

# Visual perception and social foraging in birds

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**Birds gather information about their environment mainly through vision by scanning their surroundings. Many prevalent models of social foraging assume that foraging and scanning are mutually exclusive. Although this assumption is valid for birds with narrow visual fields, these models have also been applied to species with wide fields. In fact, available models do not make precise predictions for birds with large visual fields, in which the head-up, head-down dichotomy is not accurate and, moreover, do not consider the effects of detection distance and limited attention. Studies of how different types of visual information are acquired as a function of body posture and of how information flows within flocks offer new insights into the costs and benefits of living in groups.**

It is said that, when a physicist was asked to explain why a horse was not winning races, she started her reply with ‘Let’s assume that horses are spherical, have punctual mass, and can deliver infinite power...’. The point made by this joke also applies to theoretical behavioural ecology. Although simplification is essential in developing theory, it is also true that conclusions drawn from models can be highly sensitive to the very first assumptions made in their formulation and that, unfortunately, these assumptions are often not corroborated when models are tested empirically. Here, we discuss how details of visual perception in birds, including variability in visual fields, factors affecting visual acuity, and costs of visual attention affect the predictions and tests of social foraging theory. We argue merging research on social foraging and visual perception is necessary because inappropriate assumptions that are prevalent in the field limit the validity of empirical tests (Box 1).

Much foraging in birds is social [1], and foraging decisions in groups are affected not only by detection of food resources or potential predators by individuals, but also by the behaviour of conspecifics [2–7]. Compared with individuals foraging alone, group members can benefit and/or suffer from: (i) food being snatched by neighbours (scrounging); (ii) information about food location (local enhancement) and food quality (public information) being shared; (iii) foraging performance being hindered by others

(interference) or by the effects of others on food supply (pseudointerference); (iv) predator detection being enhanced by the vigilance of others (collective detection); (v) mortality per predator attack being diluted by the presence of conspecifics; and so on. For most birds, the information required to exploit these opportunities and/or minimize these costs is obtained mainly through vision and, hence, differences between visual systems generate differences in information gathering, which affects what we can infer about social foraging from behavioural observations.

A common theoretical assumption in many empirical studies is that feeding and SCANNING (see Glossary) are mutually exclusive activities that occur in head-down and head-up postures, respectively [8,9]. This mutual exclusivity influences both theoretical studies [10] and empirical research, because behaviour is categorized as being either foraging or scanning [11]. For predation, this implies a sharp tradeoff between foraging and safety from predators and, for foraging, a sharp compromise between attention to the substrate and to others, because intake can depend on searching by others [5]. Whereas ‘head up’ has a net feeding cost in predation models, it is part of a foraging strategy in social foraging models. However, both types of model assume that head up is a ‘scanning’ posture, opposite to the ‘head down’ posture of a bird exploiting the substrate. Recent evidence suggests that there is no such

## Box 1. The big picture

- Foraging animals use their senses to respond to food distribution and predator danger, and many forage in groups to deal appropriately with these needs.
- Social foragers receive information through their own monitoring of external events and through monitoring the behaviour of their neighbours.
- These different information inputs conflict with each other, and maximally efficient predator detection, food finding and neighbor monitoring are achieved by different body postures and head orientation.
- Current models rarely take into account that, to infer visual targets from body postures, it is necessary to consider the organization of vision, which can vary dramatically among species.
- We argue that specific features of visual systems should be incorporated into theoretical social foraging models and that doing so will change predictions and validate the use of behavioural observations as tests of functional hypotheses.

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## Glossary

**Scanning:** the process of gathering visual information about predators, conspecifics, resources (e.g. food), surroundings (e.g. distance to cover), and so on.

**Visual acuity:** the minimum angular separation between two points or objects in the visual field that are just perceived as distinct.

**Visual fields:** the limits of the space around an animal from which visual information can be obtained.

**Attention:** the mechanism that filters out stimuli perceived and processed by the central nervous system from moment to moment, so that only some of them modify later action.

all-or-nothing difference in information input between extreme body postures in many species of birds, and that the pattern of information gathering associated with body postures varies according to the visual system. Obviously, characteristics of the environment (e.g. tall grass or large boulders) also affect the amount and quality of visual information that is accessible in a particular body posture (e.g. head down), and thus would need to be taken into

account in specific studies. For the purposes of this discussion, we ignore this additional complication.

