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## **Weaponry and defenses in fighting animals: how allometry can alter predictions from contest theory**

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## Abstract

Theoretical models have been developed to understand how animals decide to withdraw from a contest. They provide testable predictions regarding the relationship between resource holding potential (RHP) and contest duration that assume linear relationships among RHP traits. However, RHP traits might scale with body size according to power laws. Furthermore, investment across different RHP traits may vary. Herein, we provide a model that encompasses the allometric relationship between body size and other RHP traits. First, we partition RHP traits into “offensive” traits (i.e., the ability to inflict damage) and “defensive” traits (i.e., persistence in a contest). Defensive traits may in turn be subdivided into “damage endurance” (DE) or the ability to absorb damage and “stamina.” We then model scenarios where: 1) there are power relationships among RHP traits; 2) individuals invest differently in defensive and offensive traits; 3) offensive traits and DE have a positive/negative relationship with body size. We modeled sized-matched injurious contests where 1) offensive capacity (OC) increases superlinearly with body size, 2) DE increases superlinearly, and 3) OC increases superlinearly but DE increases sublinearly. Our analyses indicate that if RHP traits scale linearly current predictions are upheld for injurious contests—contest duration increases with body size. However, with power relationships we can expect nonlinear relationships. Here, contest duration increased with body size until a maximum, decreasing afterwards. Thus, considering allometric relationships between body size and RHP traits may lead to new insights in animal contest theory and may help to solve discrepancies between current theory and empirical data.

Key words: assessment models, agonistic behavior, resource holding potential, contest duration, allometric scaling.

## Introduction

Animal contests resolve disputes over the ownership of a resource that influences fitness either directly (e.g., mating opportunities; Buzatto and Machado 2008) or indirectly (e.g., food, shelter; Bergman and Moore 2003). Typically, contests are terminated when 1 individual makes a decision to withdraw, and thus it is the losers rather than the winners that determine the duration of contests. This feature has been core to the analysis of how the giving up decision is made (e.g., Taylor and Elwood 2003; Arnott and Elwood 2009; Briffa and Elwood 2009). In such contests, a variety of components that contribute to the animals’ fighting abilities (i.e., resource holding potential, RHP sensu Parker 1974) are important in determining which opponent will win, because these traits determine how much the loser can endure before deciding to give up. RHP is thus typically associated with traits that increase/decrease the probability of winning a contest, such as body size, weaponry, and energy reserves (Arnott and Elwood 2009; Vieira and Peixoto 2013). However, the relationships between the different traits that contribute to an individual’s RHP are often assumed to be linear, whereas there are clear examples showing that this may not be the case (Copeland et al. 2011; Garcia et al. 2012). Analyses of RHP and contest duration typically focus on one (Garcia et al. 2014; Costa et al. 2016) or more (e.g., Briffa 2008; Rudin and Briffa 2011; Arnott and Elwood 2009; Junior and Peixoto 2013; Palaoro et al. 2014) of the traits that might contribute to overall RHP. However, there are, in fact, 2 types of within-individual relationship involving traits that could contribute to overall RHP and hence influence the duration of contests. First, there is the relationship between specific RHP traits and an individual’s overall RHP. Second, there are relationships

among the different traits that contribute to RHP. In both cases, the implicit assumption of the framework (Taylor and Elwood 2003) used to investigate giving up decisions is that these relationships should be linear. Later, we describe how this framework has been derived. We then go on to show that, while it is logical, its predictions should be modified if there is evidence for nonlinear relationships among RHP traits. We argue that such nonlinear relationships may be quite common in fighting animals and may have been overlooked. We show that nonlinear relationships can be important for contest duration whenever this is influenced by the difference in RHP between opponents (i.e., contests settled by both mutual- and self-assessment but involving damage; Briffa and Elwood 2009).

