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The point of the triangle and utility of repeated measures: a response to comments on Chapin et al

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of assessment mechanisms. After many decades of modeling, game theory has not delivered this richer set of models, but it remains a worthy challenge.

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The point of the triangle and utility of repeated measures: a response to comments on Chapin et al.

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We appreciate the diversity of commentaries on our recent review on animal contests (Chapin et al. 2019). Here we respond to some key points to highlight how our suggested approach could be used. In summary, we suggested that: 1) variation in information use might be continuous, in contrast to the usual mutual assessment versus self-assessment dichotomy, 2) individuals in a population might vary in how they use information, 3) if we include information about resource value that an individual has access to, we can represent these continua in a ternary plot. Finally, 4) we suggested an experimental design based on repeated fights that could reveal individual-level variation in information use.

Our central suggestion is that individual-level variation in contest assessment strategies might be present in wild populations. Given other contexts in which information use is known to vary across individuals, it seems entirely possible that the same might be true of contest behavior though empirical evidence is needed to test this idea. We agree that imperfect decision making may affect the assignment of individual-level assessment strategies (Elwood 2019). However, as we suggested, one could first test if there is individual-level variation in a population (Chapin et al. 2019) before proceeding with tests focused on individual strategies. In case individual-level assessment strategies are determined, additional tests, such as analysis of contest dynamics, may be carried out to establish if a given model (e.g., cumulative assessment, sequential assessment) explains how individuals make decisions during the contest.

The ternary plot can be used to classify contests in two senses: to show where current theoretical models (focusing on those frequently tested in experiments) sit and relate to each other (Chapin et al. 2019), and to classify empirical data obtained from real fights. We agree with Parker (2019) that resource value comprises both objective and subjective components and that the latter may differ between opponents. However, the ternary plot represents information use by focal individuals so should only include one axis for RV, representing focal RV assessment. Elwood (2019) suggested that opponent only assessment (OA-only) is unlikely in real systems. There is some initial evidence for OA-only (or predominant) assessment but the possibility also remains largely unstudied. Furthermore, OA-only provides a necessary theoretical extreme and allows for a framework that presents mutual assessment as occurring on a spectrum along which the proportions of information on self and opponent RHP vary.

We note that many studies involving repeated contests have overcome the potential ethical and logistical issues voiced by Elwood (2019), and suitable data might even exist already (Kasumovic 2019). Indeed, research on animal personality and behavioral syndromes holds repeated trials as a critical step in understanding individual-level variation (Bell et al. 2009). Further, additional variables like winner-loser effects or delays between fights, for example, could be incorporated into random regression models (Chapin et al. 2019; Reichert 2019) as covariates. We agree that error in the data will make patterns harder to uncover, but this is true for any experiment.

Mesterton-Gibbons (2019) highlighted the importance of consistent terminology. Extremes on the ternary plot represent "pure" strategies in that individuals only use one information source (self resource holding potential, opponent resource holding potential, or resource value). This phrasing has been used elsewhere (e.g., Arnott and Elwood 2009), but we agree that the term "pure" had already been used in the sense of a pure evolutionarily stable strategy. Perhaps describing the extremes as OA-only, SA-only, and RV-only would be an alternative.

We reiterate that the Taylor–Elwood approach is useful, but we agree that most things in biology are more complicated than they first appear (Leimar 2019; Parker 2019). We hope that our approach can be used to reveal new information about fighting, even if we might have to wait (Leimar 2019; Parker 2019) for theory to catch up with the data (Mesterton-Gibbons 2019). Investigating individual-level assessment strategies could further elucidate the complexity, plasticity, and evolution of animal contests. Taken together, our review and the commentaries highlight the need for research that

integrates theoretical models with richer empirical data to understand animal contests. Although there might be challenges, we feel that such studies would be well worth undertaking.

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