## Variability in avian visual systems and foraging in groups

In comparison to other vertebrates, avian eyes are relatively large in proportion to body size. This reflects the need of birds for higher acuity at longer focal distance and the resultant higher image magnification (Box 2). Assuming similar photoreceptor densities, VISUAL ACUITY increases with eye size, and eye size with body size [12,13]. Thus, larger species have a greater ability to identify objects at any given distance. Whereas osprey *Pandion haliaetus* can identify prey brought by conspecifics at a breeding colony from beyond 50 m [14], the smaller oystercatcher *Haematopus ostralegus*, with one-third of the body mass of an osprey, only gathers such information from a few metres away [15]. Information flow in foraging groups can differ greatly among species of different size [13]. Thus, the opportunity for local interactions, such as kleptoparasitism and local enhancement, probably scales allometrically. The positive correlation between body (and hence eye) size

## Box 2. Avian eyes

Avian eyes have a central MACULA with an associated FOVEA (see Box Glossary), which defines a visual axis for each eye. The eyes of most birds are aligned laterally, and each visual axis gives a lateral, or monocular, view (Figure 1, [44]). This lateral visual field serves to monitor predators and conspecifics, as well as to detect food at some distance [45,46]. Most birds also have a second retinal macula/fovea, located in the temporal retina [47], which increases the acuity of forward, frontal (in some cases binocular) vision, and provides vision relevant to handling food items (e.g. identification, position and speed of approach towards the target) as well as the control of pecking (Figure 1). Some ground-foraging birds have a localized myopia that represents an adaptive matching of the focal length of the temporal region of the eye to the eye-to-ground distance [48]. This probably enables the bird in a head-up position to maintain an in-focus panoramic view (e.g. looking for predators) whilst inspecting the ground for food. The cyclopean area is the combination of the frontal and lateral visual fields whose placement defines a blind area at the rear of the head (Figure 1).

Factors associated with variations in the size of the blind area might be the result of adaptations for selective pressures that are not necessarily related to social foraging. Species with large eyes (e.g. ostriches, eagles or albatrosses) have developed sunshade structures (e.g. eye-brows or eye lash-type feathering) and larger blind areas to minimize sunlight glare [49]. Large blind areas reduce the cyclopean field, which might be affordable in large species owing to their lower risk for predation. However, species with small eyes generally have smaller blind areas and larger cyclopean fields, because they are not so strongly affected by sunlight and need a wider visual field with which to detect predators [49]. Thus, differences in the size of visual fields seem to be determined by tradeoffs between high acuity, predator vulnerability and sensitivity to light.

Visual fields have recently been categorized into three types (Figure 1). An additional category corresponds to the combination of two basic classes [46].

## Box Glossary

**Macula:** thickened area of the retina with a high concentration of photoreceptors.

**Fovea:** a pit or thinning of the inner retina corresponding to the region of maximum visual acuity.

- Type 1 (Figure 1a). Visual guidance to food items taken in the bill (e.g. rock pigeon *Columba livia*, starling *Sturnus vulgaris* and cattle egret *Bubulcus ibis*)
- Type 2 (Figure 1b). Non-visual guidance to food items taken with the bill (e.g. Eurasian woodcock *Scolopax rusticola*, mallard *Anas platyrhynchos* and teal *Anas crecca*).
- Type 3 (Figure 1c). Non-visual guidance to food items taken with the feet (e.g. tawny owl *Strix aluco*).
- Combination of Types 1 and 3: similar to Type 1 in that individuals visually follow and take mobile prey; but prey is taken in the feet, which is akin to Type 3 (e.g. short-toed eagle *Circaetus gallicus*).

Figure modified with permission from [50].

