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of the call correlated with male body mass and the likelihood of females responding (Humphries 2014; Ridley AR, unpublished data).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’ sparrow’s 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.

**REFERENCES**


**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.
Indeed, they formalized this idea into their “prediction 2”: small stable societies should lack quality signals. Though they point out that robust phylogenetic comparative studies that directly address this prediction have not been conducted, they cite Bridge et al.'s (2008) study on *Aphelocoma* scrub-jays as a source of indirect support. In this study, sex- and age-related color differences were not associated with cooperative breeding. A problem with this argument, however, is that using the presence of sex- or age-dependent plumage coloration as a proxy for signaling is tenuous. Sexual dichromatism, for instance, could be reduced in cooperative breeders either because 1) quality signaling is less important in such systems (as argued by Sheehan and Bergman) or 2) quality signaling is still important in such systems and both males and females have evolved it (counter to Sheehan and Bergman).

We can discriminate between these 2 possibilities. Sheehan and Bergman’s hypothesis predicts that reduced sexual dichromatism in cooperative breeders arises through males evolving less elaborate ornamentation. The alternative predicts that reduced sexual dichromatism in cooperative breeders evolves through females getting more elaborate. Rubenstein and Lovette (2009) have tested this in the African starlings and their results were clear: sexual dichromatism was reduced in cooperative breeders (as in the scrub-jays) and this was the outcome of females evolving increased ornamentation in such species. Rubenstein and Lovette (2009) interpret their results as evidence for “increased selection on females for traits that increase access to reproductive opportunities, other resources, or higher social status.” Under Sheehan and Bergman’s framework, such traits would not be necessary because social recognition in these small stable societies should suffice.

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Received 27 August 2015; accepted 29 August 2015; Advance Access publication 24 September 2015.

doi:10.1093/beheco/arv138

Editor-in-Chief: Leigh Simmons

**REFERENCES**


**The evolution of signaling complexity: a comment on Sheehan and Bergman**

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Two questions should be asked of a novel theoretical framework: first, is the argument sound? Second, what are the potential implications or applications? As to the first, Sheehan and Bergman (2016) make a compelling case for an evolutionary antagonism between quality signaling and social recognition, such that mechanisms for assessing groupmates evolve either toward advertising quality or toward the capacity to disseminate and process highly variable information.

The interesting question then becomes how and where best to apply the framework. The authors propose that small-scale societies should evolve toward monitoring variable, rich social information, and large aggregations toward badges or other easily recognized signals of quality.

Yet Sheehan and Bergman also acknowledge that complex social systems often feature both mechanisms. We suggest, therefore, that a productive application may not be comparing between species, rather starting by evaluating signaling strategies within species. There should be a differentiation in strategies between interactions with close associates versus those with unfamiliar, or infrequently encountered, social partners. Using such an approach, this framework may also provide a resolution to outstanding questions about the relationship between social, communicative, and cognitive complexity.

Multilevel animal societies with differentiated relationships are precisely the kinds of systems that should possess multimodal communication using both variable and quality signals. Individuals that move between smaller stable groups might rely on social recognition to navigate their close-knit networks, while individuals in larger populations may use quality signals to identify familiar members of the larger population. Harem-forming equids and primates, such as plains zebra and gelada baboons, are characterized by small, stable reproductive units that regularly coalesce with other harems and groups of bachelor males into larger aggregations. Although harem membership is stable over multiple years, males move in and out of bachelor status and can form affiliative relationships with other males. In light of the proposed framework, the component elements of staged signaling contests may be better understood as distinct evolved strategies for providing different types of information, rather than simply as escalations on a gradient of intensity, as has been previously suggested. In male–male signaling contests among feral horses (Rubenstein and Hack 1992), olfactory signals reinforce social knowledge about more stable traits related to individual identity, fitness, and dominance, whereas acoustic signals provide timely new information about more transient qualities such as the current motivational state. Similarly, the disproportionate participation in contest signaling by closely ranked competitive dyads—as in chacma baboons (Kitchen et al. 2003)—may reflect the different affordances of social recognition and signal assessment. Quality signaling refined by abundant social information may provide the most precise temperature-tapping between known individuals. When social recognition helps me identify my closest rivals, signals will be the lowest-cost strategy for gauging their formidable right now.

Longer-term movement between social groups is another example where individuals might shift between social recognition to badges or other quality signals. Dispersing individuals, particularly males, must navigate new networks and hierarchies across 1 or more dispersal events and encounter high levels of intrasexual competition with unknown adversaries. Where females forgo dispersal, they remain in stable social units wherein social information is abundant and strictly attended to. Thus, we would expect differentiated signaling between males and females, with the former engaging more in quality advertisement. Spotted hyena clans provide an example of differentiated signaling as males far outstrip females in producing the hypothesized “display” variant of the long-distance whoop vocalization (East and Hofer 1991). Although this signal serves