### *Models of the giving up decision and tests of their assumptions*

Several models have been developed to understand how individuals make the decision to quit. These models are based on how individuals accrue costs and what kind of information they use during contests—do they use information only about themselves (i.e., self-assessment; Arnott and Elwood 2009), do they incorporate information about their opponent into their decision (i.e., mutual assessment; Arnott and Elwood 2009), or do they only use information about their opponent (i.e., opponent-only assessment; Elwood and Arnott 2012)? These different assumptions underpin some of the most influential models of animal contests. All self-assessment models assume that individuals only use information about themselves, and war of attrition type models predict that individuals give up when they reach a threshold of costs (Bishop and Cannings 1978; Payne and Pagel 1997; Payne 1998). In contrast, models based on an assumption of mutual assessment, such as the Sequential Assessment Model (SAM) predict that losers should give up as soon as they perceive that they are the weaker opponent (Enquist and Leimar 1983), and, therefore, persisting until a cost threshold is reached is unnecessary. The opponent-only assessment is not a theoretical model but was proposed to explain some studies in which only the winner's RHP influenced the decision to quit—the loser reaches their cost-threshold based solely on the winner's RHP and not on information about his own RHP or cost-threshold (Elwood and Arnott 2012). Self-assessment models can be further subdivided into energetic wars of attrition (EWOA; Payne and Pagel 1997) and the cumulative assessment model (CAM; Payne 1998). The main difference between EWOA and CAM is that costs are accrued only through performance of costly displays under EWOA, whereas under CAM individuals can inflict damage on one another, with high RHP individuals inflicting more damage than individuals of lower RHP. Although most of these models make predictions regarding contest escalation patterns, most researchers focus on testing their assumptions (self-, mutual-, and opponent-assessment) based on the frameworks provided by Taylor and Elwood (2003), Arnott and Elwood (2009), Briffa and Elwood (2009), and Elwood and Arnott (2012). This empirical framework is based on relationships between RHP traits and contest duration (Table 1). These tests assume linear relationships between RHP traits and contest duration, which are evidenced by the widespread use of parametric regression to test predictions (e.g., Rudin and Briffa 2011; Junior and Peixoto 2013; Palaoro et al. 2014; McGinley et al. 2015; McLean and Stuart-Fox 2015; Wofford et al. 2015).

## *Animal growth and RHP*

A fundamental aspect of animal growth is the allometric nature of relationships between overall body size and the size of other traits including weapons (Emlen 2008), defenses (Lease and Wolf 2010; Swanson et al. 2013), and physiological capacities (Nilsson and Östlund-Nilsson 2008). Typically, as body size (e.g., length and mass) increases during development all other traits develop alongside it according to power relationships ( $\gamma = a_0 \times X^{a_1}$ , where  $\gamma$  is the trait size,  $X$  is body size,  $a_0$  is the normalization constant, and  $a_1$  is the scaling exponent; Huxley 1924) rather than linear relationships. Huxley (1924) also noted that you could linearize this power relationship by log transforming the variables before regressing it ( $\log(\gamma) = b_0 + b_1 \times \log(X)$ , where  $\log(\gamma)$  is the log-transformed trait size,  $\log(X)$  is the log-transformed body size,  $b_0$  is the intercept, and  $b_1$  is the slope; Huxley 1924)—but this is not the same as linearly scaling variables and you are assuming that the traits have a common developmental pathway (Pélabon et al. 2014). Consequently, it is expected that the capacities of specific RHP components (e.g., the ability to inflict damage, to absorb damage, and physiological endurance) might also show nonlinear changes with overall body size. Such differential investment across different RHP traits is well documented because it may lead to extreme morphologies (Nijhout and Emlen 1998; Emlen and Nijhout 2000). An example of this in the context of weaponry is the horns of beetles, which in some species increase with a slope of 2.5, whereas legs, wings, and elytra increase with a slope of 1 with body size, and the eyes increase with a slope of 0.65 (Johns et al. 2014). This means that there may be a disconnection between the RHP itself and how we deal with the relationships among RHP traits. Copeland et al. (2011) and Garcia et al. (2012) highlighted this disconnection between RHP and body size/physiological competence—because RHP is an overall complex of different traits, it may not increase linearly with body size as previously thought. This leads to the key reason why growth allometries need to be considered in analyses of animal contests: if overall RHP scales nonlinearly with overall size, then RHP differences between larger and smaller individuals could be markedly greater or smaller than would be expected if linear relationships between RHP and body size are assumed. Moreover, if relationships between body size and the different traits that contribute to different aspects of RHP are not equivalent, then our ability to infer decision rules from RHP–duration relationships would be further complicated. This could be one of the reasons why Vieira and Peixoto’s (2013) meta-analysis did not find support for the role of physical strength in contests that involve physical contact or for physiological endurance in contests that do not involve physical contact. The problem is not in the selection of RHP traits (Vieira and Peixoto 2013), but maybe in how we are incorporating the relationship among the RHP traits and between RHP and contest duration. The possibility of differential relationships between different RHP components and overall body size seems particularly important in contests that involve direct physical contact. Such contests involve both inflicting and absorbing damage, each of which is dependent on different components of RHP. Causing damage should be related to the weapon used by the attacker, whereas enduring damage is related to defensive components of RHP, such as the thickness of exoskeletons and physiological endurance (e.g., Green and Patek 2015). As different parts of RHP are being used, there is the potential for differential investment in the relative abilities to inflict and to resist damage, such as the aforementioned example of the beetle. In this case, the empirical predictions for the assessment models about the relations between RHP and contest duration (Table 1) may not hold true. Thus, different types of allometric relationship between weapons, endurance, and stamina may offer a potential explanation for the discrepancy between current models and empirical