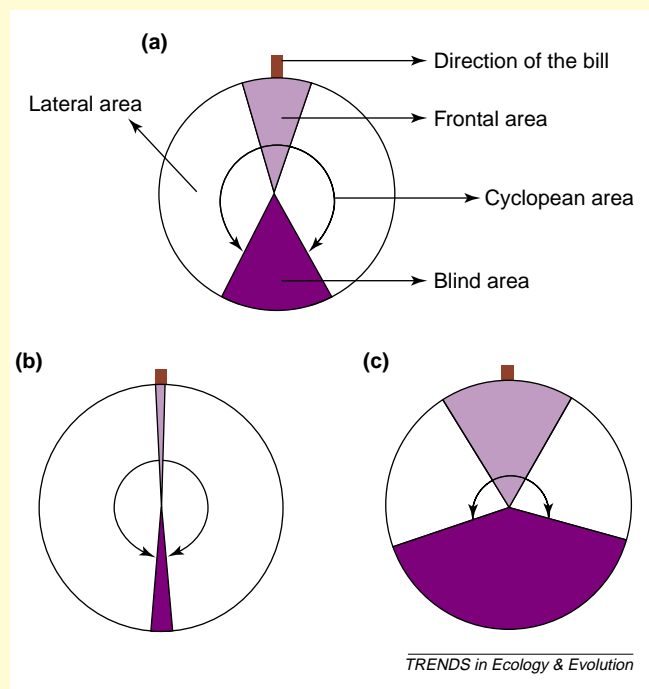


Figure 1.

and distance between conspecifics might be causally related to the ability to gather visual information, although this functional link has been relatively unexplored (Box 3).

The strength of competition in information gathering between body postures depends on the visual coverage from each posture, which, in turn, depends upon the design of VISUAL FIELDS. According to one recently published analysis, avian visual fields have been classified into three basic types according to the foraging ecology of the species (Type 1, Type 2, Type 3, and a combination of Type 1 and 3; Box 2). This classification scheme is a good starting point for assessing the effects of the extent of cyclopean visual fields and blind areas on information gathering in different body postures, and the implications for group foraging. Species with Type 2 visual fields (e.g. large cyclopean and very small blind area) face a small loss in detection ability when head down relative to head-up posture owing to the

### Box 3. The extent of information transfer in groups: flock size versus flock density

Social foraging research has often used group size as the critical independent factor for assessing the costs and benefits of living in groups. However, the flow of information (and hence the effects of the behaviour of conspecifics) will be stronger within the distances at which the visual system can distinguish different types of stimulus (e.g. the prey type caught by a neighbour or simply its body posture). This is related to eye size and the density of photoreceptors in the retina, which affects visual acuity. Therefore, group size without a quantitative measure of spatial structure is unlikely to characterize adequately the different behavioural mechanisms that occur in flocks.

Group size and group density are often confounded in modelling and empirical studies, but they have very different functional implications. For models of the dilution effect, the main issue is the number of subjects that are simultaneously exposed to attack by a predator; but for vigilance or food information transfer effects, the separation between adjacent flock members is important [2]. For instance, the chances of a foraging starling being kleptoparasitized might depend on the birds within a range of a few metres, irrespective of whether, beyond this area, the flock contains a dozen or a hundred individuals. Information transfer is expected to decrease nonlinearly with distance from neighbours, leading to the prediction that animals will reduce foraging time as the distance to neighbours increases to compensate for the loss of antipredator information [51,52]. The relatively scarce empirical evidence from natural circumstances that relates to this issue shows that: (i) redshanks *Tringa totanus* react later to the flushing behaviour of conspecifics upon a predator attack as distance to neighbours increases [53]; and (ii) head-up scanning in the teal *Anas crecca* increases with distance to neighbours, controlling statistically for group size [54].

Although group size can be considered a proxy for neighbour distance (if the area occupied by a flock does not change with variations in the number of group members), groups of similar sizes can and do vary in density. It is likely that neighbour distance is a more relevant factor to be predicted, manipulated and measured in the field than is group size. Individuals can control the distance to neighbours by aggression and attraction, responding flexibly to environmental, social and visual conditions, but group sizes might oscillate around the optimum, whereas density might be maintained [55,56]. Field studies reporting changes in foraging and scanning behaviour as a function of group size should include an assessment of flock area and/or density to rule out the effects of a decrease in information spread with increasing separation between flock mates. Comparative studies including several species with different degrees of visual acuity are necessary to understand fully the relationship between the distance at which information can be obtained and flock density.

