

## Using ternary plots to investigate continuous variation in animal contest strategies.

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## **Abstract**

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 been recently 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 (RV) 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.

**Keywords:** Contest, fighting, assessment, decision, RHP, RV, resource, winner, loser,

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 self assessment (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). In contrast, in models founded on an assumption of mutual assessment, 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 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 categorised 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 et al. 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 broad scale 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 characterising 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 utilise information on self RHP, while mutual assessment 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 (a) no information or (b) perfect information about opponent RHP in addition to perfect information about self RHP (Crowley, 2000). By extension, this implies that in cases of mutual assessment, 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 and 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. Prenter et al. (2006) discussed the possibility of partial mutual assessment by male amphipods fighting over ownership of pre-copula females. They suggested that each contestant would have good information about their own ability but might have less information about that of their opponent 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 in the social cichlid fish *Neolamprologus pulcher* (Reddon, Voisin, Menon *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 & 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 mutual assessment 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 (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, Peixoto, & Briffa, 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 MA as a continuum, defined by the proportional contribution of information on self and opponent RHP. Viewed in this way, any example of mutual assessment 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 (a) its reliability and (b) 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 the value of the resource (see Humphries, Hebblethwaite, Batchelor, & Hardy, 2006 for a discussion of resource value 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 represent the information contribution of self RHP, opponent RHP and resource value on decision rules made by losers (Fig. 1; see below for detailed discussion). We previously used this type of ternary plot to summarise 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 those 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 figure 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 2017)). If losers give up using a strategy of SA-only, all the information that they use to reach this 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 figure 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 mutual assessment, 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 figure 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, Elwood, & Taylor 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 resource value 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 the value of the resource, 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 (a) the proportion of the theoretical maximum persistence time that they are willing to fight up to in the case of a SA-only strategy, (b) the strength of opponent

that they are willing to persist against in the case of a OA-only strategy and (c) 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 figure 1, the point marked OA & RA represents a strategy based on a combination of information on the strength of the opponent and the resource value, 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 figure 1 is dragged from the midpoint 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 in 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 emphasised 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 characterising 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 emphasises 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 characterise 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 re-visiting 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 (i) injuries and (ii) 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 actually settled through SA (as assumed for example by the cumulative assessment model, CAM; 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 opponent assessment 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 opponent assessment 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 non-injurious, 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 a SA scenario without resource

assessment (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 dataset, checking that the expected correlations (specified above) were still present (Pearson correlations: duration v self RHP;  $r_{98} = 0.8$ , duration v opponent RHP;  $r_{98} = 0.2$ , duration v RV;  $r_{98} = -2.8 \times 10^{-17}$ , self RHP v 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 & 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 dataset (Table 2a). 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 Figure 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). It is important to 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 figure 2a, the solid point for simulated self assessment 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 self-assessment 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 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, figure 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 opponent assessment. Operationally, this would simply mean setting opponent RHP partial  $R^2$  value to zero if the slope of opponent RHP and contest duration is positive.

In the case of genuine mutual assessment, 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 figure 2b represents an analysis of data that simulate MA. Following the process described above, we generated a dataset 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 dataset yielded the following correlations (duration v self RHP,  $r_{98} = 0.7$ ; duration v opponent RHP  $r_{98} = -0.6$ ; duration v RV,  $r_{98} = 0.1$ ; self RHP v 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 2b). As expected, plotting the partial  $R^2$  values of the three predictors resulted in a point on the ternary plot close (but not directly on) to the side linking SA and OA, and closer to the SA vertex than to the OA vertex (Fig. 2b). Thus,



this example represents a mutual assessment 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 resource value, 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 mutual assessment combined with resource value 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 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 value resource. 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 v self RHP,  $r_{98} = 0.3$ ; duration v opponent RHP,  $r_{98} = -0.4$ ;

duration v RV,  $r_{98} = 0.5$ ; self RHP v 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 2c). The plot of this result (Fig. 2c) again represents contests that are settled by mutual assessment. In contrast to the result plotted in figure 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 resource value. 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, Hebblethwaite, Batchelor & Hardy, 2006). In these cases, data should be cross-tabulated by role and outcome, to subset into 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 utilised by individuals adopting different roles.

