



Commentary

Using ternary plots to investigate continuous variation in animal contest strategies

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Studies on the strategic rules used by fighting animals usually attempt to categorize fights as falling into one of two discrete types: self-assessment and mutual assessment. With self-assessment, losers give up when they cross an individual costs threshold, without reference to the fighting ability (resource-holding potential, RHP) of their opponent, while in mutual assessment, losers compare their own RHP to that of their opponent and give up if and when they determine themselves to be the weaker rival. However, it has recently been suggested that this discontinuous view of variation in assessment strategy might be an oversimplification. This is because use of information on self-RHP, opponent RHP and resource value is likely to show continuous variation across individuals, populations and species. While the possibility of this continuous variation is often ignored, we suggest that we can gain a better understanding of decision making during fights by considering the relative contributions of these three information sources to the giving-up decisions of losers. Here, we use ternary plots to demonstrate how the relative contribution of self-RHP, opponent RHP and resource value to decision rules can be illustrated using simulated and real contest data, as an aid to achieving greater depth in discussions of variation in assessment rules.

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A prevailing question about animal contests is what strategies animals should use to determine when to give up a fight. This decision is made by the loser and key assumptions about the sources of information that contribute to this decision underpin theoretical models of animal contests (Arnott & Elwood, 2009). In a broad sense, these models assume that losers arrive at their decision to give up in one of two ways: self-assessment (SA) or mutual assessment (MA). In models based on an assumption of SA (Mesterton-Gibbons & Heap, 2014; Payne, 1998; Payne & Pagel, 1997), losers base their giving-up decisions on information about their own resource-holding potential (henceforth 'self-RHP'). Here each individual has a maximum cost threshold, and the first individual to cross its own threshold (due to depletion of energy, accumulated injuries or simply time budget constraints) will withdraw and lose the fight. Thus, the maximum cost threshold of an individual (i.e. the individual's capacity to allocate expenditure to the fight) is equivalent to its RHP (but see below for the effects of

resource value, RV). In contrast, in models founded on an assumption of MA, the loser will base its decision on the RHP asymmetry between itself and its opponent, that is, through comparing information about self-RHP with information that it has either gleaned about the RHP of its opponent during the fight (Enquist & Leimar, 1983; Enquist, Leimar, Ljungberg, Mallner, & Segerdahl, 1990; Hammerstein & Parker, 1982; Parker & Rubenstein, 1981) or inferred by relation to RHP distribution across the population (Mesterton-Gibbons, Marden, & Dugatkin, 1996; henceforth 'opponent RHP' in both cases). Therefore, under MA, if an individual determines that its opponent can bear greater costs (e.g. allocate more energy, cope with more injuries) than itself, it can give up the contest before reaching its own cost threshold. For both SA and MA the individual threshold of costs or the estimated RHP differential that triggers a giving-up decision might be adjusted based on a third parameter, the value that the individual places on the contested resource (RV) (Arnott & Elwood, 2008). The higher the RV, the more motivated an individual is to continue fighting and therefore the higher the cost threshold that it is willing to reach before giving up the contest. Note that an individual's absolute maximum ability to pay costs is fixed, but the

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cost threshold an individual is willing to fight to may decrease if the resource in question is of relatively low value.

One approach commonly used to investigate whether strategic decisions made by losers are best categorized as being based on SA or MA involves testing for correlations between contest duration and traits linked to RHP (Taylor & Elwood, 2003). Although there are some limitations on the interpretation of these analyses (for example, in fights where injuries are important: Briffa & Elwood, 2009; where defences and weaponry grow at different rates: Palaoro & Briffa, 2017; or where assessment rules vary within populations: Chapin, Peixoto, & Briffa, 2019a), the basic procedure is as follows. Absolute measures of winner and loser RHP are included as predictors in a model where duration (the time from the onset of fighting until the point at which the loser makes a clear decision to withdraw) is the response variable (but see McGinley, Prenter, & Taylor, 2015 for an alternative approach). In the case of SA, only loser RHP should be important, with contests lasting longer for losers with higher RHP values. In the case of MA, we should still see this positive correlation between loser RHP and duration but there should also be a negative correlation between winner RHP and duration, since losers should discover that they are the weaker opponent more quickly when the disparity between self-RHP and opponent RHP is high.

Based on the approach proposed by Taylor and Elwood (2003), much empirical testing of assessment rules has categorized fights as being resolved on the basis of either SA or MA (Pinto, Palaoro, & Peixoto, 2019). However, although this broadscale binary classification (SA or MA) of contest data is conceptually useful because the MA–SA dichotomy underpins current theory, it is also a relatively blunt tool for characterizing real fights. In fact, there are many examples in which the results are treated as inconclusive because the data provide partial support for both SA and MA (reviewed in Pinto et al., 2019). Therefore, by limiting our discussion of contests to the constraints of this binary framework, we risk overlooking more nuanced (but equally relevant) sources of continuous variation in information use that are already captured in the data typical of most contest studies.

CONTINUOUS VARIATION IN DECISION RULES

With respect to fighting ability, self-assessors utilize information on self-RHP, while MA involves a combination of information from two sources, self-RHP and opponent RHP. The initial suite of models of contest behaviour (see Kokko, 2013 for a review) assumed that fighting animals would either have (1) no information or (2) perfect information about opponent RHP in addition to perfect information about self-RHP (Crowley, 2000). By extension, this implies that in cases of MA, information on self and opponent RHP is equally weighted, that is the two sources of information contribute equally to the giving-up decisions of losers. Therefore, correlations between contest duration and winner and loser RHP should provide slopes with similar magnitudes but opposing directions (Taylor & Elwood, 2003). In contrast, empirical evidence shows that the contribution to the giving-up decision of each of these two sources of information may be unequal. Thus, Prenter, Elwood, and Taylor (2006) discussed the possibility of 'partial MA' by male amphipods fighting over ownership of pre-copula females. They suggested that each contestant would have good information about its own ability but might have less information about its opponent's RHP, presumably because the latter source is more difficult to access. Therefore, the relative contribution of opponent information on decision rules may vary.

Since private information (e.g. about self-RHP) is easier to obtain than public information (e.g. about opponent RHP; Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005), we might assume that information on opponent RHP will never have a stronger influence than self-RHP. Furthermore, we might even assume that information on self-RHP will be of high quality. In this case, the continuum of strategies would vary from SA-only to a form of MA where information on opponent RHP and self-RHP have equal weights. However, this need not always be the case. In some types of fight, information on opponent RHP might be more salient than information on self-RHP (Briffa & Elwood, 2002). During shell fights in hermit crabs, for example, there is a strong asymmetry in the agonistic behaviour used by an attacking individual and a defending individual that resists the attacker's attempts to evict it from its gastropod shell. Attackers but not defenders perform energetically demanding shell-rapping behaviour. Defenders, on the other hand, gather information on the attacker's RHP by monitoring the vigour of this shell rapping. Thus, in defending hermit crabs, information on opponent RHP might make a relatively important contribution to an opponent-assessing individual's giving-up decision (Briffa & Elwood, 2002). In other more extreme examples, such as the salamander *Plethodon cinereus* (Wise & Jaeger, 1998), the cricket *Gryllus bimaculatus* (Rillich, Schildberger, & Stephenson 2007) and the social cichlid fish *Neolamprologus pulcher* (Reddon et al., 2011) there is evidence that losers might reach their giving-up decision without any reference to information on self-RHP. Instead, they rely solely on information about the opponent, a strategy discussed by Arnott and Elwood (2009) as 'opponent assessment' (OA). While there has been some subsequent debate about the interpretation of these results (specifically whether the same measures of RHP could be assessed by both opponents, see Elwood & Arnott, 2012), situations in which individuals base their decisions only on OA remains a theoretical possibility for the basis of giving-up decisions by losers. Thus, we may draw an axis representing the proportions of information on self- and opponent RHP that extends beyond a form of MA where the maximum contribution of information on opponent RHP is 50%. Rather, the axis should extend into a region where the contribution of information on opponent RHP outbalances that on self-RHP, and continues all the way to an extreme point where the loser's decision is based only on opponent RHP (e.g. see Xu & Fincke, 2015). Although only a few studies so far indicate that fights of this type occur, it represents an important theoretical possibility (see Chapin et al., 2019a, b).

Therefore, the typically assumed 'balanced' form of MA, where information on self- and opponent RHP contribute equally, only represents one specific scenario within a continuum of possible weightings for information on self- and opponent RHP. Rather than thinking of MA as a single strategy, or even as a set of distinct strategies (e.g. balanced versus partial MA), we can instead conceive of MA as a continuum, defined by the proportional contribution of information on self- and opponent RHP. Viewed in this way, any example of MA that has been uncovered in an experiment will actually sit at some point along an axis bounded by what have been described as 'pure-SA' and 'pure-OA' strategies (Arnott & Elwood, 2009) at each extreme (henceforth 'SA-only' and 'OA-only' assessment). Indeed, more recent theory (Mesterton-Gibbons & Heap, 2014) has formally demonstrated how the use of information on opponent RHP can vary according to (1) its reliability and (2) the extent to which weaker individuals can afford to invest in gathering this information. By ignoring this potentially continuous nature of variation in self- and opponent assessment we may be overlooking a salient aspect of differences in strategic decision making across different examples of animal contests.