nearly total visual coverage of their surroundings. Species with Type 1 visual fields (with somewhat larger blind area) probably experience greater loss of information when head down, but without compromising its acquisition entirely (Box 2). Recent research challenges the assumption of mutual exclusivity of visual coverage. This is illustrated by juncos *Junco hyemalis*, which, even when head down, can detect a predator model approaching, albeit less effectively than when in a head-up position [16]. In teals *Anas crecca* and shovelers *Ana clypeata*, head up is more frequent when feeding with eyes underwater than when foraging with the eyes above the water, suggesting that they scan during shallow but not during deep-water feeding [17]. Moreover, wigeons *Anas penelope* spend a larger proportion of their foraging time scanning (14.6%) than do shovelers (8.8%), and they also have a larger blind area [18]. This suggests that the size of the blind area constrains and correlates with the patterns of scanning behaviour, although more studies with larger sets of species are necessary. Consequently, in species with small blind areas, the transition between head up and head down is unlikely to eliminate visual coverage, in spite of what is usually assumed by many models. Instead, the loss of visual information might be positively related to the size of the blind area. This partial overlap in function implies a continuous rather than discrete tradeoff [16]. Species with Type 3 visual fields, along with species with a combination of Types 1 and 3 (Box 2), have larger blind areas that could significantly reduce, if not block completely, detection whilst head down and, hence, might match more closely the mutual exclusivity assumption.

Gathering visual information also entails ATTENTION COSTS. Paying attention to a difficult task in the frontal field (e.g. distinguishing between prey that are similar in size and colour) could limit performance in secondary tasks (e.g. processing information from the lateral fields about predators or conspecifics) [19]. Recent evidence from blue jays *Cyanocitta cristata* selecting virtual food items on a computer screen demonstrates that attention does bear a cost, affecting their ability to detect peripheral targets or two prey types simultaneously [20,21]. This suggests another interdependence: individuals performing a difficult food detection task might have a greater need to interrupt foraging to monitor predators. Attention costs might lead to the paradox that the more cryptic the prey, the higher the amount of time spent in the head-up position.

### Social foraging theory and the configuration of visual fields

Social foraging theory encompasses information-sharing (IS) and producer–scrounger (PS) models [22]. In IS models, individuals share finding successes; all search and, once a patch is found, the discoverer is joined by neighbours [23]. Groups find and deplete patches faster than do individuals, so that average intake might be unaffected. In PS models, some individuals (scroungers) forego searching to exploit others, so that less food is found overall [5,22]. These models are based on different assumptions regarding information flow: searching and exploiting others are mutually exclusive in PS but not in IS models.

Both local enhancement and scrounging do occur. However, the difference in intake consequences between PS and IS models poses difficulties for solving simultaneously the problems of stability of group size (which is mostly addressed in an IS context) and of equilibrium between producer and scrounger strategies within groups (which is mostly addressed by PS models). Realistic assumptions regarding information flows in different body postures would validate the use of one or other approach and increase testability.

A model by Vickery *et al.* [24] includes individuals that both search and exploit others, with parameters that might reflect the visual systems of different species. They examined within-group stability among three strategies: producers that consume only their own findings; scroungers that exploit the findings of others; and opportunists that do both with lower efficiency than either specialist.

We incorporated variation in visual fields into Vickery *et al.*'s model (Box 4), and calculated the proportion of

individuals in each strategy as a function of group size for divisible food patches (or patchily distributed food). Figure I in Box 4 shows that, for starling-like species (Type 1 visual field), there are many situations in which exclusive producers will not occur, so that the population includes many opportunists and fewer scroungers. For mallard-type birds (Type 2 visual field), only opportunists occur, and for eagle-type birds (Types 1 + 3 visual field), producers and opportunists coexist in small groups, whereas scroungers become commoner in larger groups, without producers being represented. The implication is that, in the last case, increases in group size considerably reduce per capita intake at equilibrium.