evidence (Fawcett and Mowles 2013; Vieira and Peixoto 2013), especially those from contests with injuries. This possibility seems most important for contests settled by self-assessment, as assumed in the CAM and EWOA models. In the case of CAM, for example, it is assumed that the damage caused by the opponent has a fixed value, rather than increasing with size (Payne 1998). Similarly, in tests of the EWOA, we assume that physiological endurance scales linearly with body size. Therefore, we model scenarios in which defensive (i.e., resisting damage and endurance) and offensive capacities (i.e., causing damage) are separate RHP traits that might scale differently from each other (e.g., offensive RHP might scale faster with size than the defensive RHP, e.g., sea anemones; Rudin and Briffa 2011), and compare our results with current predictions. Second, we model scenarios in which these traits might scale nonlinearly with size and also compare these with current predictions (Table 1). First, we provide a predictive model for contest duration based on underlying assumptions of the CAM. Our goal is to expand the empirical framework proposed by Taylor and Elwood (2003) by accounting for RHP traits that scale nonlinearly with body size. As described above, weapons might increase in size and strength during development at a different rate than defenses (e.g., the thickness of the cuticle or epithelium) or other physiological traits that contribute to endurance. We therefore compare scenarios with linear and power relationships for the development of RHP traits and make predictions in each case for relationships between body size and contest duration. We show that under these conditions we should not necessarily expect a positive linear relation between RHP and contest duration in contests settled via self-assessment. Second, we test whether the RHP of a pair of larger-sized individuals will vary more than the RHP of a pair of smaller-sized individuals for RHP under both scenarios (i.e., linear and nonlinear scaling). We argue that although the role of damage and trait allometry has been investigated empirically, it has yet to be incorporated into the body of contest theory dealing with assessment rules. Thus, we hope to pave the way for further development of this subject.

