter k. We performed this procedure for each of the four parameters. In the example shown in Fig. 6, α increased as r and d increased but decreased as f increased. Speed sensitivity α did not strongly depend on c.

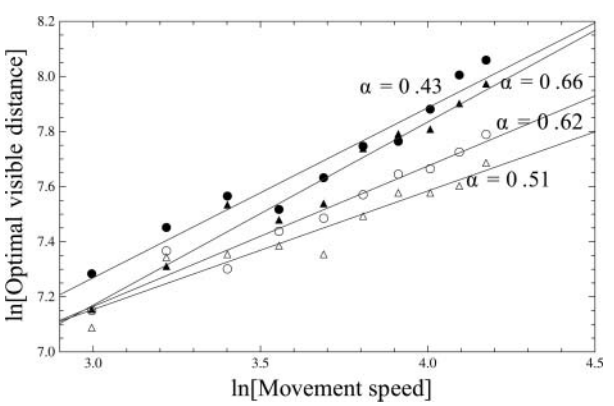

Fig. 4. Optimal visible distance versus movement speed. The horizontal axis is the logarithm of movement speed $\ln v$, and the vertical axis is the logarithm of optimal visible distance $\ln R_{opt}$. Different symbols indicate different sets of values for the number of food items f and the number of obstacles r. Other parameters: $c = 3$, $d = 5$. The slope of the regression line is denoted by α and is called the 'speed sensitivity'.

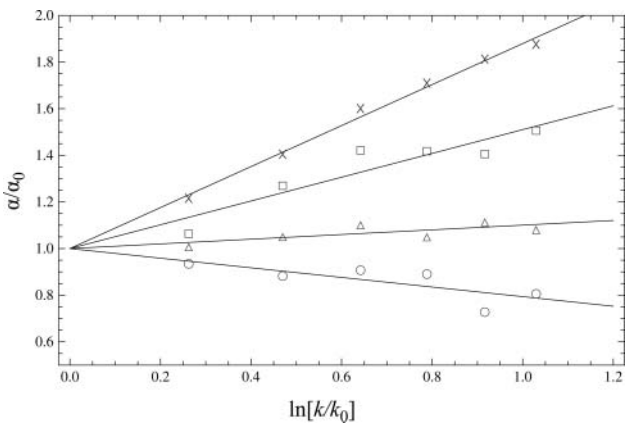

Fig. 5. Speed sensitivity α depends on four parameters (*r*, *f*, *c*, and *d*). We chose the standard values of parameters as follows: $f = 40$, $r = 20$, $c = 3$, and $d = 3$. We increased the four parameters (e.g. *k*) by multiplying them by 1.3, 1.6, 1.9, 2.1, 2.4, and 2.7, with the other parameters unchanged. The horizontal axis is the change in the logarithm of *k* (i.e. $\ln[k/k_0]$), and the vertical axis is the change in α (i.e. α/α_0). Different symbols represent different parameters that were changed: crosses represent the number of obstacles *r*; circles represent the number of food items *f*; triangles represent the cost of eyes *c*; and squares represent the damage caused by collisions *d*.

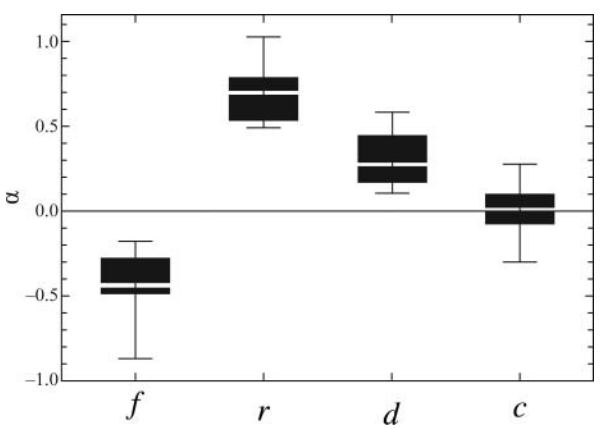

Fig. 6. Sensitivity of α for each parameter. We performed the analysis shown in Fig. 5 for 16 different parameter sets, generated by combinations of high and low values of four parameters (ranges differed by two-fold). Parameters: $f = 20$ and 40, $r = 10$ and 20, $c = 3$ and 6, $d = 3$ and 6.

The observed parameter dependence of α may depend on the choice of the standard set of parameters. To determine the variability of the slope for each parameter when the choice of the standard set of parameters changed, we performed a similar analysis for 16 different parameter sets, generated by considering high and low standard values for each parameter, the ranges of which differed by two-fold. We performed a sensitivity analysis for each of these 16 sets of parameters, as shown in Fig. 5. We then obtained the variability of the slope, namely the sensitivity of α to each parameter. Despite considerable variability in the slope, we never observed a change in the sign (see Fig. 6), which confirms that α

increased with the number of obstacles r and the collision damage d but decreased with the number of food items f. α was almost independent of the cost of eyes c.