In the following section we describe a means of illustrating the three different types of assessment strategy that we have already mentioned (SA-only, the MA continuum and OA-only) in relation to these two sources of information (self-RHP and opponent RHP) in a vector space. We also incorporate the third source of information that is likely to influence persistence times in fights: the loser's perception of the value of the contested resource (RV) (Enquist & Leimar, 1987). Doing so introduces an additional extreme strategy, resource assessment only (RA-only), where losers reach their decision to give up using only information on RV (see Humphries, Hebblethwaite, Batchelor, & Hardy, 2006 for a discussion of RV effects). Adding this third source of information also has the effect of extending the strategy space out from a one-dimensional vector linking SA and OA. The contribution of information on RV would drag strategies away from their position on that vector, and towards the interior of a two-dimensional space; a triangle in which each side represents the information contribution of self-RHP, opponent RHP and RV on decision rules made by losers (Fig. 1; see below for detailed discussion). We previously used this type of ternary plot to summarize the assumptions about information use that underpin a range of influential models of contest behaviour (Chapin et al., 2019a). While these models assume that information (including costs accrued) accumulates during a contest, as noted above, empirical tests of these assumptions typically rely on inferences that can be gained at the point of decision (i.e. when the loser quits the contests). Here we extend the scheme of Chapin et al. (2019a) to show how the same kind of diagram can be used to illustrate such data (gained at the point of decision) from real contests, avoiding the typical division between SA and MA. We then show that ternary plots used in this way would allow ready comparison of typical contest data across studies.

A TERNARY PLOT RELATING STRATEGIES TO INFORMATION SOURCES

If all strategies can be described by the relative contributions of information on self-RHP, opponent RHP and RV, any strategy (see Table 1 for definitions of sources of information and the strategies that they are used in) can be represented as a point on a ternary diagram. A ternary diagram consists of three axes (representing different factors that may affect a given process) arranged as an equilateral triangle, such that each axis is a side of the triangle. Each axis is scaled from 0 to 100% (on which the proportionate contribution of the relevant variable is plotted, e.g. 0.27 would be plotted as 27% on this scale) and these minimum and maximum values join to form the three vertices (points) of the triangle. Any location inside the ternary diagram represents the relative contribution of each variable depicted on each side of the diagram.

Ternary plots are typically used when the relative contributions of three variables to an end result need to be illustrated. For example, vision scientists use them to illustrate the contribution of red, green and blue channels to a perceived colour and geologists use them to illustrate the proportions of different minerals in soils. For animal contests, we can use ternary diagrams to plot the relative contributions of the three sources of information discussed above (self-RHP, opponent RHP and RV). Such a plot would illustrate the relative contributions (i.e. 0–100) of each information source to the loser's giving-up decision.

Example strategies plotted in this way are illustrated in Fig. 1 (see Appendix 1 for R code used to generate this plot; all plots have been produced using the 'Ternary' package, running under R 3.4.1 (Smith, 2017, R Core Team 2019). If losers give up using a strategy of SA-only, all the information that they use to reach this

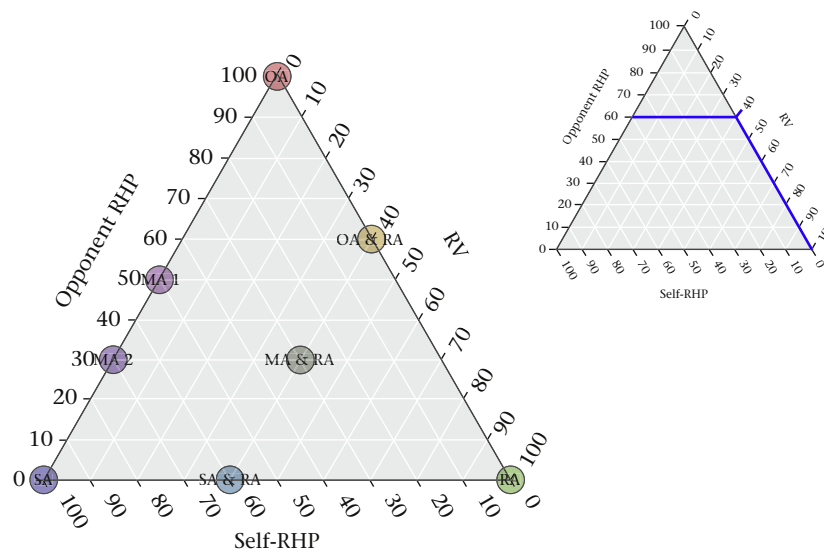


Figure 1. Ternary plot representing the sources of information used by losers across a range of different strategic decision rules. Axes (sides of the triangle) represent sources of information and labelled points represent strategies that utilize each source of information to a greater or lesser degree. The three vertices of the plot represent extreme strategies where losers make their decisions based exclusively on self-assessment (SA), opponent assessment (OA) or resource assessment (RA). The self-RHP axis runs from left to right along the lower side of the triangle, the opponent RHP axis from the base to the apex of the triangle and the resource value (RV) axis runs from the apex back down to the base. Correct interpretation of these plots is dependent on identifying the direction of the gridlines extending from each axis into the interior of the plot area. The direction is indicated by the orientation of the axis tick marks, which matches the direction of the gridlines. Thus, MA1 represents an MA strategy where giving up is based on combined and equally weighted information about self- and opponent RHP. For this reason, MA1 appears at the mid-point along the side linking SA and OA (note that MA1 could also be called SA & OA, but by convention we refer to this combination of information sources as MA). Similarly, MA2 has a score of 70 on the self-RHP axis, 30 on the opponent RHP axis and 0 on the RV axis, and therefore plots out on the side linking (i.e. scores of 100) SA-only and OA-only. Similarly, the strategy marked OA & RA has a score of 0 on the self-RHP axis, 40 on the RV axis and 60 on the opponent RHP axis. Since the decision in this case is based on a combination of information on opponent RHP and RV (without any contribution from self-RHP) it plots out on the side linking the OA-only and RV-only strategies (see inset). In contrast, the strategy marked MA & RA (which could also be called SA & OA & RA) combines information represented on all three axes and is therefore dragged away from all sides of the triangle to the interior of the plot area.

Table 1
Strategies that losers could use to reach their giving-up decision and the sources of information on which these strategies depend

Name	Abbreviation	Definition and notes
Strategies		
Self-assessment	SA-only	Loser bases its giving-up decision on information about its own RHP (self-RHP), usually envisaged as a threshold of the maximum costs it can absorb
Opponent assessment	OA-only	Loser bases its giving-up decision on information about its opponent's RHP, typically envisaged as being advertised through the use of agonistic signals or inferred directly through assessment of indices such as body size
Resource assessment	RA-only	Loser bases its giving-up decision on information on the value it places on the resource
Mutual assessment	MA	This could also be described as 'SA and OA'. The loser reaches its giving-up decision by comparing self- and opponent RHP. This is the only strategy outlined here that uses a combination of information sources. Although they do not have specific names, other strategies based on any combination of the sources of information described below are also possible
Sources of information		
Self-RHP		Private information that the loser has on its own fighting ability
Opponent RHP		Public information concerning the opponent's RHP, accessed by the loser
Resource value	RV	The subjective value that the loser places on the contested resource

In Fig. 1, the strategies described in this table are plotted as points within a ternary plot where the three sources of information represent the axes.

decision concerns self-RHP. This strategy can be represented by proportional values of self-RHP = 100, opponent RHP = 0, RV = 0. Therefore, the SA-only strategy appears at the lower left vertex of the plot in Fig. 1. Similarly, if losers reach decisions using an OA-only strategy, all the information used to reach this decision concerns opponent RHP. This strategy can be represented by scores of self-RHP = 0, opponent RHP = 100, RV = 0. Therefore, the OA strategy appears at the upper vertex of the plot. Under MA, losers should combine information on self- and opponent RHP. Assuming that both sources of information contribute equally to the loser's decision, this strategy of balanced MA can be represented by scores of self-RHP = 50, opponent RHP = 50, RV = 0. Under this scenario, MA (MA1 in Fig. 1) appears at the mid-point of the side linking the top and lower left vertices of the triangle (i.e. mid-way between the extreme points that represent SA-only and OA-only strategies). On the ternary plot, different points along this continuum can be represented with ease. Consider, for example, a scenario in which losers use information on both self-RHP and opponent RHP, but their decision is influenced by self-RHP to a greater extent than by opponent RHP. This could occur because information on self-RHP is more attainable, or can be gathered with greater accuracy, leading losers to place greater weight on this information during decision making. MA2 represents this type of scenario which has been described as partial MA (Prenter et al., 2006). In the example illustrated here, the giving-up decision is based 70% on information about self-RHP with a contribution of 30% from information about opponent RHP. As in the case of MA1, this strategy appears on the side of the plot that represents the continuum linking SA-only and OA-only as extreme strategies but plots closer to the SA-only extreme, compared with MA1. It would be equally possible to plot out a strategy where the influence of information on opponent RHP was greater than that of self-RHP. In this case, the strategy would also appear on the side linking SA-only and OA-only but would plot out closer to the OA-only extreme.

