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.

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**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, multilevel 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 are already 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...
is difficult (Grueter et al. 2015), providing further support for our argument. Dale (2016) correctly points out that dimorphism is only a proxy for signaling traits as not all quality signaling traits are dimorphic and not all dimorphism is a signal of quality. Specifically, he notes a lack of plumage dimorphism could result from the presence of signals in both sexes rather than an absence of quality signaling in either sex. We agree with this statement. Dale (2016) offers the example of plumage monomorphism in cooperative African starlings as a result of females evolving bright feathers similar to males (Rubenstein and Lovette 2009). However, we do not know if there is elevated variation in plumage coloration in either males or females of these species (much less whether the starlings attend to this variation) as would be expected in a quality-signaling situation. Although we feel that Dale’s interpretation of the starling plumage data is somewhat premature, we agree that robust tests of this framework need to actually test for the phenotypic indicators of quality signals, rather than relying on the poor proxy of sexual dimorphism or the presumed ornamental value of plumage or other traits.

Shultz and Gersick (2016) also suggest that for less stable traits, signals can “refine” social information suggesting a more complementary relationship. We agree, as social recognition is only useful for traits that remain stable across interactions (see Figure 1 in Sheehan and Bergman 2016). In Bergman and Sheehan (2013), we elaborate on the use of signals in relation to less stable phenomena (e.g., signals of intent or fertility), but these are not signals of quality, the only types of signals that we expect to trade-off with social recognition.

Finally, Shultz and Gersick (2016) propose that the costs of recognition per se are minimal and that keeping track of and integrating information about individuals from disparate contexts are costly. We agree that integrating information across contexts is likely to be more complex and taxing, though it is important to note that this can only happen via social recognition. If a species relies solely on quality signaling, by default animals would not be tracking individuals across multiple contexts as they would not invest in learning about and remembering others. Explaining the distribution of signaling and social cognition across animals remains a major challenge for behavioral ecologists. We look forward to future theoretical and empirical work at the interface of signaling and recognition.

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