Next, we performed a multivariate analysis to assess how α depends on the four parameters r, d, f, and c. It is important to note that interactions between different parameters are possible, which was excluded from the above analysis. We pooled all simulation α-values for different combinations of the four parameters and performed a regression analysis on $\ln r$, $\ln d$, $\ln f$, $\ln c$, and their combinations – for example, $(\ln r)(\ln d)$ or $(\ln r)(\ln f)$. This is a standard method for a generalized linear model (Kasuya, 2012). We then obtained the following regression formula, which excludes terms whose weights were not significant:

$$\alpha = 0.106 + 0.744 \ln r - 0.387 \ln f + 0.237 \ln d + 0.260 \ln r \ln d - 0.432 \ln r \ln f \quad (3)$$

The results again indicate that α depends on r, f, and d, but is independent of c. However, the interaction terms between $\ln d$ and $\ln r$ and between $\ln f$ and $\ln r$ were statistically significant. Therefore, we present parameter dependence as contour plots in Figs. 7 and 8. Figure 7 is a contour plot of α. The horizontal axis is the logarithm of the number of obstacles, and the vertical axis is the logarithm of the damage owing to collisions. This figure suggests that a large r and a large d result in larger α-values. Figure 8 includes two contour plots of α for f and r. The horizontal axis represents the logarithm of the number of obstacles, and the vertical axis the logarithm of the number of food items. From these results, we can conclude that large f (food abundance) and small r (obstacle density) result in smaller α-values.

DISCUSSION

Leuckart's law predicts that faster-moving animals tend to have larger eyes than slower-moving animals, because large eyes improve visual ability. Additionally, faster-moving animals need high visual acuity to avoid obstacles and to forage. Although this law seems plausible, the few empirical studies conducted to date have reached conflicting conclusions. In the present study, we examined the conditions under which Leuckart's law holds, i.e. when there is a strong correlation between the speed of movement of an animal and the optimal visible distance. We conducted computer simulations of an animal moving on a plane that contained many food items to consume as well as obstacles to avoid. After a sufficiently long simulation run, we obtained the number of food items consumed and the number of collisions with obstacles. The results confirmed that fast-moving animals need a long visible distance, whereas slow-moving animals need only a short visible distance. Because long visible distance is made possible by a large eye size (Land and Nilsson, 2012), these results suggest that faster-moving animals are likely to have larger eyes, supporting Leuckart's law. Walls (1942) stated that faster-moving animals have large eyes because of the need to avoid colliding with obstacles, whereas others have concluded that avoiding collisions and navigating food resources over greater distances are the mechanisms behind this law (Brooke *et al.*, 1999; Hall and Heesy, 2011; Heard-Booth and Kirk, 2012). Our theoretical analysis supports the argument that avoidance of obstacles and foraging for food items are the mechanisms behind Leuckart's law.

Next we examined the strength of the positive correlation between speed of movement and the advantage of a long visual distance. We obtained the optimal visual acuity based on the number of food items consumed by a moving animal, the number of obstacles with which it collides, and a small cost of visual acuity. The optimal visible distance tended to increase with movement speed, forming a linear relationship when plotted on a logarithmic