Although our example is only illustrative and ignores the problem of what determines group size, it indicates that visual specialisation can be an essential ingredient for making social foraging models testable. The stability predictions of Vickery *et al.*'s model suggest that considering only two mutually exclusive strategies (producer and

#### Box 4. Incorporating variability of visual fields into a producer–scrounger model

Vickery *et al.* [24] presented a model with three foraging strategies [producers, scroungers and opportunists (a combination of the first two)] that captures the tradeoff involved in being an opportunist in two parameters:  $c$  (relative producing ability) and  $h$  (relative scrounging ability), which are inversely related and represent the proportional searching ability that an opportunist experiences as compared with a producer and a scrounger, respectively. The intake rate of an opportunist is given by  $R_o = c * R_p + h * R_s$ , where  $0 \leq c, h \leq 1$ , and  $R_p$  and  $R_s$  are the intake rates of a producer and scrounger, respectively.

Three scenarios can be explored: (i) when improvements in the foraging performance of opportunists are compensated for by losses in the ability to exploit others ( $c + h = 1$ , 'perfect compensation'); (ii) when it is possible to do well at both food finding and sharing the success of others ( $c + h > 1$ , 'overcompensation'); and (iii) when any foraging effort implies a bigger loss in proportional ability to monitor others ( $c + h < 1$ , 'undercompensation'). Under these assumptions (and additional parameters), systems can be identified where the evolutionarily stable distribution of the strategies varies widely between extreme cases [24], from only opportunists being present at the point where all strategies achieve equal payoff to cases in which opportunists are completely excluded but producers and scroungers coexist.

Vickery *et al.* [24] emphasize the need for empirical tests of models to identify the values of the parameters that define how much monitoring ability is lost by engaging in food searching. In the case of estimating the parameters  $c$  and  $h$ , we suggest that a primary source of information might be the visual type of the species under study (Box 2). Comparing different group-foraging species, it seems justified to hypothesize that

species of Type 2, such as the mallard *Anas platyrhynchos*, can search for food and monitor conspecifics simultaneously with little loss of information; hence, their value of  $c + h$  should be large, perhaps close to the maximum of 2. Species of Type 1, with a rather large cyclopean area, such as the starling *Sturnus vulgaris*, will have lower but still considerable ability to do both things at once. Their  $c + h$  is likely to be (1, but considerably  $< 2$ ). Finally, species with a combination of Type 1 and 3 visual fields and that forage in groups but pursue mobile and evasive prey, such as bald eagles *Haliaeetus leucocephalus* (assuming they have visual field types similar to short-toed eagles *Circaetus gallicus*), will face a sharp tradeoff between their ability to find prey and monitor other foragers, and hence their  $c + h$  will be just above unity, representing an almost mutually exclusive choice (Figure I). To illustrate the expected differences in visual fields between species, we employed arbitrary values of  $c + h$  of 1.40, 1.95 and 1.05 for species in Type 1 ('starling'; Figure Ia), Type 2 ('mallard'; Figure Ib) and Type 1 + 3 ('eagle'; Figure Ic), respectively.

We computed and plotted evolutionarily stable proportions of the three strategies as a function of group size using the equations provided by Vickery *et al.* [24] (Figure I: solid line, producers; dashed line, scroungers, dotted line, opportunists). We used an arbitrary value of food distribution, which indicated the fraction of patch content shared between the finder and those who join it ( $\psi = 0.8$ ).  $\psi$  was defined as  $[(F - a)/F]$ ; where  $F$  is the number of items within a food clump;  $a$  is the number of food items consumed by a scrounger and/or opportunist in a food clump discovered by a producer or opportunist.