### **Partitioning RHP traits: the role of damage endurance, stamina, and offensive capacity**

In our model, we focus on how much damage an individual can endure (henceforth “damage endurance” [DE]) and how much damage an individual can inflict (henceforth “offensive capacity” [OC]). Before considering the role of DE it is necessary to partition it from other variables that can influence an individual’s maximum persistence time in a fight. First, there is another form of endurance commonly discussed in studies of animal contests. This is generally defined as the ability to sustain demanding activity and is described as stamina or “endurance capacity.” In fact, stamina and DE are often considered together, such that fighting animals must pay a single pooled cost: the sum of injuries received and the metabolic costs of fighting that have accrued. We further note that these combined forms of endurance are often referred to as “RHP”; but during injurious fights, RHP will also be influenced by OC. Therefore, we consider DE, stamina, and OC as distinct RHP traits. Stamina and DE are the only traits that should influence a focal individual’s maximum persistence (although in real animals the 2 traits might covary; Figure 1), whereas OC affects the time taken to push the focal individual’s opponent towards its own maximum threshold. Finally, there is a third source of variation that could interact with stamina and DE to produce an individual’s maximum persistence time. We denote this (loosely) as “motivation,” which could be influenced by a range of intrinsic and

extrinsic factors (i.e., resource value). We do not deal specifically with variation in motivation here, but we note its potential role in modifying maximum persistence. Motivation does not influence the maximum OC, DE, and stamina of a fighting individual. Rather, motivation will determine what proportion of these capacities an individual is willing to commit to the contest. Therefore, motivation interacts with these RHP traits to produce the behavioral outputs that researchers measure in studies. Figure 1 shows the relationships between these different sources of variation and maximum persistence time.

### *Nonlinear scaling of offensive and defensive RHP*

Endurance is a property of an individual's morphology and physiological state, and should not be influenced by any other factors. Crucially, both types of endurance are intrinsic traits of the individual, liable to variation with a tendency to increase during growth. In the case of stamina, it is well recognized that greater energy reserves in larger individuals (mammals: Lindstedt and Boyce 1985; fish: Schultz and Conover 1999; insects: Hahn and Denlinger 2007) can allow them to persist for longer in a fight, both by being able to bear greater costs and by having more energy to perform costly aggressive acts. Similarly, in the case of DE there might be increased defences against damaging weapons in larger individuals. For example, thicker exoskeletons in larger arthropods (Lease and Wolf 2010) should increase the DE, again allowing for greater persistence. The same reasoning can be applied to OC. As the individual develops, weapons can increase in efficiency thus causing more damage, as seen in crustaceans' claws (Palaoro et al. 2014), lizards' jaws (Lappin and Husak 2005), and mammalian jaws and forelimbs (Morris and Carrier 2016), for example. This increase in efficiency usually occurs because of the steep allometric slopes (or high scaling exponent) these weapons show. Beetles are a good example of steep allometric slopes, because some species can scale their horns with a slope of up to 4.67 (McCullough et al. 2015). Frogs can also show high scaling exponents when we regress body size with their arm girth, which can also change according to the competition they face during mating season—sites with lower male densities have frogs with thicker arms (Buzatto et al. 2015). Literature is laden with examples of steep allometric slopes and high scaling exponents between body size and weapons, thus, it is clear that weapons are increasing damage at a nonlinear rate (McCullough et al. 2015; Voje 2016). During development, both DE and OC may vary. In some instances, causing damage may be more important and so OC may increase at a greater rate during development in comparison with DE (e.g., damages in the claws of crustaceans or the broken beetle horns; Rojas et al. 2012; McCullough 2014, respectively), while in other instances the opposite may be true (e.g., mantis shrimps' abdomen carapace that absorbs the damage of the striking appendage, Green and Patek 2015). In the case of damage, the capacities to inflict and endure it might be dependent upon different traits (e.g., Green and Patek 2015). If these traits associated with injurious fighting scale differently, this may lead to a decoupling of offensive and defensive capacities (e.g., physical contact in fallow deer; Jennings et al. 2010), a possibility that does not have formal predictions based on any model of contest behavior. Indeed, although models such as the CAM allow attack rate to vary, they do not incorporate the possibility that the severity of damage inflicted can vary (Payne 1998; Kokko 2013). In the next section, we present our model that considers the variation in DE and OC, also considering 2 types of trait scaling—linear and power scaling.