The MA strategies plotted thus far always plot on the side linking the SA and OA extremes because they represent a combination of these two sources of information, without any contribution from information on RV represented by the third axis. As in the case of SA-only and OA-only strategies, if losers make their decision solely on the basis of information about RV, this RA-only strategy (self-RHP = 0, opponent RHP = 0, RV = 100) plots on the third vertex of the triangle, at the lower right position. In some cases, losers may combine information on RV and RHP. Motivational effects, for example, might influence (1) the proportion of the theoretical maximum persistence time that they are willing to fight up to in the case of an SA-only strategy,

(2) the strength of opponent that they are willing to persist against in the case of an OA-only strategy and (3) the known differential in fighting ability (relative to a stronger opponent) that they are willing to persist against in the case of an MA strategy. Simultaneous contributions from information on RV, SA and OA thus have the effect of dragging the positions of strategies inwards, away from any one side of the ternary plot. For example in Fig. 1, the point marked OA & RA represents a strategy based on a combination of information on the strength of the opponent and RV, but without any contribution from information on self-RHP (self-RHP = 0, opponent RHP = 60, RV = 40). But by adding an effect of RV, the strategy has been dragged from the extreme OA end of the side linking SA and OA down towards the RV vertex. Similarly, in a scenario where information on opponent RHP is not used, but losers use a combination of information on self-RHP and RV (self-RHP = 60, opponent RHP = 0, RV = 40), the resultant SA & RA strategy is dragged from the extreme SA end of the same side across towards the RV vertex. Finally, mutual assessors might also incorporate information on RV into their strategic decision. In this case, the position of the resultant MA & RA strategy (self-RHP = 30, opponent RHP = 30, RV = 40) in Fig. 1 is dragged from the mid-point of the side linking SA and OA (since information on self- and opponent RHP contributes equally) into the inside of the triangle (note that the tick marks on each axis inform the direction of each gridline representing the proportions of each axis).

For convenience (because RHP is often at the forefront of our thinking about contests) we have thus far emphasized the side of the plot linking SA and OA, and we have described the effect of RV as 'dragging' strategies away from this axis and towards the vertex representing pure RA. However, we could have equally emphasized the side linking OA and RV, or that linking SA and RV. Thus, the ternary plot describes a plane defined by three axes representing the three sources of information assumed by theory to underpin strategic decision making in fights. Depending on the relative contribution of information sources in making contest decisions, strategies can plot on any position bounded by the sides of the ternary plot. Representing dyadic animal contests using the ternary coordinates demonstrated above and illustrating the resultant positions on a ternary plot (Fig. 1) provides a means of characterizing contests with a greater degree of precision than the typical allocation to a single category, as in the SA versus MA dichotomy. Instead, this approach emphasizes that MA is, in fact, a continuum based on the combination of at least two sources of information. In the sections below, we consider how the ternary approach could be used to characterize contest data, first

illustrating our approach using simulated data and then with data from real contests.

Weapons, Defences and Intraspecific Variation

As noted above, there are some limits to our ability to make inferences about assessment rules based on contest duration and RHP data. These have been discussed previously and are worth revisiting here because they would also apply to interpretations of ternary illustrations. Specifically, we should be cautious about our ability to discern the sources of information used by losers in fights where injuries (Briffa & Elwood, 2009), and therefore disparities between weapons and defences (Palaoro & Briffa, 2017), are important. This is because the effects of injuries and information on opponent RHP on decision rules can both produce the same pattern: negative correlations between contest duration and winner RHP measures (Taylor & Elwood, 2003). Therefore, in injurious contests that are settled through SA (as assumed, for example, by the cumulative assessment model; see Payne, 1998), the effect of injuries caused by rivals could produce the pattern expected under MA (Briffa & Elwood, 2009). Even in contests that are settled by genuine MA, the contribution of information on opponent RHP could be exaggerated if individuals are able to damage each other during the contest. Since correlations between contest duration and individual traits are used in the construction of the ternary plots, the SA–OA axis may not exclusively represent the relative contribution of OA to decision rules if injuries also influence the outcome. It may also represent the effect of agonistic behaviours that impose direct costs on the recipient. Therefore, if fights occur with injuries, additional approaches will be needed to disentangle the effect of OA and injuries on decision rules. In particular, data on contest dynamics are important to make such distinctions (Briffa & Elwood, 2009; Briffa, 2015; see also ; Payne & Pagel, 1997). Furthermore, if intraspecific variation in information use during contests is indicated (see Chapin et al., 2019a), the suggested plots (like previous approaches) will indicate the average population decision rule.

EXAMPLES WITH SIMULATED DATA

Simulations Based on Continuous Measures

To illustrate a procedure that allows ternary plots, like the one described above, to be used for the classification of results from empirical studies, we generated data sets to simulate contests where losers use either SA or MA strategies and adjust their fighting investment according to RV to reach their giving-up decision (see Appendix 2 for example R code). In each case, we assumed that contests were noninjurious, and thus settled on the basis of information alone. To simulate data for contests settled by SA, we specified four sets of 100 values selected at random from a normal distribution (mean = 50, SD = 10). The four sets are simulated values for contest duration, self-RHP, opponent RHP and RV. These represent the response variable (contest duration) and predictor variables (self-RHP, opponent RHP and RV) that would be included in typical analyses of contest duration. To simulate an SA scenario without RA (as described by Taylor & Elwood, 2003), we initially specified a strong positive correlation between self-RHP and contest duration ($r = 0.8$), a weaker positive correlation between opponent RHP and contest duration ($r = 0.2$) and no correlation between RV and contest duration ($r = 0$). In this simulation, and all subsequent simulations, we ensured that there were no additional correlations among the RHP and RV variables (see Appendix 2). To add a further element of realism, we multiplied loser (self-) RHP by 0.8, such that winner (opponent) RHP was greater than loser RHP

(paired t test: $t_{99} = 8.3$, $P = 0.0001$), because in real fights losers are expected to have lower RHP than winners. We then validated the final version of the data set, checking that the expected correlations (specified above) were still present (Pearson correlations: duration versus self-RHP: $r_{98} = 0.8$; duration versus opponent RHP: $r_{98} = 0.2$; duration versus RV: $r_{98} = -2.8 \times 10^{-17}$; self-RHP versus opponent RHP: $r_{98} = -5.8 \times 10^{-17}$).

Next, we subjected the data to an analysis that would be typical of an empirical study based on the recommendations of Taylor and Elwood (2003). We ran a linear model where self- (loser) RHP, opponent (winner) RHP and RV were treated as predictors of contest duration, which represents the persistence of losers across the 100 fights in the data set (Table 2, simulated self-assessment). As described above, the aim of the ternary plot is to illustrate the proportional contribution of information on the three key parameters that should contribute to giving-up decisions, and (by reference to Fig. 1 for example) to allow a ready comparison between the data and assumptions that underpin contest theory. Translated to this analysis, these contributions are equivalent to the proportional contributions of each of the predictors in the model to variance in contest duration, without considering the unexplained (i.e. residual) variation. Thus, we calculated the partial coefficient of determination (partial R^2) for each term in the model and used these to provide relative measures of the proportion of variance explained by each term. This generated a set of three contributions to variation in contest duration (equivalent to loser persistence), one for each parameter, and we plotted the resultant position on a ternary plot (Fig. 2a). Note that the ternary plots only contain the relative contribution of each information source in relation to the explained variance of the model. For this reason, information about the effect of the predictor variables in determining contest duration and victory probability must be considered before interpreting the results of the ternary plot (see below).

In Fig. 2a, the solid point for simulated SA data plots out close to the expected position of the extreme pure SA vertex, but with some displacement away from the 0% contribution of opponent RHP expected under SA. This displacement represents the contribution from the weakly positive correlation between opponent RHP and contest duration that we simulated. In real contest data, such weak positive correlations between opponent RHP and contest duration are most likely to occur under SA when the RHPs of winners and losers show a positive correlation. This is due, for example, to size-assortative fighting, but positive correlations do not indicate that information about the opponent's RHP is contributing to the loser's

Table 2
Summary statistics for linear models on simulated data sets

	<i>df</i>	<i>b</i>	Partial R^2	<i>F</i>	<i>P</i>
Simulated self-assessment					
Self-RHP	1	1.0	0.67	192	< 0.0001
Opponent RHP	1	0.2	0.11	12	< 0.001
RV	1	2.8×10^{-16}	3.3×10^{-16}	0	1
Residuals	96				
Simulated mutual assessment with a small RV contribution					
Self-RHP	1	0.88	0.78	336	< 0.0001
Opponent RHP	1	-0.60	0.72	246.86	< 0.0001
RV	1	0.10	0.07	3.86	0.01
Residuals	96				
Simulated mutual assessment with a categorical RV contribution					
Self-RHP	1	0.37	0.13	15.39	< 0.0001
Opponent RHP	1	-0.40	0.22	27.36	< 0.0001
RV	1	-9.88	0.25	32.26	< 0.0001
Residuals	96				

Effects of self- (loser) RHP, opponent (winner) RHP and resource value (RV) on contest duration. The analyses shown are illustrated in Fig. 2.

giving-up decision (only a negative correlation would indicate this). Such correlations could be avoided in experiments based on staged encounters but may be unavoidable when data are collected during field studies of naturally occurring fights.

