Invited Commentaries

Is information from both quality signaling and social recognition really redundant? A comment on Sheehan and Bergman

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Sheehan and Bergman (2016) have put together a thought-provoking and timely article on the importance of different types of assessment strategies in animals. They focus on quality signaling and social recognition and argue that there is an evolutionary trade-off between the two, in that those that have developed quality signaling have little need for social recognition and vice versa. Sheehan and Bergman have done a commendable job of reviewing an extensive literature to look for consistent themes to support their hypotheses and generate some clear testable predictions for future studies to address. Although we in general agree with much of what is written, we feel that some areas have been oversimplified and need further consideration.

IS INFORMATION FROM BOTH ASSESSMENT STRATEGIES REALLY REDUNDANT?

Sheehan and Bergman (2016) argue that quality signaling and social recognition trade-off against each other because they serve different functions: social recognition works well in small social groups but becomes more costly in larger networks of individuals. In contrast, quality signaling may not be required in small social groups because group members are so familiar with one another but is more useful when there are many individuals around. As such, Sheehan and Bergman argue information gained from both is redundant, not additive. We disagree with this. We do not see a situation where recognition does not provide additional information to quality signaling or vice versa. Without social recognition, inbreeding avoidance via familiarity may be a lot more difficult for example. Sheehan and Bergman use the example of dispersal to illustrate how the 2 assessment strategies cancel one another out. When individuals try to disperse, they argue that quality signals should be most relevant and social recognition not needed (as illustrated in Figure 3 of their article). We disagree: when individuals disperse, if they are seeking breeding opportunities not only would they want a good quality mate (quality signaling), but they may also want to avoid inbreeding (social recognition) as well as avoiding trying to disperse into areas containing socially dominant competitors (recognizing such competitors could come via quality signaling *and* social recognition). There is evidence in a number of species that inbreeding avoidance does

exist (Keller and Waller 2002), and we think it highly debatable that quality signaling would provide individuals with reliable information about the presence of relatives. If we consider an alternative scenario, where an individual is seeking to disperse, but not necessarily only for the purpose of a mate, it may be more likely to be accepted onto a territory by a relative than a nonrelative (nepotistic tolerance). In this scenario, both social recognition *and* quality signaling would be useful to dispersal decisions.

Although Sheehan and Bergman argue that stable social groups should rely on social recognition and not quality signaling, we argue that it is unlikely that quality signaling ever becomes obsolete. Stable social groups tend to be kin-structured, and mating opportunities will often lie in the wider population (Clutton-Brock 1989), and hence quality signaling would still be useful. The relative lack of physical ornaments in individuals that live in social groups does not suggest that signaling of quality is not happening. Quality signaling may be transmitted in a number of ways, such as signals that travel long distances (e.g., vocalizations) or persist in the environment (e.g., scent marks). Indeed, the discovery of the importance of UV coloration for signaling in Great Tits (*Parus major*, Sheldon et al. 1999) emphasizes how difficult it can sometimes be to readily detect and measure the quality signals that individuals may be giving one another.

Sheehan and Bergman acknowledge that there is unlikely to be complete trade-offs between the two, arguing that there are many cases that both assessment strategies are likely to be present in a species, and we agree. However, much of their opinion throughout the article focuses on the concept of one mode of assessment being redundant in the presence of the other. We suggest that although the 2 assessment strategies may provide different types of information, and one may be more useful in one context than another, they are not mutually exclusive: it is likely that both assessment strategies remain useful.