### **Using ternary plots to characterise real contests**

In order 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 neo-tropical 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 (a) the extrinsic RHP of both opponents prior to fighting (through exposure to either hypoxic or normoxic conditions) and (b) resource value 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 seawater; low RV = still seawater). 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 only contribute to RHP 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 (Vieira & Peixoto 2013, Pinto et al. 2019), 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 opponent assessment, and resource assessment. However, it is obvious from the  $R^2$  values that none of these variables contribute 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 the vast majority of variation in contest duration.

Further inspection of the results give another reason to be cautious about figure 3a. As well as being non-significant, the coefficients for both self and opponent RHP are negative (Table 3a). 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 (non-significant) effects in both cases, suggest that perhaps body size is not an appropriate measure of RHP in this dataset. Body size has previously been shown to reliably predict contest outcome in *A. equina*, but only in non-injurious fights (Rudin & Briffa 2011). As the majority of fights in the current dataset 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. Rudin & Briffa 2011, Briffa 2014). 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 non-significant 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 (figure 3a), we would not recommend doing this routinely. While figure 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 (figure 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 all a point that represents all three parameters on the ternary plot because the proportionate effect of a non-significant variable would be very low in relation to the other parameters of interest; alongside a second point that excludes the influence of non-significant effects. In the following paragraph, we describe this exact situation, based on further analyses of the anemone data (Lane & Briffa 2018). In figure 3b-c, described in detail below, we compare the plots that result from excluding and including non-significant 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 self assessment. The ternary plots produced using the partial  $R^2$  taken from the linear model illustrates these relative contributions. Regardless of whether the non-significant 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 & 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 (non-significant) correlation with winner RHP, again predominantly characteristic of self assessment (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 resource value, 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 principle components 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 & 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 among 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 lift their hind legs repeated times. Some fights may escalate to the second phase in which males orient in opposite directions against each other, cross their hind legs and perform pushes and kick attempts. Once in the second phase, fights never de-escalated and 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 loser's hind femur length ( $r_{37} = 0.42$ ,  $P = 0.008$ ) and presented a near significant negative trend with winners 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 vs 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 figure 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 circles 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 circles. Figure 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 figure 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 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, Peixoto, & Briffa, 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) only describes 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 resource value 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 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 resource value (with subjective resource value 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 individual 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 figure 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 mutual assessment (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. Due 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 broad scale information on where future modelling efforts would be best focussed (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.