We included this small amount of correlation between opponent RHP and duration here because it illustrates why the inspection of correlation coefficients is still an important step prior to plotting the data on a ternary diagram. If we envisage MA as a continuum of strategies between SA-only and OA-only extremes, Fig. 2a gives the impression that the data represent a point along this continuum (albeit one very close to pure SA). This, however, is a false impression, because MA predicts a negative correlation between opponent RHP and contest duration, rather than the positive one simulated here. Thus, care would need to be taken in the interpretation of ternary plots where points deviate from the pure SA vertex due to positive correlations with opponent RHP. We suggest that the positive correlation between opponent RHP and contest duration be treated as part of the residual variance in the model, which is ignored for the purposes of the ternary plot. This would clearly illustrate a situation such as the one simulated here, where SA cannot explain the total amount of variation in contest duration, but this unexplained variation is not then erroneously attributed to OA. Operationally, this would simply mean setting the opponent RHP partial R^2 value to zero if the slope of opponent RHP and contest duration is positive.

In the case of genuine MA, we should expect a negative correlation between contest duration and opponent RHP. In this situation, the amount of variance in contest duration explained by that negative correlation would represent the contribution of information about the opponent's RHP to the loser's giving-up decision. Thus, when there is a negative correlation between opponent RHP and contest duration, this value should be included on the ternary plot. For example, the point on Fig. 2b represents an analysis of data that simulate MA. Following the process described above, we generated a data set where we initially specified a strong positive correlation between self-RHP and contest duration ($r = 0.7$), a weaker negative correlation between opponent RHP and contest duration ($r = -0.6$) and a positive but low correlation between RV and contest duration ($r = 0.1$). Again, we multiplied loser (self-

RHP by 0.8, such that opponent RHP was greater on average than self-RHP (paired t test: $t_{99} = 7.18$, $P < 0.0001$). Validation of the final version of the data set yielded the following correlations (duration versus self-RHP: $r_{98} = 0.7$; duration versus opponent RHP: $r_{98} = -0.6$; duration versus RV: $r_{98} = 0.1$; self-RHP versus opponent RHP: $r_{98} = 3.2 \times 10^{-18}$). The effect of the three predictors (self-RHP, opponent RHP and RV) on contest duration were then analysed using a linear model as above (Table 2, simulated mutual assessment with a small RV contribution). As expected, plotting the partial R^2 values of the three predictors resulted in a point on the ternary plot close to (but not directly on) the side linking SA and OA, and closer to the SA vertex than to the OA vertex (Fig. 2b). Thus, this example represents an MA situation where there is a disparity between the contributions of information on self- and opponent RHP. In this example, information on self-RHP makes a greater average contribution to the giving-up decisions of losers than information on opponent RHP, and a small contribution from information on RV has pulled the point away from the side linking pure SA and OA vertices, down towards the RV vertex.

A Simulation Based on Discontinuous RV

Thus far we have simulated data where our predictors are always continuous. In many examples of contest behaviour, predictors of RHP (e.g. body or weapon size), are continuous variables, but this does not need to be the case. For example, discontinuous variation such as morph type (e.g. major and minor males in rhinoceros beetles) or reproductive status may predict fighting ability. Further, experiments can involve the manipulation of RV, where staged fights are often allocated to treatments of high and low RV (e.g. Briffa, Elwood, & Dick, 1998; Peixoto & Benson, 2012; Palaoro, Velasque, Santos, & Briffa, 2017). We can also apply data obtained from experiments with categorical predictors to these plots because ternary plots can illustrate proportional contributions derived from the estimates of any predictor variable. In our final simulation, we first produced a data set to simulate a scenario of MA combined with RV assessment, such that there was a positive correlation between self-RHP and duration (0.3), a negative correlation between opponent RHP and duration (-0.4) and a positive

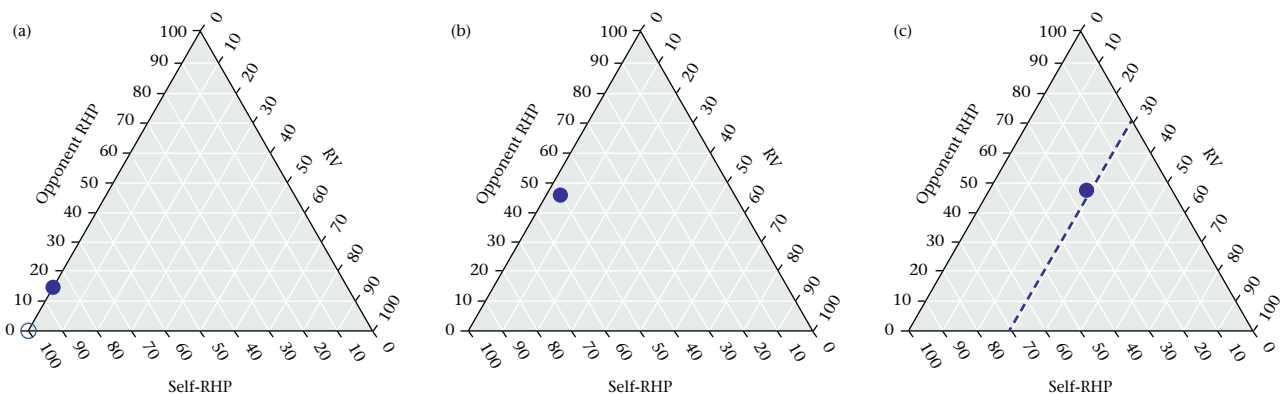


Figure 2. Ternary plots for data simulating fights settled through different types of decision rule. (a) Self-assessment. The solid point represents a plot where the variance due to the positive correlation between opponent RHP and duration is included. Since this positive correlation implies that losers are not using information on opponent RHP, this variance contribution could be excluded from the plot as the intention is to illustrate the sources of information used by the loser. Excluding this information produces the point illustrated by the open circle. (b) Mutual assessment. Here the variance contributions of the positive correlation between self-RHP and duration and negative correlation between opponent RHP and duration are plotted. Since the effect of RV is small the point representing these data plots close to the axis linking OA-only (the apex) and SA-only (the lower left vertex) strategies. In this case, information on self-RHP has a greater contribution to the loser's giving-up decision than information on opponent RHP. (c) Mutual assessment and resource assessment. Owing to the contribution of RV, the point has been dragged away from the side linking pure SA and pure OA towards the pure RV assessment strategy. Nevertheless, we can still gauge the relative contributions of self- and opponent RHP, by locating the position of the plotted data on a gridline parallel to that side (illustrated by the dashed blue line). In this example, information on the opponent's RHP has a greater influence on the giving-up decisions of the loser than information on self-RHP, since the data plots out closer to the OA-only strategy than to the SA-only strategy.

correlation between RV and duration (0.5). In this case, as well as combining information on self- and opponent RHP, eventual losers will persist for longer when fighting for a higher RV. As above, we ensured that there were no correlations among self-RHP, opponent RHP and RV. We adjusted self-RHP by a factor of 0.8, to ensure that winners had greater average RHP than losers (paired t test: $t_{99} = 8.21$, $P < 0.0001$) and then validated the simulated data to check that expected correlations were still present (duration versus self-RHP: $r_{98} = 0.3$; duration versus opponent RHP: $r_{98} = -0.4$; duration versus RV: $r_{98} = 0.5$; self-RHP versus opponent RHP: $r_{98} = 9.7 \times 10^{-18}$). Finally, we factorized the RV variable, such that values greater than the mean were designated as high RV and values equal to or below the mean value were designated as low RV. We then used a linear model to determine the effects of self-RHP, opponent RHP and factorial RV on the duration of contests (Table 2, simulated mutual assessment with a categorical RV contribution). The plot of this result (Fig. 2c) again represents contests that are settled by MA. In contrast to the result plotted in Fig. 2b, however, information about opponent RHP has a greater influence on loser giving-up decisions than information on self-RHP. Therefore, the result plots out at a point that is closer to the OA-only vertex than the SA-only vertex. Note also that the point is now located in the interior of the plot area, because of the relatively strong influence of RV on the persistence of losers.

In the simulation model described here, both opponents were assumed to have had access to the resource and were equally affected by RV. However, there are many instances when competing animals adopting different roles (e.g. owner versus intruder) may have differential access to information on RV (e.g. Bridge, Elwood, & Dick, 2000) or place a different subjective value on the resource (e.g. Humphries et al., 2006). In these cases, data should be cross-tabulated by role and outcome to give subsets of fights lost by each role. Then each of the two subsets could be separately analysed and the results for each subset shown separately on ternary plots (e.g. different symbols or entirely different plots for each role). This would allow one to distinguish between the assessment strategies utilized by individuals adopting different roles.

