A testable definition of individual recognition

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In their letter [1], Steiger and Müller propose a definition of individual recognition (IR) that differs from the definition used in our review [2]. The difference between our definition of IR and the definition proposed by Steiger and Müller [1] can be highlighted using Sherman *et al.*'s [3] recognition framework. Sherman *et al.* [3] suggest that recognition involves (i) cue production by the signaller, (ii) cue perception and template matching by the receiver and (iii) a behavioural response by the receiver. We [2] defined IR as occurring when cue, template and response are all individual specific. Steiger and Müller [1] posit that IR occurs whenever the cue and the template are individual specific. In contrast to our view, they suggest that individual-specific receiver responses are not a requirement for IR.

Our definition of IR matches definitions used in previous IR research [4–7], and it includes the range of behaviours described in our original review. Our definition encompasses all situations where receivers learn the unique cues of one individual and treat that individual differently from others. For example, *Polistes fuscatus* wasps fit our criteria for IR because they have unique facial features and a linear dominance hierarchy where particular individuals are treated differently based on their specific position in the hierarchy [8].

Contrary to Steiger and Müller's [1] assertion, monogamous mate recognition and offspring recognition in species with a single offspring fit our criteria for IR.

Although some previous researchers have suggested that 'true' IR requires receivers to learn more than one different individual [9,10], we do not define IR based on the number of individuals learned. As such, monogamous mate recognition is compatible with our definition of IR because receivers treat their own mate uniquely. Mate recognition would only be considered class-level recognition if receivers treat multiple individuals like their mate. Similarly, offspring recognition in species with a single offspring (e.g. emperor penguins *Aptenodytes forsteri*, free-tailed bats *Tadarida brasiliensis*) is IR because parents learn the unique features of their offspring and treat that individual differently from all others. Therefore, we believe these examples should be unambiguously considered individual recognition.

A major challenge of Steiger and Müller's definition of IR is that it is impractical to empirically test. In fact, it might not be possible to determine whether cue and template are unique *without* considering the behavioural response of the receiver. Cues that appear individually distinctive to researchers might not be perceived as unique by the receiver's sensory system. Cues that are perceived as unique by the receiver's sensory system might not be used for recognition decisions. Even if unique cues are involved with recognition, the receiver's template might be generalised rather than individual specific. For example, the acoustic structure of meerkat (*Suricata suricatta*) alarm calls suggests the calls are individually distinctive, but meerkats do not appear to distinguish among individual calls [11]. Of course, the absence of a unique receiver response does not rule out the possibility that meerkats can perceive the differences among calls or that receivers have individual-specific recognition templates. Unfortunately, it simply is not possible to test the specificity of the template without a unique behavioural response.

References

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