#### **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)
```

```
## 4. APPLYING SPECIFIED CORRELATION STRUCTRE AND SPECIFIED MEAN
#AND SD ACCROSS ALL COLUMNS
```

```
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)
```

```
### 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")
```

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**Table 1:** Strategies that losers could use to reach their giving up decision, and the sources of information that these strategies depend on.

<b>Name</b>	<b>Abbreviation</b>	<b>Definition and notes</b>
<i>Strategies</i>		
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.
<i>Sources of information</i>		
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 figure 1, these strategies described above are plotted as points within a ternary plot where the three sources of information represent the axes.

**Table 2:** Summary statistics for linear models on simulated datasets.

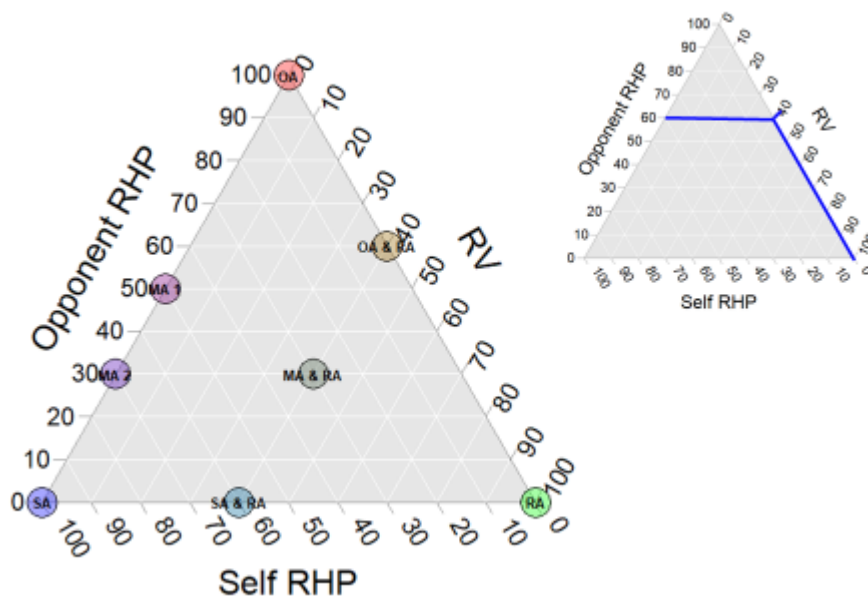
	df	<i>b</i>	partial $R^2$	<i>F</i>	<i>P</i>
<i>Simulated self-assessment</i>					
Self RHP	1	1.0	0.67	192	< 0.0001
Opponent RHP	1	0.2	0.11	12	< 0.0008