USING TERNARY PLOTS TO CHARACTERIZE REAL CONTESTS

To further assess the value of ternary plots, and to illustrate some key considerations, we now generate ternary plots using data taken from recent studies of animal contests. First, we use data from fights between beadlet sea anemones, *Actinia equina*, and then we turn to contests in the neotropical cricket *Melanotes ornata*.

RHP Traits in Sea Anemones

These data were taken from a study in which the effect of extrinsically manipulated RHP and RV on contest decisions was investigated (Lane & Briffa, 2018). We manipulated (1) the extrinsic RHP of both opponents prior to fighting (through exposure to either hypoxic or normoxic conditions) and (2) RV during the fight (through the presence or absence of flowing water in the contest arena). This resulted in categorical predictors for both extrinsic RHP (hypoxic or normoxic seawater) and RV (high RV = flowing sea water; low RV = still sea water). Alongside these categorical variables, we also measured body size and the average length of nematocysts (the harpoon-like weapons used by cnidarians) for each individual, providing two continuous measures of intrinsic RHP (Rudin & Briffa, 2011, 2012). For the purposes of the current illustration, the effect of each RHP measure on contest duration was

analysed separately using a linear model. All three linear models also included RV as a predictor. As nematocyst length has previously been shown to contribute to RHP only in injurious fights, only escalated fights were included when analysing the effect of nematocyst length on contest duration.

Although body size is widely regarded as an important contributor to RHP (Pinto et al., 2019; Vieira & Peixoto 2013), the results of our analyses suggest that this may not be the case in *A. equina*. An initial inspection of a ternary plot (Fig. 3a) based on the partial R^2 values from a linear model (Table 3) would indicate that if body size is an RHP trait in anemones, then losers are using OA and RA. However, it is obvious from the R^2 values that neither of these variables contributes significantly to contest duration, each explaining only a tiny part of the total variance (Table 3). This illustrates an aspect of ternary plots that has to be treated with caution when plotting out real data: since ternary plots illustrate the relative (to one another) contributions of three variables, they do not account for residual variance, which in the current example accounts for most of the variation in contest duration.

Further inspection of the results gives another reason to be cautious about Fig. 3a. As well as being nonsignificant, the coefficients for both self- and opponent RHP are negative (Table 3). While a negative association between opponent RHP and contest duration is not surprising, the negative association between self-RHP and duration and the very weak (nonsignificant) effects in both cases suggest that perhaps body size is not an appropriate measure of RHP in this data set. Body size has previously been shown to reliably predict contest outcome in *A. equina*, but only in noninjurious fights (Rudin & Briffa, 2011). As the majority of fights in the current data set did escalate to injury, this high incidence of injury may explain why body size does not appear to be an appropriate measure of RHP in this case. Thus, as with any study of fighting behaviour, care should be taken to identify the most appropriate proxy for RHP a priori (e.g. Briffa, 2014; Rudin & Briffa, 2011). This is particularly important if, as noted above, a single proxy for RHP that is relevant to both opponents is difficult to identify.

Dealing with Nonsignificant Results

In both the simulated and these real data, we have dealt with a mixture of scenarios, ranging from those where all three variables have clear (judged by statistical significance) effects on contest duration, cases where only some of the variables have a significant effect, through to examples like the one above where there are no significant effects in the analysis. Although we have plotted this example of no significant effects for illustrative purposes here (Fig. 3a), we would not recommend doing this routinely. While Fig. 3a still correctly illustrates the variance contributions of each parameter of interest relative to each other, there is the danger that a plot such as this could give the erroneous impression of significant effects, especially for opponent RHP and RV (Fig. 3a), to a reader who did not cross reference the figure with the underlying analysis (or other parts of the paper such as figure legends or discussion). On the other hand, an analysis may indicate that some (but not all) of the three parameters of interest have an effect on contest duration. In this case, we suggest plotting a point that represents all three parameters on the ternary plot, because the proportionate effect of a nonsignificant variable would be very low in relation to the other parameters of interest, alongside a second point that excludes the influence of nonsignificant effects. In the following section, we describe this exact situation, based on further analyses of the anemone data (Lane & Briffa, 2018). In Fig. 3b and c,

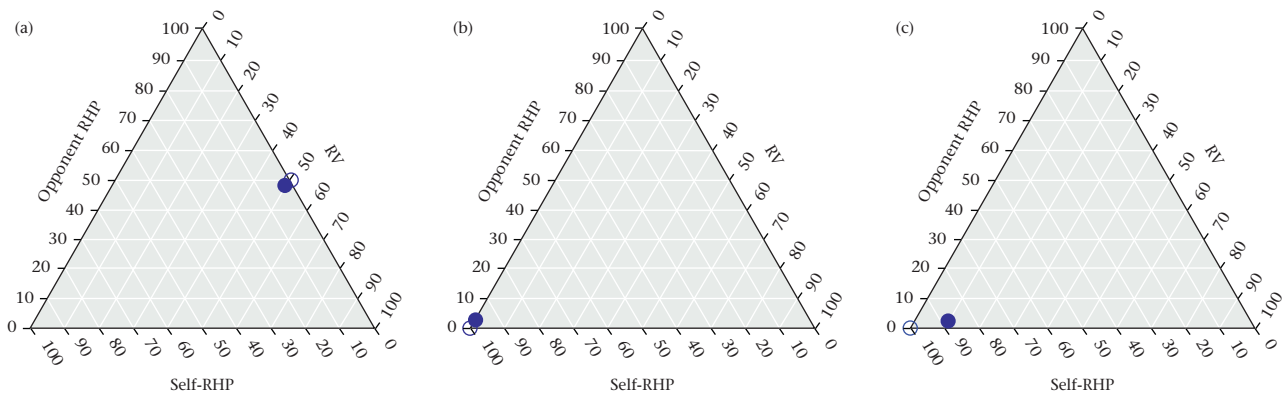


Figure 3. Ternary plots for real contest data from sea anemone fights with (a) body size, (b) nematocyst length (injurious fights only) and (c) oxygen concentration (categorical) as measures of RHP. Closed circles represent plots that have partial R^2 values for all effects in the models whereas open circles represent plots where (a) only effects that are consistent with the directions expected for known assessment strategies have been used or (b, c) only effects that are statistically significant have been used.

Table 3
Summary statistics for linear models on real contest data from sea anemone fights

	df	b	Partial R^2	F	P
Continuous RHP (body size)					
Self-RHP	1	-0.008	0.001	0.34	0.57
Opponent RHP	1	-0.03	0.022	0.53	0.47
RV	1	0.28	0.021	0.57	0.46
Residuals	27				
Continuous RHP (nematocyst length)					
Self-RHP	1	7.34	0.30	8.05	0.01
Opponent RHP	1	-1.12	0.01	0.08	0.78
RV	1	0.04	0.002	0.03	0.88
Residuals	13				
Categorical RHP (oxygen consumption)					
Self-RHP	1	0.53	0.37	20.22	<0.0001
Opponent RHP	1	0.07	0.01	0.37	0.55
RV	1	0.14	0.04	1.54	0.22
Residuals	36				

Effects of self- (loser) RHP, opponent (winner) RHP and resource value (RV) on contest duration, with body size, nematocyst length (injurious fights only) and oxygen consumption (categorical) as RHP measures. The analyses shown above are illustrated in Fig. 3.

described in detail below, we compare the plots that result from excluding and including nonsignificant effects when other effects are important.

Weapon Size as a Proxy for RHP in Sea Anemones

When analysing the effect of RHP quantified by nematocyst length on the duration of injurious contests, we found a significant positive correlation between loser RHP and contest duration ($r_{15} = 0.60$, $P = 0.01$), and no correlation between winner RHP and contest duration ($r_{15} = 0.11$, $P = 0.67$), indicative of SA. The ternary plots produced using the partial R^2 taken from the linear model illustrates these relative contributions. Regardless of whether the nonsignificant contribution of opponent RHP is included or not, nearly 90% of the information used by the loser is on self-RHP (Fig. 3b).

Categorical RHP in Sea Anemones

As described above, ternary plots can also be used to illustrate the relative contributions of categorical predictors, including

experimentally manipulated RHP levels and manipulated RV. In the data from Lane and Briffa (2018), sea water oxygen concentration was a categorical RHP variable because it influenced the chance of victory. We can infer the direction of the effect between this categorical predictor (normoxia or hypoxia) and the continuous response (contest duration) by inspecting the parameter estimates from the summary of the linear model performed. These parameter estimates showed that contest duration increased with loser RHP and with winner RHP, indicating a positive correlation between loser RHP and duration and a weaker (nonsignificant) correlation with winner RHP, again predominantly characteristic of SA (with a very small contribution from RV). These relative contributions can now be illustrated using a ternary plot (Fig. 3c) which shows that, similar to the results for nematocyst length, 90% of the information used by the loser is on self-RHP and in this case less than 10% is from RV, while virtually no information on opponent RHP is used.