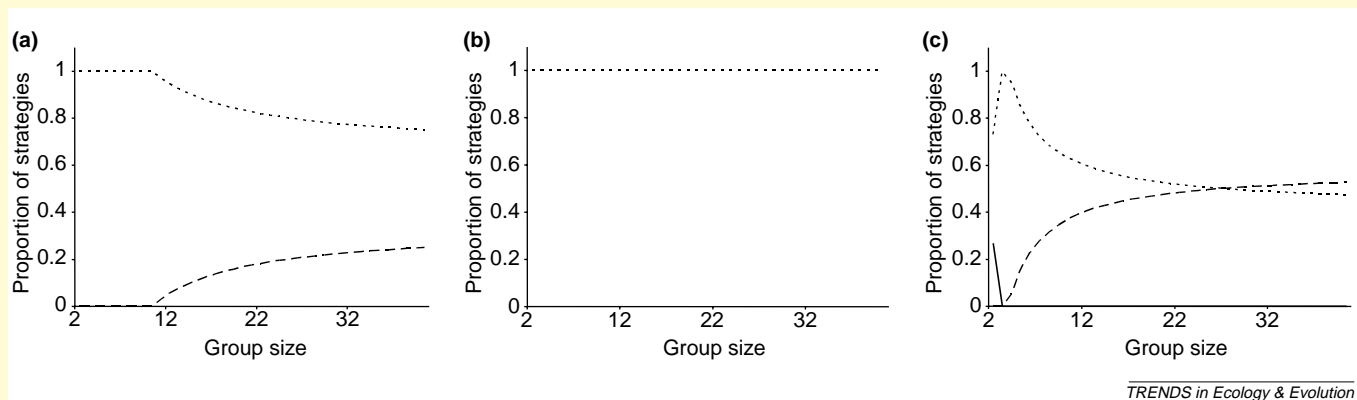


Figure I.

scrounger) lacks generality for species with ample visual coverage and that, when the mutual exclusivity assumption is relaxed, a third strategy (opportunist) could be common or even exclusive in species with partial (Type 1) and total (Type 2) visual coverage, respectively. Studies of how the proportion of different strategies respond dynamically to manipulations of group size and resource distribution in species with different visual configurations could eventually be grouped and subject to meta analyses so as to test the differential response to ecological conditions according to visual properties.

Even though we only assessed the effects of visual fields, other visual properties, such as visual acuity and limited attention, might affect the predictions of current models by generating independent effects or by interacting with the configuration of visual fields.

### Information transfer and body posture

Insights into interspecific differences in avian visual systems could help us to understand the extent to which birds monitor the behaviour of conspecifics. Some granivorous birds, for instance, appear not to monitor the level of vigilance of flock mates [25–27]. These species might benefit only from dilution effects or might not need to monitor the vigilant behaviour of conspecifics because of the large extent of their own visual fields to detect predators through personal detection [28] or through the escape behaviour of conspecifics [25,29,30]. Other birds do show conspicuous conspecific scanning in specific foraging situations [31,32]. For instance, in spice finches *Lonchura punctulata*, a higher frequency of hopping with the head up was associated with joining other individuals to share food patches; conversely, hopping with the head down increased the chances that individuals engaged in searching for food [33]. Although these studies confirm that information transfer does occur within flocks, we have little knowledge about the quality and quantity of information gathered by flock members.

Available studies are limited on at least two grounds. First, the assumption that conspecific scanning is costly because animals divert time from foraging to monitor the behaviour of conspecifics [9,34] is likely to be questionable under certain circumstances. For example, in birds with small blind areas, it seems reasonable to expect that individuals can scan to some extent whilst head down, thus reducing the overall need for head-up scanning [18]. A recent study shows that there is no obvious tradeoff between time devoted to personal foraging and time devoted to monitoring conspecifics for kleptoparasitism opportunities [35], but see [33]. In fact, it is possible that the lack of a negative relationship between group size and vigilance reflects the fact that, in some species, vigilance can be maintained whilst foraging with the head down.

Second, most studies measure the transmission of either predation or foraging information in situations that exclude one or the other, whereas, in natural conditions, both information categories might flow simultaneously and might be acquired (and passively emitted) by subjects showing the same body posture. Flock members probably need to interpret the significance of the posture of a neighbour according to context. For instance, if a bird that

is foraging head down sees a neighbour with its head up, it could interpret this as signalling by the neighbour that it is in a poor feeding patch and is therefore seeking an opportunity to scrounge, or that the neighbour has seen something suspicious and hence there is an increase in predation risk. Therefore, it is necessary to understand how different species decode and respond to information contained in the postures of others based on their visual systems. This also calls for the reassessment of the role of certain brain structures involved in the gathering and processing of social information (e.g. the neostriatum [36,37]) from a broader ecological perspective. Models should incorporate different types of information [38] and include decoding of the position of the observed animals: head up cannot be measured in the field by researchers and taken to mean a single thing to the receiving birds, because body postures have a range of completely different biological determinants.