## Model specifications

We only modelled contests between size-matched opponents because this is the situation where the importance of both offensive (i.e., the ability to inflict damage) and defensive RHP is likely to be starkest in most taxa (Hardy and Briffa 2013). Indeed, when opponents are size-matched other traits than size become more important in deciding contests (e.g., weaponry, Sneddon et al. 2000; Lailvaux et al. 2005; Kelly 2006; physiological competence, Copeland et al. 2011; Junior and Peixoto 2013). Nevertheless, our model could also be parameterized for asymmetric (in terms of body size) contests. OC, DE, and stamina scaled either linearly or nonlinearly with body size (see below). We used body size values between 1 and 100 in intervals of 1, using the following equation for linear relationships between RHP and body size:

$$\gamma = 1 + b \times x \quad (1)$$

Where  $\gamma$  is the RHP trait, 1 is the value of the intercept,  $b$  is the slope, and  $x$  is the body size. We kept the value of the intercept at 1 because altering it would mainly increase the starting value of the RHP trait, which in turn could prevent the comparisons between the models starting value due to the additive or multiplicative nature of this part. By keeping it at 1, we simplified interpretations and made both models more directly comparable due to the low influence of the intercept and the normalization constant. When RHP traits scaled nonlinearly, we used the following equation:

$$\gamma = 1 \times x^a \quad (2)$$

Where  $\gamma$  is the RHP trait, 1 is the normalization constant,  $a$  is the scaling exponent, and  $x$  is the body size. The slopes (Equation 1) and scaling exponents (Equation 2) were modelled between 0.5 and 2 because values beyond these limits are rare in nature (Voje 2016). Although we modelled a range of values, only the most representative were used for the figures and analyses here. We also provide the model in the Supplementary Files alongside an R-code. Stamina and motivation were considered invariant and did not covary with OC and DE. Note that in the case of motivation this means that any damage that an individual attempts is equal to its OC, because low motivation could reduce the amount of damage attempted (e.g., Condon and Lailvaux 2016) but high motivation cannot increase it beyond the upper limit of OC. Furthermore, the individual that starts the contest and inflicts the damage on the opponent is decided by chance—this rule was used when calculating contest duration, but not when we only calculated the RHP of the individuals (see below). To calculate contest duration, we used the following equation:

$$Cd = \text{Stamina (receiver)} + \text{OC (initiator)} - \text{DE receiver} \quad (3)$$

Where  $Cd$  is the contest duration, OC is the offensive capacity, and DE is the damage endurance. In case of negative  $Cd$  we considered it zero. We highlight that we kept motivation fixed at 1 and that is why OC, DE, and stamina are directly used in the calculation of contest duration. For simplicity, motivation was fixed at 1 in each of the following simulations. Therefore, we assume that both opponents are equally motivated (i.e., place the same value on the resource) and that both will commit all available offensive and defensive capacities to the contest. Within the 2 types of RHP scaling patterns we developed 3 scenarios. The first scenario is where OC scales with an exponent higher than 1 (i.e., it increases super-linearly) and DE is fixed at 1 (i.e., it increases linearly). The second scenario is where DE scales with an exponent higher than 1 and OC is fixed at 1. In the last scenario, we tried to simulate a more biologically relevant result. As it is perfectly plausible that OC and DE might covary, we simulated a



