multiple functions in hyena social life (including recruitment to resource defense and mother-cub contact communication), males are more likely to whoop spontaneously, perhaps because this individually recognizable call allows them to advertise quality to potential mates or rivals. Moreover, similar male long-distance vocalizations signaling quality is seen in male, but not in female primates.

Understanding how individuals partition and differentiate signaling leads to questions about signaling complexity between social systems. We predict that multilevel societies require a suite of finely tuned social information deployed in regular social interactions together with quality signals for infrequent social interactions. We would also suggest that rather than individual recognition imposing cognitive costs, it is coordination and decision making across multiple modalities. Animals that are not typically considered cognitively complex can excel at recognizing individuals (reviewed by Tibbetts and Dale 2007), whereas solving group coordination and consensus decision-making problems are computationally expensive (David-Barrett and Dunbar 2013). These costs should be exacerbated where individuals must process information from disparate sources (e.g., kinship group membership, physical condition, dominance rank, reproductive state, motivation).

The argument for multimodal complex signaling may best be evidenced by humans. We rely heavily on both quality and individually recognizable signals. In the Western World, quality signals include the cars we drive, the phones we use, the houses we occupy, and the clothes we wear, which all convey salient information about economic resource holding potential and social class/group identity. However, humans also have a remarkable ability to remember individuals and to use social information to maintain relationships despite temporal and spatial absences.

**FUNDING**

S.S. is supported by a Royal Society University Research Fellowship (UF110641). A.G. is funded by the Princeton Class of 1877 Biology Fund.

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Received 5 August 2015; accepted 6 August 2015; Advance Access publication 23 September 2015.

doi:10.1093/beheco/arv155

**Editor-in-Chief:** Leigh Simmons

**REFERENCES**


**Understanding antagonism: a comment on Sheehan and Bergman**

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Sheehan and Bergman (2016) point to Rohwer’s (1982) classic paper as the source of their central insight regarding antagonistic evolution stating that “to our knowledge, he was the first to propose that social recognition may limit the evolution of a quality signal by eliminating the need for a signal in certain social systems.” Although this may not have been the authors’ intent, this phrasing generates the impression that badges of status are some kind of “default setting” and the possibility for social recognition thus “prevents” such signals from evolving, whereas, as originally formulated, and as Sheehan and Bergman (2016) themselves report, the argument is that, when group size is small and social recognition sufficient, badges of status are simply not advantageous. When put this way, it all seems much less antagonistic. To be fair, the authors state explicitly that limitation occurs through the “elimination of need” but, again, this phrasing suggests the presence of something that was subsequently removed. Rohwer’s (1982) argument can equally well be interpreted to mean simply a complete absence of need, and not its elimination. This is a small and trivial point, but the phrasing does help generate the impression that antagonism is central and important, but perhaps this needs more elaboration for why this should be the case.

We have 2 further issues for the authors’ consideration, as we are interested to know whether and how these fit into their proposed framework. First, Butynski et al. (1992) reported on the “pyow” calls of male blue monkeys. They found that these were individually recognizable and that the calls of the resident male in one of their study groups remained stable over a 10-year period. They concluded that “[a]coustic analysis of pyow calls may provide a relatively easy and reliable method to document tenure lengths of adult male blue monkeys resident in groups.” (p. 183). Given that the ability to hold tenure in a 1-male group arguably qualifies as a measure of male quality, does this mean that pyow calls are badges of status? If so, given that they can also be used as an indicator of tenure length, do such calls qualify as a measure of social knowledge combined with a badge of status?

Second, resident blue monkeys and vervet monkeys both experience seasonal influxes of novel males during the breeding season. Hence, both species have to deal with unfamiliar conspecifics. This suggests badges of status should evolve (and this much is suggested by Bergman and Sheehan 2013, with respect to vervet monkeys). For the rest of the year, blue monkeys live in 1-male groups, and vervets live in multimale groups. Generally speaking, then, only novel males have to deal with both unfamiliar and familiar males regularly (although presumably male blue monkeys have some familiarity with floating males in the population [Henzi and Lawes 1987]). Vervet monkeys possess distinctively colored genitalia that may function as badges of status (Bergman and Sheehan 2013), but blue monkeys apparently do not (unless one considers “pyow” calls to be badges of status, as suggested above, but as these are individually distinctive they could also fall under signals of identity, according to the authors’ scheme). The question then is, why does the species that would seem to have a greater need for, and would
benefit from, social knowledge also have the more overt badge of status, if social knowledge limits quality signal evolution? If the answer is that there is no requirement for social knowledge and quality signals to be antagonistic in this sense, why are social knowledge and signal quality presented as somehow imposing limits on each other? These questions are not intended as refutations, nor do we have the answers, but we consider them sufficiently interesting to raise and would be interested to know the authors’ views.