THE VALUE OF DIFFERENT TYPES OF INFORMATION

Throughout an animal's life, it acquires information about conspecifics that can be useful for decision making, including mate choice and rival assessment, the decision to collaborate with conspecifics, etc. Thus, different information is required for different contexts, and it is for that reason that we argue that both types of assessment strategies would prevail and that information provided by one is not redundant in the presence of the other. Social recognition can be useful for territory defense (the "dear enemy effect" for example, Temeles 1994) and decisions regarding who to cooperate/collaborate with. Quality signaling can be useful for mate assessment, rival assessment, and decisions of where to establish a territory. Both can be useful for dispersal and reproductive investment decisions (for identifying a

quality mate, finding collaborators that may help to raise young, and to avoid inbreeding). It is the final point, where *both* can be useful in the same context, that our opinion diverges most strongly from that of Sheehan and Bergman, who suggest that the targets of social recognition and quality signaling are likely to differ.

We have intensively studied a species for the last decade that employs both assessment strategies. Although this may bias our view, we believe this makes a good case study of why the 2 assessment strategies do not necessarily trade-off against one another. In the pied babbler (*Turdoides bicolor*), we have considerable evidence for social recognition (Humphries 2014). This fits with the hypothesis that Sheehan and Bergman acknowledge that species living in small stable social groups should develop social recognition (Tibbetts and Dale 2007). We also have considerable evidence for quality signaling. There is large individual variation in the male advertisement call in pied babblers, with the duration of the call correlated with male body mass and the likelihood of females responding (Humphries 2014; Ridley AR, unpublished data). Males typically bias the production of these calls toward extra-group females that are available to mate, further suggesting the use of the call as a quality signal (Humphries et al. 2015). Pied babblers therefore employ both assessment strategies on a regular basis, with the information in some cases being additive (using calling as a quality signal, but only directing it toward nonrelatives and extra-group females) rather than redundant. This is similar to that of the Harris' sparrow (*Zonotrichia querula*) originally mentioned by Rohwer (1982) in his theoretical development of badge stability, where although Harris' sparrows in large groups may find the use of a quality signal more reliable than in small groups, social recognition was still useful.

BEHAVIORAL PLASTICITY FAVORS THE RETENTION OF BOTH ASSESSMENT STRATEGIES

In a number of species, the formation and dissolution of social groups is fluid according to prevailing ecological and social conditions (e.g., Hatchwell et al. 2013). Under the predictions of Sheehan and Bergman (2016), this would therefore mean that the value of quality signals versus social recognition would vary over time. We agree that this could be true but argue that this means that the presence of either assessment strategy would not be selected against because both may become more or less important over time according to changing conditions. Take the example of the Seychelles warbler (*Acrocephalus sechellensis*, Komdeur 1992), which breeds cooperatively when the available habitat is saturated (favoring social recognition under Sheehan and Bergman's predictions) and breeds in pairs when the habitat is not saturated (favoring quality signals). Because the social system varies over time, this species should theoretically retain both assessment strategies, as should most species that facultatively form social groups.

In summary, we believe that Sheehan and Bergman have written a great article about a very important topic that will help direct researchers in the field, as well as acting as a catalyst to a lively debate. From our point of view, we believe that Sheehan and Bergman have oversimplified the relationship between the 2 assessment strategies. We emphasize that we believe the two can be additive. Social recognition, for example, could make quality signaling more effective because it allows a comparison between current and previous information

about the quality of a known individual. However, we agree wholeheartedly with Sheehan and Bergman that more rigorous and directed testing will help lead to useful information regarding the cost, use, and value of the assessment strategies employed by individuals, giving us greater evolutionary insight into signal selection.

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Quality signals may be common in species with social recognition: a comment on Sheehan and Bergman

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Sheehan and Bergman (2016) have crafted together an ambitious framework that addresses an area in dire need of attention: the nature of the interaction between social recognition and quality signaling. The perspective the authors take is broad—social recognition includes individual and class-level recognition, and quality signaling includes all forms of putatively costly signals used in, but not limited to, rival assessment and mate choice. Citing primates and corvids as model systems, the authors argue that "few quality signals have been reported from groups that tend to rely on individual recognition." Sheehan and Bergman (2016) have a lot riding on this assertion because they go to great length at providing a theoretical framework to explain it.