scenario in which OC increases superlinearly (slope or scaling exponent  $> 1$ ), and DE increases sublinearly (slope or scaling exponent  $< 1$ ). In other words, both OC and DE could be either linearly or nonlinearly related to body size. In each case, we analysed the effects of RHP variation on contest duration, across a range of scaling component values, thus providing similar predictions as what is currently used for the assessment models. Modelling was performed with Microsoft Excel. To test if RHP varies more between fights of larger individuals than between fights of smaller individuals, we extracted the 30 highest and 30 lowest body sizes from a simulated population ( $N = 200$ , mean = 50, standard deviation = 20) and these were our focal individuals. To generate RHP-matched opponents with a difference corresponding to what is regularly used in the current animal contest literature (Briffa et al. 2013), we multiplied the body size of the focal individual by 0.75, thus generating individuals that were 15% smaller than the focal individual. We then calculated the RHP component for both individuals (i.e., focal individuals and opponents) in the same way we did for first scenario. Specifically, we used Equations 1 and 2 and varied only the OC slope or scaling exponent superlinearly ( $>1$ ). Although we ran the same slopes and scaling exponents as in the previous analysis, we chose only the most relevant to show here. As our goal is to test the difference in the RHP components between the pair, we used only the component that scaled superlinearly (i.e., OC) to test that prediction. We thus subtracted the OC of the focal individual by the OC of the opponent. We tested the differences among groups (i.e., large vs. small pairs and linear vs. nonlinear scaling) using a 2-way Anova. These analyses were run in the R software (R Development Core Team 2015).

## **RHP trait scaling and model predictions**

### *Linear and nonlinear scaling for RHP traits with body size*

Figure 2 illustrates how RHP traits might scale according to body size across the range of scenarios that we simulated. In comparison with simple linear relationships, subtle increases in body size can result in large differences between RHP traits when they scale in a power relationship with body size (e.g., Figure 2f). This is in accordance with weaponry growth studies, where changes in body size are accompanied by a large growth in the morphological trait (Emlen et al. 2012). The scaling factor of DE might also show nonlinear variation with overall body size. For instance, the relationship between exoskeletal chitin mass and body mass differs between flying insects (slope: 0.97) and nonflying insects (slope: 1.03; Lease and Wolf 2010). Although similar and near linear, these slopes are different from each other and from a linear scaling (slope: 1). *Uca* crabs are another potential example of disproportionate investment in weapons and defenses. Although their claws rarely break during combat, the cephalothorax can be easily indented (Swanson et al. 2013). Overall, these examples illustrate the point that we should expect disproportionate investment across different RHP traits during development.

## **Effects of linear and nonlinear scaling of RHP on contest duration**

Figure 3 illustrates differences in contest duration among scenarios where RHP traits scale linearly with body size and those with a power relationship with body size. When RHP traits scale linearly with body size (Figure 3a–c), Taylor and Elwood’s (2003) predictions for self-assessment size-matched contests are upheld—contest duration increases with loser body size indefinitely, regardless of the scenario. However, when RHP traits scale in a power law (Figure 3d–f), the predictions for contests resolved by self-assessment change dramatically. First, a nonlinear relationship between offensive RHP and body size (e.g., Figure 2d) produces a nonlinear relationship between duration and body size, i.e., a power relationship. Thus, the relationship can be sublinear (downward bend; Figure 3d), or superlinear (upward bend; Figure 3e), depending on the type of allometric relationship between body size and weapon size. When the OC (e.g., weapon size) increases sublinearly with body size, but DE increases linearly or superlinearly, DE will be greater than OC. This would lead to an upward bent curve indicating that contest duration increases exponentially (Figure 3e,f). On the other hand, when OC increases superlinearly with body size—and DE increases linearly or sublinearly—an interesting scenario that is not predicted arises. Under these scenarios, OC is increasing faster than DE. Thus, once a particular threshold of body size has been exceeded, OC will be greater than DE. This produces a curve with a maximum peak, which then decreases. In other words, damage will be so massive that losers will withdraw from the contest at an early time and contests will be short. Thus, as body size increases so does the mismatch between body size and the severity of damage. This scenario is possible when animals are under selective pressure to invest in powerful and efficient weapons. Weapons may increase in performance as the individuals grow such as claws and jaws (Lappin and Husak 2005; Dennenmoser and Christy 2013), and may have a larger investment than DE (or stamina) due to sexual selection (e.g., claws that break their opponent’s exoskeleton; Rojas et al. 2012). In some cases, weapons cause so much damage that they seem very likely to have increased in efficiency at a rate greater than the DE capacity. Examples include the forelimb spines of gladiator frogs, *Hypsiboas rosenbergi*, that can pierce opponent’s eyes or eardrums (Dyson et al. 2013), or the specialized fighting tentacles of the sea anemone, *Actinia equina*, that cause necrosis in the skin of the opponent (Rudin and Briffa 2011). These extreme forms of damage probably have very large contributions to the total costs of fighting, leading to the maximum persistence threshold being rapidly exceeded. This possibility was not considered either in the CAM (Payne 1998) or its predictions (Taylor and Elwood 2003; Table 1), which explicitly incorporates the costs of receiving damage but increasing in proportion with the accrual of energetic costs. In other words, the individual is always causing the same damage, what changes is the number of strikes delivered during the fight. When significant damage costs accrue very rapidly, however, the OC of the winner will have the most immediate effect on the loser’s decision to withdraw, while the loser’s stamina or DE will be less important. Therefore, during self-assessment contests the positive relationships between RHP traits and duration predicted by Taylor and Elwood (2003) might not describe such contests accurately. This increased importance of the winner’s RHP could also be a viable explanation for the opponent-only assessment. In this type of assessment the winner’s RHP is the most important factor to settle contests, being negatively correlated with contest duration (e.g., Rillich et al. 2007; Prenter et al. 2008; Reddon et al. 2011; Jennings et al. 2012; Peixoto and Benson 2012). It is possible that, in some of these studies, the winner is inflicting more costs than the loser is able to bear, which although not predicted in any of the current models, is predicted in our model. If true, then the opponent-only assessment may not be a model on its’ own, but rather an extension of the CAM in which