### Conclusions

Considering the different visual constraints and capabilities of different bird species is particularly important for social foraging studies because of the central role of vision as the conduit for information flow among group members, whether this be about food location and/or predator attacks. The predictions of prevalent models of social foraging, which almost universally assume discontinuous variation in information input with body posture, are only applicable to species with narrow visual fields. They cannot be used to make precise predictions for large categories of social-foraging species that have wide visual coverage even when their heads are down. Another factor that might lead to interesting insights is that, because the ability to detect objects (prey, conspecifics or predators) as a function of distance scales allometrically, the interplay between the extent and the acuity of visual fields must modify the environmental and social determinants of group foraging. The properties of visual systems might also affect the ability to gather information relevant to group foraging in other taxa, such as mammals [11], and thus should be considered in theoretical and empirical studies of their behaviour, as we are suggesting for birds.

We call for a strong interaction between theoretical, experimental and comparative perspectives from different disciplines: behavioural ecology, sensory ecology, neurobiology and evolutionary biology (Box 5). One reason why oversimplified assumptions of social foraging models persist without challenge is that empirical studies tend to devote little attention to critical tests of the assumptions and, instead, focus on the predictions of the models (but see [4,10]). Because predictions are often qualitative and almost never unique to the specific model being discussed, prediction testing is only meaningful when the assumptions are corroborated. It is therefore important to incorporate general properties of the visual system into models of group foraging and, from empirical data, to estimate specific parameters relative to information gathering to generate more realistic predictions. Empirical studies also need to use the known properties of the visual systems of the species under consideration to avoid misleading interpretations.

### Box 5. Outstanding questions and problems

- How do visual adaptations affect the flow of social information within foraging flocks and how do differences in information quality (e.g. predation or foraging information) and quantity (e.g. number of flock mates per unit area from which information can be obtained) determine the interactions among social foragers?
- Because visual properties determine how the available visual information decreases with distance among flock mates, differences in inter-neighbour distances between species should be related to the interplay between visual systems and the foraging and vigilance demands imposed by their ecology [56]. This implies that there is an opportunity for comparative analyses linking specific visual systems to the degree of flock cohesion. An obvious prediction (if food abundance and distribution are controlled) would be for neighbour distance to increase (and flock density to decrease) with eye size.
- Antipredator- and foraging-oriented scanning both occur in bird flocks, but how does monitoring differ between species with different visual coverage? Species with wider visual fields might face smaller information tradeoffs between body positions and hence have very different head-up and head-down dynamics than do others with narrower fields. Wider visual fields might also entail several different kinds of cost. Perhaps the benefits of wider visual fields (increased detection abilities in different postures) are counterbalanced by the costs of allocating attention to different portions of the field. Studies comparing attention costs across species with different visual designs should shed some light on this question.
- Theoretical models of predation generally assume that predators are detected immediately after they emerge from cover [57], without consideration of the differences in detection latency among species. Interspecific differences in visual acuity and visual fields might generate corresponding differences in detection latencies for any within-flock information. Species with small eyes tend to have wide visual fields, but reduced acuity, properties that reduce the probability of early spotting of predators as they enter the danger zone for an individual. How do social species with small eyes cope with these sensory constraints? One strategy would be to increase flocking propensity to benefit from the dilution of risk, but, to our knowledge, no formal test of this has been conducted.

We need better measures of body postures and their significance. This can be accomplished by detailed analysis of head movements [39,40], which can vary in relation not only to the target of attention, but also with distance to the target [41]. Some studies have used head orientation as an adequate estimator of gaze; that is, where a bird is looking [42], because of the limited movements of avian eyes [43]. Manipulating visual obstructions [26,27,40] and neighbour distance [26] are valuable tools for assessing the quality and quantity of information passed under different circumstances. They can be combined with more detailed descriptions of scanning to create a finer picture of what information is there, what information is picked up and what receivers do with it. Finally, comparative analyses can help resolve evolutionary questions related to the association between design of sensory systems and social structure.

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