These analyses of contests in *A. equina* illustrate that the directions of correlations between self- and opponent RHP (as well as their strength) should be carefully considered prior to deciding which parameters should be added to ternary plots where the intention is to illustrate the balance between information sources that contribute to giving-up decisions. They also show how ternary plots can allow a ready comparison between the results of different analyses. When body size is used as the measure of RHP (Fig. 3a), RV appears to be relatively important in the losers' giving-up decision, but when other (more pertinent) measures of RHP are analysed, we can quickly see that RV is in fact unimportant. In studies where several measures of RHP have been taken, it might be more desirable to simplify these measures by means of factor analysis. Ternary plots are versatile enough to cope with these sorts of data and the raw measures of RHP traits used here. For example, one could test for correlations between principal component scores and contest duration for winners and losers and then treat these in the same way as raw measures of RHP have been treated in the examples above.

Variable Assessment Rules in *M. ornata* Cricket Contests

Our second example comes from the study of Lobregat, Kloss, Peixoto, and Sperber (2019) on fighting in the cricket *M. ornata*. Males of this species defend mating territories located in tree trunks in Brazilian Atlantic Forest. Fights between males may

consist of two different phases. Males initiate the fight by touching each other with their antennae. During this phase, they elevate their bodies and repeatedly lift their hindlegs. Some fights may escalate to the second phase in which males orient in opposite directions against each other, cross their hindlegs and perform pushes and kick attempts. Once in the second phase, fights never de-escalate and the authors found that hind femur length was the best predictor of victory. Evaluations of whole contest dynamics indicated the losers perform MA, while analysis separated per phase indicated two possibilities: (1) individuals adopt MA in the first phase and change to SA in the second phase or (2) some individuals always adopt MA, while others always adopt SA.

By employing simple correlations on the original data, we found that whole fight duration (log-transformed) was positively associated with the loser's femur length ($r_{37} = 0.42$, $P = 0.008$) and presented a near significant negative trend with the winner's femur length ($r_{37} = -0.27$, $P = 0.09$). However, in the original study it was noted that contest dynamics (i.e. patterns of escalation and de-escalation) differed across phases. Furthermore, for winners (but not for losers) these patterns also differed within the first phase between contests that were resolved at the end of that phase and contests that escalated to the second phase. Since theory predicts different escalation patterns across assessment rules (see Payne & Pagel, 1997), it was concluded that assessment modes differed between phases, and this is borne out by analyses of RHP versus duration specific to each phase.

By using the same patterns described in the original study, we evaluated the correlations between fight duration and loser and winner RHP for each phase separately. For winners, we also divided the data into individuals that escalated and individuals that did not escalate the contest to phase 2. In contests that were resolved in phase 1 there was a positive association between duration and the hind femur length of losers ($r_{37} = 0.40$, $P = 0.01$). For winners there was no significant association between duration and hind femur length for fights that escalated to phase 2 ($r_{18} = 0.29$, $P = 0.22$) but for fights that did not escalate, there was a marginally significant negative trend ($r_{17} = -0.44$, $P = 0.06$). During phase 2, no associations between loser ($r_{18} = 0.28$, $P = 0.22$) or winner ($r_{18} = -0.20$, $P = 0.39$) RHP and duration were detected. A ternary plot can be used to illustrate this type of pattern by plotting both the whole contest and each phase on the same figure. In Fig. 4, we have followed the same convention used above, where points representing clear evidence for assessment rules (as described by Taylor & Elwood, 2003) are represented by solid symbols whereas points that do not fit into that framework (i.e. where there is no convincing association in the expected direction) are represented by open symbols. Fig. 4 illustrates that during fights in *M. ornata*, MA is being used under some circumstances (i.e. when fights are resolved without escalation) but not in every fight. Furthermore, if fights are considered as a whole, the influence of opponent RHP on the loser's giving-up decision appears to be lower than during phase 1 (the only specific circumstance where there is clear evidence of MA). This is because the point representing whole fights plots out closer to the SA-only vertex in comparison to the point representing phase 1 only for fights that were resolved during this phase.

These data show how ternary plots can be used to illustrate two aspects of real contests that are often overlooked. First, as described above, information on the relative contributions of self- and opponent RHP has been illustrated, emphasizing the continuous nature of variation in the use of these information sources. Second, even within the same study system (or experiment) not all fights are equal. In Fig. 4 we have illustrated differences in decision rules across contest phases. We might also plot out differences between species, between experiments or between any other units that are biologically interesting. For instance, males and females might both

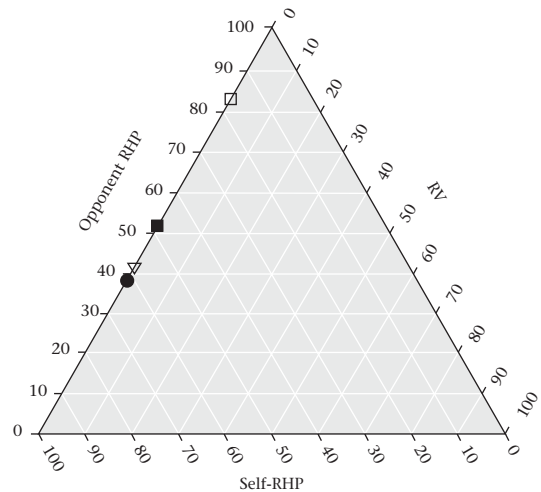


Figure 4. A ternary plot illustrating intercontest variation in assessment rules in the cricket *Melanotes ornata*. As this experiment did not involve variation in RV, all points plot out on the axis linking SA with OA (the contribution of RV is 0). Although these fights could equally well be plotted on a line (as described above), rather than a ternary plot, illustrating them in this way would allow for comparison across studies (for example if future experiments on this species incorporated variation in RV). The solid circle shows data from all fights whereas the solid square shows data from fights that were resolved during phase 1. The open square shows phase 1 for fights that escalated to phase 2 and the open triangle shows data from phase 2 of these fights. These latter two categories are represented by open symbols because they did not contain any significant associations between RHP and contest duration.

fight (Stockley & Campbell, 2013) but in different ways (Briffa & Dallaway, 2007), agonistic behaviour might vary across genotypes (Lane, Wilson, & Briffa, 2020) and individuals within populations might differ in how they use information (these differences could be detected when focal individuals fight multiple times; Chapin et al., 2019a). Such individual level data could also be shown on a ternary plot to illustrate the pattern of variation in decision rules within populations.

CONCLUSIONS

It is increasingly clear from recent empirical and theoretical studies that the traditional classification of contests as either SA-only or MA-only (relying equally on information about self- and opponent RHP) describes only part of the story (Chapin et al., 2019a; Mesterton-Gibbons & Heap, 2014). Here, we have shown how ternary plots provide a versatile way of illustrating and visually comparing continuous variation in contest decision rules. This approach is not intended as a replacement for the initial steps of (1) identifying significant RHP traits, (2) establishing how subjective and objective values of a resource determine the total RV for each individual and (3) testing the assumptions and predictions of contest theory. Rather, we suggest that presenting data in this way provides an additional third step that will allow us to consider contest data in more depth. Specifically, we hope that ternary plots will provide a means of visually comparing assessment strategies within and between data sets and of encompassing the possibility that information use could vary continuously across contests. We suggest that such an approach will be particularly useful in studies that investigate contests in an integrated way, involving the simultaneous analysis of the RHP of both contestants alongside RV (with subjective RV quantified from the perspective of the loser where possible). As would be expected for any study on animal contests, the concomitant information on self-RHP, opponent RHP and RV will provide a more complete picture on how decisions are

made. But, even in studies that do not incorporate RV, the approach advocated here can be used to illustrate the relative contributions of information on self- and opponent RHP. These could be represented by a point plotted onto the axis linking SA and OA, either including the other two axes of the triangle (as in Fig. 4) or omitting them.

Our simulated and empirical examples show how ternary plots can be used to illustrate the relative contributions of information on self-RHP, opponent RHP and RV to the outcome of contests. Furthermore, ternary plots can easily be adapted to allow comparisons across fights from different study systems, populations, age categories and levels of fighting experience within the same population. In conclusion, if used in conjunction with existing approaches for the study of agonistic interactions, ternary plots can provide a way of achieving a greater level of granularity from contest data, particularly when MA is evident, by illustrating the relative contributions of information on self- and opponent RHP, as well as that of RV. Although several studies have presented evidence for MA (Benítez, Pappano, Beehner, & Bergman, 2017; Tedore & Johnsen, 2015; Tibbetts, Mettler, & Levy, 2010), it is difficult to gauge the balance between the contributions of information on self- and opponent RHP to the giving-up decision. However, this information is likely to be present already in data sets that contain contest duration and the RHP of both opponents, and these data could be used to populate ternary plots. Finally, if the parameter space within a ternary plot encompasses all possible rules (based on opponent RHP, self-RHP and RV) for giving up in a fight, only a limited subset of that space has thus far been explored by theory. Owing to the challenges of modelling fights, this situation may persist for some time (Leimar, 2019; Parker, 2019). Populating ternary plots with empirical data might provide broadscale information on where future modelling efforts would be best focused (see Mesterton-Gibbons, 2019). Moreover, until we have new theory, by supplementing current analyses with additional ternary plots, we can build a general picture illustrating the occurrence of different decision rules. Furthermore, we could potentially expand on the current prevailing view of assessment rules as an MA versus SA dichotomy.