RV	1	$2.8 \times 10^{-16}$	$3.3 \times 10^{-16}$	0	1
Residuals	96				
<i>Simulated mutual assessment with a small RV contribution</i>					
Self RHP	1	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				
<i>Simulated mutual assessment with a categorical RV contribution</i>					
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 RV on contest duration. The analyses shown are illustrated in the corresponding parts of Figure 2.

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

	df	<i>b</i>	Partial $R^2$	<i>F</i>	<i>P</i>
<i>Continuous RHP (body size)</i>					
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				
<i>Continuous RHP (nematocyst length)</i>					
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				
<i>Categorical RHP (oxygen consumption)</i>					
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				

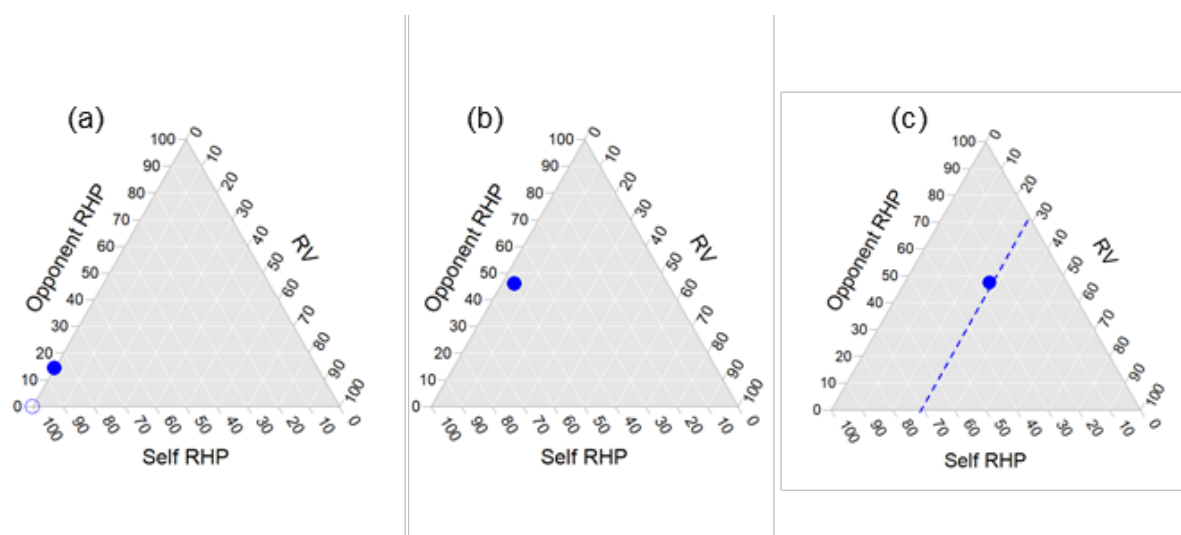
Effects of self (loser) RHP, opponent (winner) RHP and RV on contest duration, with body size, nematocyst length (injurious fights only) and oxygen consumption (categorical) as RHP measures. The analyses shown above are illustrated in the corresponding parts of figure 3.