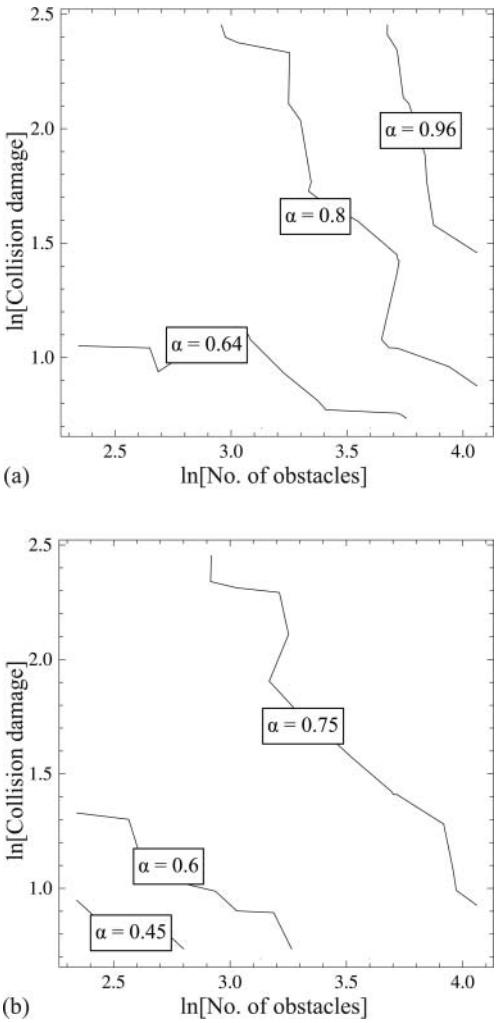

Fig. 7. Contour plot of speed sensitivity α. The horizontal axis is the logarithm of the number of obstacles (ln$r$), and the vertical axis is the logarithm of damage due to collisions (ln$d$). Other parameters: (a) $f = 30$, $c = 5$; (b) $f = 60$, $c = 5$. Contours that are not parallel to each other indicate an interaction between the two parameters.

scale. We denoted the slope of the linear regression as α, i.e. 'speed sensitivity'. We then examined the parameter dependence of α and found that a larger number of obstacles r and greater damage due to collisions d tend to see α increase, whereas a larger number of food items f tends to see α decrease. In contrast, α did not depend on the cost c of visual acuity.

Hall and Heesy (2011) measured the eye size and flight speed of birds directly and concluded that Leuckart's law does not hold for birds, whereas Heard-Booth and Kirk (2012) concluded that the law does hold for mammals. Our theoretical results suggest that birds have to navigate environments in which food availability is high and obstacles are relatively few, whereas mammals often live in environments with low food availability, many obstacles,

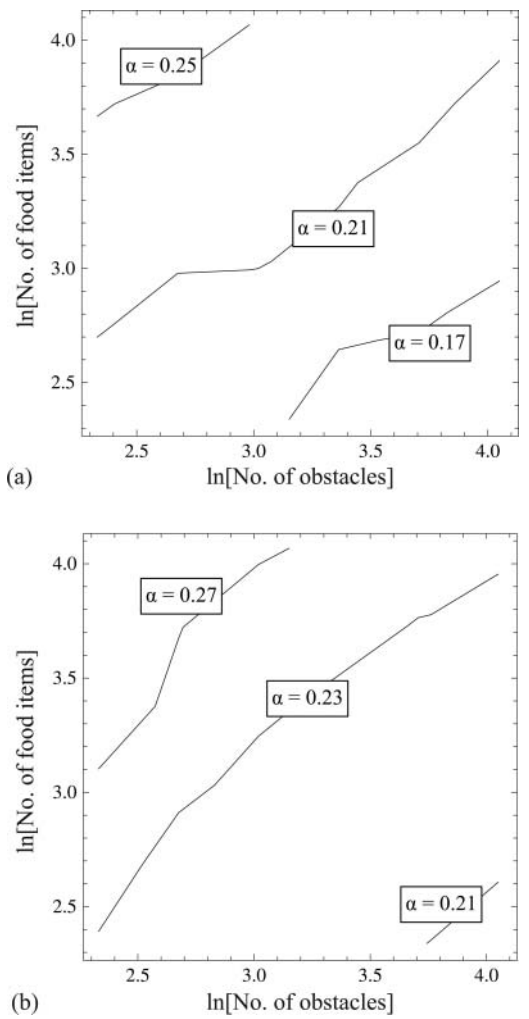

Fig. 8. Contour plot of speed sensitivity α. The horizontal axis is the logarithm of the number of obstacles (ln*r*), and the vertical axis is the logarithm of the number of food items (ln*f*). Other parameters: (a) $d = 2$, $c = 5$; (b) $d = 4$, $c = 5$.

and high levels of damage owing to collisions with obstacles. Determining the identity and numbers of specific obstacles or food items and collision damage for each species, however, would be difficult.

It should not be assumed, however, that the differences between the above two studies of Leuckart's law can be explained only by variation in the abundance of obstacles and food items, damage from collisions, and the cost of visual acuity, because eye size is likely to be determined by selection pressures and constraints other than those considered in the present study. Activity pattern is also an important determinant of eye size (Kay and Kirk, 2000; Garamszegi *et al.*, 2002; Kirk, 2006; Werner and Seifan, 2006; Hall and Ross, 2007; Hall, 2008). Although almost none of the birds analysed by Hall and Heesy (2011) were nocturnal, the dataset for mammals used by

Heard-Booth and Kirk (2012) included several types of activity patterns: diurnal, cathemeral, and nocturnal, an aspect we did not not address in the present analysis. Future simulations should also consider chasing prey versus foraging, or include more complex avoidance behaviours. However, to our knowledge, ours is the first study to consider theoretically the conditions pertinent to Leuckart's law, and we hope that our work will stimulate more theoretical research of the factors not addressed here, as well as empirical research focusing on other factors affecting eye size.

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