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References

- Arnott, G., & Elwood, R. W. (2008). Information gathering and decision making about resource value in animal contests. *Animal Behaviour*, 76(3), 529–542. <https://doi.org/10.1016/j.anbehav.2008.04.019>.
- Arnott, G., & Elwood, R. W. (2009). Assessment of fighting ability in animal contests. *Animal Behaviour*, 77(5), 991–1004. <https://doi.org/10.1016/j.anbehav.2009.02.010>.
- Benítez, M. E., Pappano, D. J., Beehner, J. C., & Bergman, T. J. (2017). Evidence for mutual assessment in a wild primate. *Scientific Reports*, 7(1), 2952. <https://doi.org/10.1038/s41598-017-02903-w>.
- Bridge, A. P., Elwood, R. W., & Dick, J. T. A. (2000). Imperfect assessment and limited information preclude optimal strategies in male–male fights in the orb-weaving spider *Metellina mengeli*. *Proceedings of the Royal Society B*, 267, 273–279.
- Briffa, M. (2014). What determines the duration of war? Insights from assessment strategies in animal contests. *PLoS One*, 9, Article 0108491. <https://doi.org/10.1371/journal.pone.0108491>.
- Briffa, M. (2015). Agonistic signals: Integrating analysis of functions and mechanisms. In D. Irschick, M. Briffa, & J. Podos (Eds.), *Animal signalling and function: An integrative approach* (pp. 141–173). Hoboken, NJ: J. Wiley.
- Briffa, M., & Dallaway, D. (2007). Inter-sexual contests in the hermit crab *Pagurus bernhardus*: Females fight harder but males win more encounters. *Behavioral Ecology and Sociobiology*, 61(11), 1781–1787. <https://doi.org/10.1007/s00265-007-0411-5>.
- Briffa, M., & Elwood, R. W. (2002). Power of shell-rapping signals influences physiological costs and subsequent decisions during hermit crab fights. *Proceedings of the Royal Society B: Biological Sciences*, 269(1507). <https://doi.org/10.1098/rspb.2002.2158>.
- Briffa, M., & Elwood, R. W. (2009). Difficulties remain in distinguishing between mutual and self-assessment in animal contests. *Animal Behaviour*, 77(3), 759–762. <https://doi.org/10.1016/j.anbehav.2008.11.010>.
- Briffa, M., Elwood, R. W., & Dick, J. T. A. (1998). Analysis of repeated signals during shell fights in the hermit crab *Pagurus bernhardus*. *Proceedings of the Royal Society B: Biological Sciences*, 20(4), 187–193.
- Chapin, K. J., Peixoto, P. E. C., & Briffa, M. (2019a). Further mismeasures of animal contests: A new framework for assessment strategies. *Behavioral Ecology*, 30(5), 1177–1185. <https://doi.org/10.1093/beheco/arz081>.
- Chapin, K. J., Peixoto, P. E. C., & Briffa, M. (2019b). The point of the triangle and utility of repeated measures: A response to comments on Chapin et al. *Behavioral Ecology*, 30(5), 1191–1192. <https://doi.org/10.1093/beheco/arz163>.
- Crowley, P. H. (2000). Hawks, doves, and mixed-symmetry games. *Journal of Theoretical Biology*, 204(4), 543–563. <https://doi.org/10.1006/jtbi.2000.2037>.
- Dall, S. R. X., Giraldeau, L. A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, 20(4), 187–193. <https://doi.org/10.1016/j.tree.2005.01.010>.
- Elwood, R. W., & Arnott, G. (2012). Understanding how animals fight with Lloyd Morgan's canon. *Animal Behaviour*, 84, 1095–1102.
- Enquist, M., & Leimar, O. (1983). Evolution of fighting behaviour: Decision rules and assessment of relative strength. *Journal of Theoretical Biology*, 102(3), 387–410. [https://doi.org/10.1016/0022-5193\(83\)90376-4](https://doi.org/10.1016/0022-5193(83)90376-4).
- Enquist, M., & Leimar, O. (1987). Evolution of fighting behaviour: The effect of variation in resource value. *Journal of Theoretical Biology*, 127(2), 187–205. [https://doi.org/10.1016/S0022-5193\(87\)80130-3](https://doi.org/10.1016/S0022-5193(87)80130-3).
- Enquist, M., Leimar, O., Ljungberg, T., Mallner, Y., & Segerdahl, N. (1990). A test of the sequential assessment game: Fighting in the cichlid fish *Nannacara anomala*. *Animal Behaviour*, 40(1), 1–14. [https://doi.org/10.1016/S0003-3472\(05\)80660-8](https://doi.org/10.1016/S0003-3472(05)80660-8).
- Hammerstein, P., & Parker, G. A. (1982). The asymmetric war of attrition. *Journal of Theoretical Biology*, 96(4), 647–682. [https://doi.org/10.1016/0022-5193\(82\)90235-1](https://doi.org/10.1016/0022-5193(82)90235-1).
- Humphries, E., Hebblethwaite, A., Batchelor, T., & Hardy, I. C. W. (2006). The importance of valuing resources: Host weight and contender age as determinants of parasitoid wasp contest outcomes. *Animal Behaviour*, 72(4), 891–898. <https://doi.org/10.1016/j.anbehav.2006.02.015>.
- Kokko, H. (2013). Dyadic contests: Modelling fights between two individuals. In I. C. W. Hardy, & M. Briffa (Eds.), *Animal contests* (pp. 5–32). Cambridge, U.K.: Cambridge University Press.
- Lane, S. M., & Briffa, M. (2018). How does the environment affect fighting? The interaction between extrinsic fighting ability and resource value during contests. *Journal of Experimental Biology*, 221, 187740. <https://doi.org/10.1242/jeb.187740>.
- Lane, S. M., Wilson, A. J., & Briffa, M. (2020). Analysis of direct and indirect genetic effects in fighting sea anemones. *Behavioral Ecology*. in press.
- Leimar, O. (2019). Game theory models of animal contests: Are we at a standstill? A comment on Chapin et al. *Behavioral Ecology*, 30(5), 1190–1191. <https://doi.org/10.1093/beheco/arz144>.
- Lobregat, G., Kloss, T. G., Peixoto, P. E. C., & Sperber, C. F. (2019). Fighting in rounds: Males of a neotropical cricket switch assessment strategies during contests. *Behavioral Ecology*, 30, 688–696. <https://doi.org/10.1093/beheco/arz005>.
- McGinley, R. H., Prenter, J., & Taylor, P. W. (2015). Assessment strategies and decision making in male–male contests of *Servaa incana* jumping spiders. *Animal Behaviour*, 101, 89–95. <https://doi.org/10.1016/j.anbehav.2014.12.014>.
- Mesterton-Gibbons, M. (2019). Squaring the information triangle: A comment on Chapin et al. *Behavioral Ecology*, 30(5). <https://doi.org/10.1093/beheco/arz106>, 1187–1187.
- Mesterton-Gibbons, M., & Heap, S. M. (2014). Variation between self- and mutual assessment in animal contests. *American Naturalist*, 183(2), 199–213. <https://doi.org/10.1086/674443>.
- Mesterton-Gibbons, M., Marden, J. H., & Dugatkin, L. A. (1996). On wars of attrition without assessment. *Journal of Theoretical Biology*, 181(1), 65–83. <https://doi.org/10.1006/jtbi.1996.0115>.
- Palaoro, A. V., & Briffa, M. (2017). Weaponry and defenses in fighting animals: How allometry can alter predictions from contest theory. *Behavioral Ecology*, 28(1), 328–336. <https://doi.org/10.1093/beheco/arw163>.
- Palaoro, A. V., Velasquez, M., Santos, S., & Briffa, M. (2017). How does environment influence fighting? The effects of tidal flow on resource value and fighting costs in sea anemones. *Biology Letters*, 13(5). <https://doi.org/10.1098/rsbl.2017.0011>.