**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 utilise 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 grid lines 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 a 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 mutual assessment). Similarly, MA2 has a score of 70

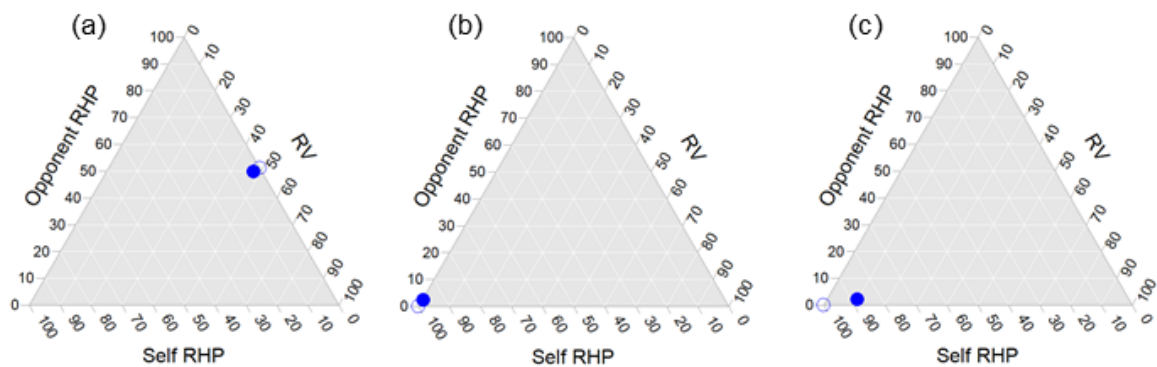


in the self RHP axis, 30 on the opponent RHP axis and 0 on the RV axis, and therefore plots out on the side linking (i.e. scores of 100) SA only and OA only. Similarly, the strategy marked OA & RA has a score of 0 on the self RHP axis, 40 on the RV axis and 60 on the opponent RHP axis. Since the decision 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.



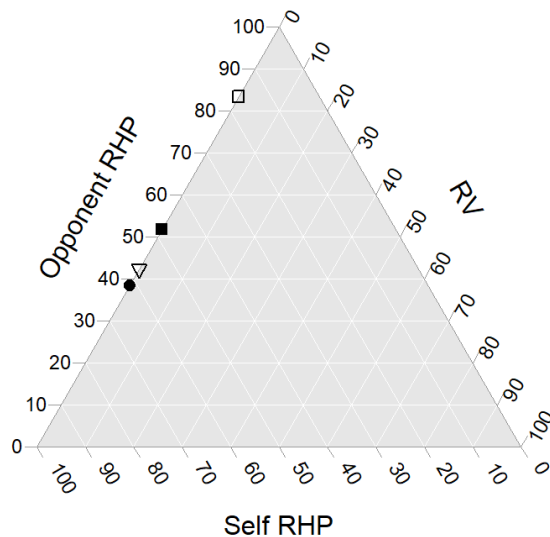
**Figure 2:** Ternary plots for data simulating fights settled through different types of decision rule. (a) Self Assessment. The solid point represents a plot where the variance due to the positive correlation between opponent RHP and duration is included. Since this positive correlation implies that 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. Due 