FUNDING
L.B. is funded by the NSERC Canada Chairs Program and Discovery Grants program, and NRF (South Africa). S.P.H. is funded by the NSERC Discovery Grants Program and NRF (South Africa).

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Received 10 October 2015; accepted 11 October 2015; Advance Access publication 28 October 2015.

doi:10.1093/beheco/arv179

Editor-in-Chief: Leigh Simmons

REFERENCES

A quality signaling–recognition trade-off at the level of the type of interaction not species: a response to comments on Sheehan and Bergman

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Our goal was to stimulate interest in the relationship between different forms of assessment so we are grateful for the thought-provoking responses. One point that needs re-emphasis is our explicit statement that the antagonism between quality signals and social recognition does not occur at the level of the species—this is obviously false—but rather at the level of the type of interaction (Sheehan and Bergman 2016). For example, male vervets regularly interact with familiar and unfamiliar males, 2 distinct contexts, which likely explains the presence of male quality signals in this species that otherwise depends largely on social recognition (Barrett and Henzi 2016). Similarly, as Ridley et al.’s (2016) pied babbler example indicates, animals may use social recognition when interacting within their group but use signals when interacting outside of their group. Indeed, recent comparative work in howler monkeys shows the greater utility of quality signaling when competing with extragroup individuals (Dunn et al. 2016), a finding that fits nicely with our proposal. Thus, we support Shultz and Gersick’s (2016) point that many species have interactions at different levels of society and more complex, multi-level societies provide a useful paradigm for testing our framework by comparing strategies across contexts. We are not arguing that species use only one strategy or the other, rather our prediction is that they will not use both quality signals and social recognition in the same interaction context. If they do, this is because either 1) the trait being signaled (e.g., intent or fertility) is too unstable to assess from social recognition and, consequently, the signal is not a quality signal, 2) it is an evolutionarily unstable situation and eventually the use of assessment strategy will prevail, or 3) there is a “spill-over” effect of a signal (or social recognition) that is maintained by selection in a different context. Although the last point may sound like bet-hedging, we merely acknowledge that if the costs of one strategy have already been paid, this may overcome the reduction in benefit (due to information redundancy) of that strategy in a different context. The reduction in benefit, and hence the evolutionary antagonism, still exists. Thus, our answer to Barrett and Henzi’s (2016) question about whether the interaction between quality signaling and social recognition is really antagonistic is yes. It is not simply the case that quality signals are inherently less useful in small social groups. Rather, quality signals are less useful in smaller groups because of the greater utility of social recognition in such scenarios. Social recognition reduces the benefits of quality signals and vice versa.

Barrett and Henzi (2016) ask about the classification of individually distinctive blue monkey pyow calls that can be used to assess breeding male tenure length. Although tenure can be inferred by long-term monitoring of pyows, the structure of pyow calls does not provide information that predicts male tenure. Quality signals allow individuals to assess quality from a single interaction or observation, which is not true of pyows.

Ridley et al. (2016) suggest that animals may want to simultaneously use both assessment strategies to assess quality and kinship. Although we agree that both of these types of information are useful, kinship is not a property of an individual but rather a relationship between individuals and is orthogonal to individual quality and therefore outside of the scope of our proposal. However, our framework does suggest that the scenario proposed by Ridley et al. (2016) (i.e., a dispersing individual assesses individuals in other groups based on quality signals but also knows their kinship status based on previous experience) is unlikely to ever occur. If the dispersers only assess familiar individuals, we would not expect a quality signal to be present and if potential mates/allies are unfamiliar, kinship could only be assessed based on phenotypic cues (not recognition).

One prediction of a quality signaling–social recognition trade-off is that species living in small stable groups should tend to invest less or lack quality signals because many of their interactions occur with known individuals compared to related taxa with larger social groups or frequent encounters with unfamiliar individuals. To support this argument, we pointed to cooperative jays in the genus Aphelocoma, which show lower levels of plumage variation than noncooperative species (Bridge et al. 2000). Recently, a new paper examining badges of status in primates demonstrates that badges evolve in larger social groups where individual recognition