- Parker, G. A. (2019). So we all choose our own assessment rules?: A comment on Chapin et al. *Behavioral Ecology*, 30(5). <https://doi.org/10.1093/beheco/arr120>, 1188–1188.
- Parker, G. A., & Rubenstein, D. I. (1981). Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. *Animal Behaviour*, 29(1), 221–240. [https://doi.org/10.1016/S0003-3472\(81\)80170-4](https://doi.org/10.1016/S0003-3472(81)80170-4).
- Payne, R. (1998). Gradually escalating fights and displays: The cumulative assessment model. *Animal Behaviour*, 56(3), 651–662.
- Payne, R., & Pagel, M. (1997). Why do animals repeat displays? *Animal Behaviour*, 54(1), 109–119. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/9268441>.
- Peixoto, P. E. C., & Benson, W. (2012). Influence of previous residency and body mass in the territorial contests of the butterfly *Hermeuptychia fallax* (Lepidoptera: Satyrinae). *Journal of Ethology*, 30, 61–68.
- Pinto, N. S., Palaoro, A. V., & Peixoto, P. E. C. (2019). All by myself? Meta-analysis of animal contests shows stronger support for self than for mutual assessment models. *Biological Reviews*, 94(4), 1430–1442. <https://doi.org/10.1111/brv.12509>.
- Prenter, J., Elwood, R. W., & Taylor, P. W. (2006). Self-assessment by males during energetically costly contests over precopula females in amphipods. *Animal Behaviour*, 72, 861–868. <https://doi.org/10.1016/j.anbehav.2006.01.023>.
- R Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Reddon, A. R., Voisin, M. W., Menon, N., Marsh-Rollo, S. E., Wong, M. Y. L., & Balshine, S. (2011). Rules of engagement for resource contests in a social fish. *Animal Behaviour*, 82, 93–99.
- Rillich, J., Schildberger, K., & Stevenson, P. A. (2007). Assessment strategy of fighting crickets revealed by manipulating information exchange. *Animal Behaviour*, 74, 823–836.
- Rudin, F. S., & Briffa, M. (2011). The logical polyp: Assessments and decisions during contests in the beadlet anemone *Actinia equina*. *Behavioral Ecology*, 22(6). <https://doi.org/10.1093/beheco/arr125>.
- Rudin, F. S., & Briffa, M. (2012). Is boldness a resource-holding potential trait? Fighting prowess and changes in startle response in the sea anemone, *Actinia equina*. *Proceedings of the Royal Society B: Biological Sciences*, 279(1735). <https://doi.org/10.1098/rspb.2011.2418>.
- Smith, M. R. (2017). Ternary: An R package for creating ternary plots. *Zenodo*. <https://doi.org/10.5281/zenodo.1123463>.
- Stockley, P., & Campbell, A. (2013). Female competition and aggression: Interdisciplinary perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368. <https://doi.org/10.1098/rstb.2013.0073>.
- Taylor, P. A., & Elwood, R. W. (2003). The mismeasure of animal contests. *Animal Behaviour*, 65(6), 1195–1202. <https://doi.org/10.1006/anbe.2003.2169>.
- Tedore, C., & Johnsen, S. (2015). Visual mutual assessment of size in male *Lysomanes viridis* jumping spider contests. *Behavioral Ecology*, 26(2), 510–518. <https://doi.org/10.1093/beheco/aru222>.
- Tibbetts, E. A., Mettler, A., & Levy, S. (2010). Mutual assessment via visual status signals in *Polistes dominulus* wasps. *Biology Letters*, 6(1), 10–13. <https://doi.org/10.1098/rsbl.2009.0420>.
- Viera, M. C., & Peixoto, P. E. C. (2013). Winners and losers: A meta-analysis of functional determinants of fighting ability in arthropod contests. *Functional Ecology*, 27(2), 305–313.
- Wise, S. E., & Jaeger, R. G. (1998). The influence of tail autotomy on agonistic behaviour in a territorial salamander. *Animal Behaviour*, 55, 1707–1715.
- Xu, M., & Fincke, O. M. (2015). Ultraviolet wing signal affects territorial contest outcome in a sexually dimorphic damselfly. *Animal Behaviour*, 101, 67–74. <https://doi.org/10.1016/j.anbehav.2014.12.018>.

Appendix 1. R code for an example ternary plot

This code plots the positions of various assessment strategies described in the animal contest literature, and can be modified to plot results from empirical analyses (or additional theoretical assumptions).

```
library("Ternary") # required package
```

#1. PLOT AREA

```
TernaryPlot(alab='Opponent RHP', blab= 'RV', clab= 'Self RHP', point='up', lab.cex=2.0,
axis.cex = 1.5, grid.minor.lines = 0, grid.lty='solid', col=rgb(0.9, 0.9, 0.9), grid.col='white',
axis.col=rgb(0.6, 0.6, 0.6), ticks.col=rgb(0.6, 0.6, 0.6), padding=0.08)
```

#2. POINTS

```
data_points <- list(
  SA = c(0, 0, 100),           #pure SA
  "MA 1" = c(50, 0, 50),      #balanced MA
  OA = c(100, 0, 0),          #pure OA
  "MA 2" = c(30, 0, 70),      #unbalanced MA (more information about self)
  RA = c(0, 100, 0),          #RA only
  "SA & RA" = c(0, 40, 60),    #SA and RA
  "MA & RA" = c(30, 40, 30),   #MA and RA
  "OA & RA" = c(60, 40, 0))    #OA and RA
```

#3. PLOT

```
AddToTernary(points, data_points, bg=vapply(data_points, function (x) rgb(x[1], x[2], x[3],
35, maxColorValue=100), character(1)), pch=21, cex=4)
AddToTernary(text, data_points, names(data_points), cex=0.8, font=2)
```

Appendix 2. Example R code for simulated self-assessment data, with subsequent analysis and plotting

```

library("rsq") # required package

#### SIMULATE DATASET

## 1. GENERATE INITIAL CONTEST DURATION DATA

x1 <- rnorm(100, 50, 10) #n=100, mean = 50, SD = 10

## 2. GENERATE THREE FURTHER COLUMNS FOR self RHP, opponent RHP, RV

# x2, x3, and x4 in a matrix, these will be modified in step (4) to meet the criteria set out in
# steps (1) and (3)

x234 <- scale(matrix( rnorm(300), ncol=3 )) #2 = sRHP, 3 = oRHP, 4 = RV
x1234 <- cbind(scale(x1),x234) # put all into 1 matrix for simplicity
c1 <- var(x1234) # find the current correlation matrix
chol1 <- solve(chol(c1)) # Cholesky decomposition for independent predictors
newx <- x1234 %*% chol1
# check for independence and x1 unchanged
zapsmall(cor(newx))
all.equal( x1234[,1], newx[,1] )

## 3. SPECIFY DESIRED CORRELATION STRUCTURE

# To specify the desired relations between predictor variables and Duration
# For SA simulation, sRHP v Duration = 0.8, oRHP v Duration = 0.2, RV v Duration = 0
# all other correlations (i.e. among predictor variables) set to zero

newc <- matrix(
  c(1, 0.8, 0.2,
    0.8, 1, 0, 0,
    0.2, 0, 1, 0,
    0, 0, 0, 1), ncol=4 )

# check that it is positive definite
eigen(newc)
chol2 <- chol(newc)

```

```

finalx <- newx %*% chol2 * sd(x1) + mean(x1)
# verify success
mean(x1)
colMeans(finalx)
sd(x1)
apply(finalx, 2, sd)
zapsmall(cor(finalx))
pairs(finalx)
all.equal(x1, finalx[,1])

# Put the final simulated data into a data frame for inspection and analysis
# Column means and SD will all be as specified in 1.
SA_data<-data.frame(finalx)

## 5. MAKE SELF RHP LOWER THAN OPPONENT RHP; RENAME COLUMNS FOR
CONVENIENCE

dur <-SA_data $X1
sRHP <-SA_data $X2 *0.8
oRHP <-SA_data $X3
RV <-SA_data $X4

## 6. VALIDATION OF SIMULATED DATA

#check desired correlations still exist
plot(dur, sRHP)
plot(dur, oRHP)
plot(dur, RV)
plot(oRHP, sRHP)

cor.test(dur, sRHP, method="pearson")
cor.test(dur, oRHP, method="pearson")
cor.test(dur, RV, method="pearson")
cor.test(sRHP, oRHP, method="pearson")

# t-test to confirm loser (self) RHP lower than opponent RHP
t.test(sRHP,oRHP,paired=TRUE)
#End of data simulation for self assessment

### ANALYSIS OF SIMULATED SELF ASSESSMENT DATA

sRHP.m <-lm(dur ~ sRHP + oRHP + RV)
summary(sRHP.m)
anova(sRHP.m)

```

(continued).

```
### TERNARY PLOT OF ANALYSIS OF SIMULATED SA DATA
```

```
## 1. EXTRACT PARTIAL R2 FOR EACH TERM (from model)
```

```
PRSQ<-rsq.partial(sRHP.m)
PRSQ$partial.rsq #list for use in tables etc.
RSQ.sRHP <-PRSQ$partial.rsq[1]
RSQ.oRHP <-PRSQ$partial.rsq[2]
RSQ.RV <-PRSQ$partial.rsq[3]
```

```
## 2. SET UP THE PLOT AREA
```

```
# use code from appendix 1, section 1. PLOT AREA
```

```
## 3. PLOT OUT PARTIAL RSQ FOR sRHP, oRHP & RV
```

```
data_point.1 <- c(RSQ.oRHP, RSQ.RV, RSQ.sRHP)
data_point.2 <- c(0, RSQ.RV, RSQ.sRHP) # positive correlation for oRHP set to 0
```

```
AddToTernary(points, data_point.1,pch=19, cex=1.5, col="blue")
AddToTernary(points, data_point.2,pch=21, cex=1.5, lwd= 2, col="blue")
```

(continued).