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 here). In this example, information on the opponent's RHP has a greater influence on the giving up decisions of loser's than information on self RHP, since the data plots out closer to the OA only strategy than to the SA only strategy.



**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 in part (a) represent plots where only effects that are

consistent with the directions expected for known assessment strategies have been used, or where only effects that are statistically significant have been used (parts b and c).



**Figure 4:** A ternary plot illustrating inter-contest 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 those fights. These latter two categories are represented by open symbols because they did not contain any significant associations between RHP and contest duration.

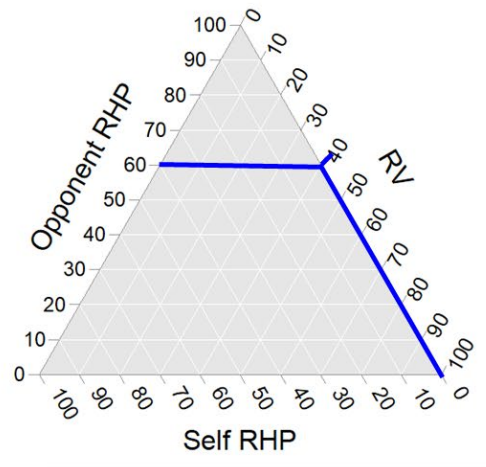
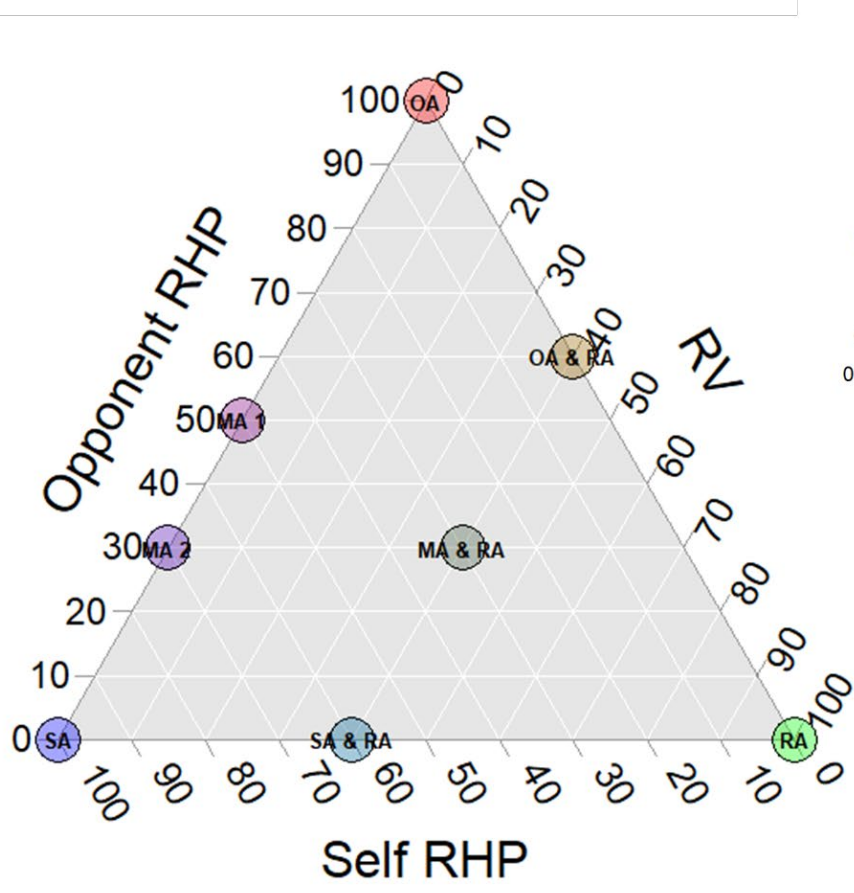
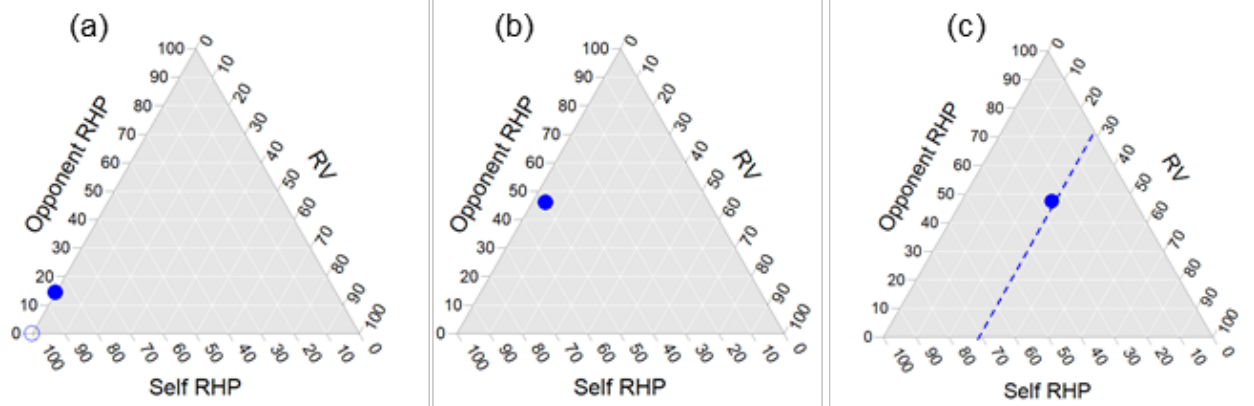


Figure 1.



**Figure 2.**

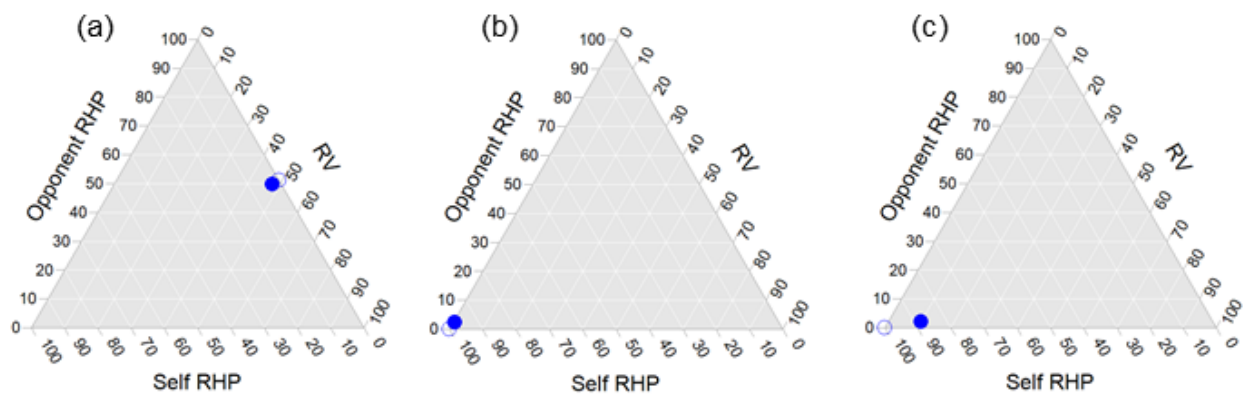


Figure 3.

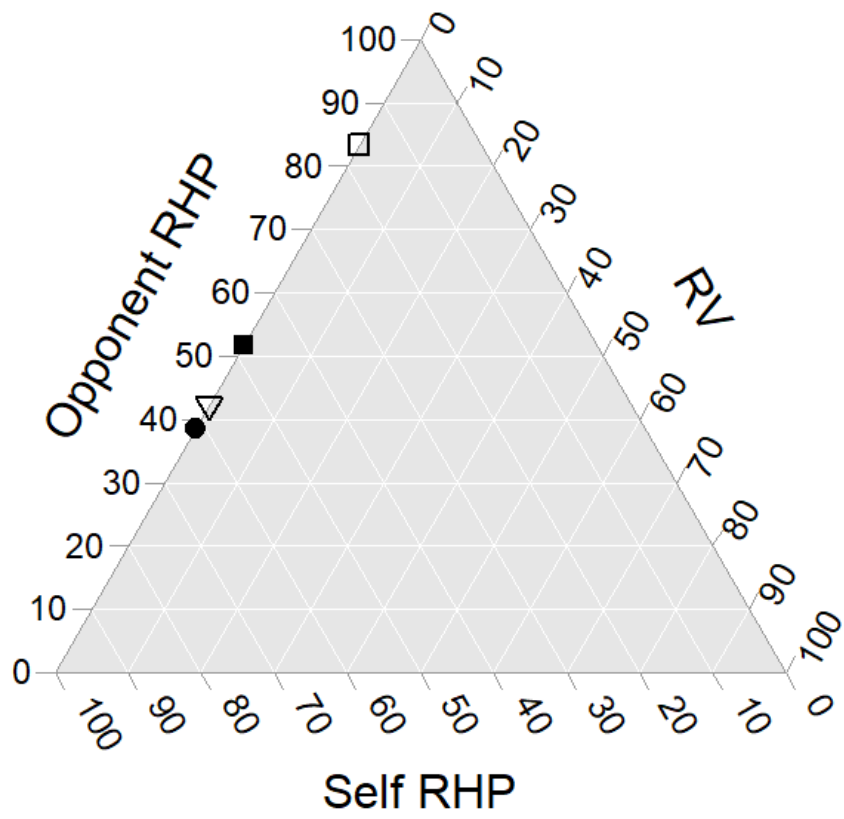


Figure 4.