damage output increases with the size of the individual and this is not expected in the theoretical model. In this scenario, our model predicts that the physical contact part of the fight would be a short interaction with a high probability that 1 of the individuals is injured or physiologically exhausted shortly afterwards. It would thus be interesting to see some of these studies reanalyzed considering our model as an alternative.

### *RHP differences between small fighting pairs and large fighting pairs*

Our prediction that RHP would differ more in paired large individuals than in paired small individuals was corroborated, but not as predicted. We predicted that this difference would occur only in nonlinear scaling, but all groups differ from each other regardless of the scaling pattern considered (Table 2; Figure 4a–c). Despite this, difference in the OC was larger in nonlinear scaling than in linear scaling—small differences in the scaling exponent of OC caused a large increase in the difference between focals' and opponents' OC (i.e., the median increases as we increase the slope/ scaling exponent, Figure 4). In addition, when comparing variance within the same size-matching method (e.g., between small pairs), the variance was always larger under nonlinear scaling. Variance also increased more under nonlinear scaling (Figure 4a–c). Our results only reinforce the idea that RHP is not scaling linearly with body size (Copeland et al. 2011; Garcia et al. 2012)—RHP is scaling faster in larger individuals than they do in smaller individuals. This could be 1 of the factors influencing the variable level of support for the assessment models provided by empirical studies—we could be misinterpreting how the overall RHP is formed, typically assuming that different components are equivalent and that they all relate to overall RHP in the same ways.

### **Future directions for contests and RHP allometries**

As all RHP traits have the same importance in decision-making in our model, the role of stamina would be to decrease the impact that OC has on contest duration. We only take into account injurious contests, but in an escalating contest, stamina and DE would surely be important in different stages of the contest. In the beginning of the contest, where most displays occur, OC and DE would be irrelevant and stamina would be the sole RHP trait that determines contest duration. If this hypothetical contest continues to escalate to physical contact, then stamina would decrease in importance while OC and DE would increase their importance. This view is similar to the recently modeled switching assessment strategy (Mesterton-Gibbons and Heap 2014), but instead of switching from self to mutual assessment (or vice versa), individuals would rely on different RHP traits during different stages of the contest. Therefore, our model can also be further developed to incorporate different views of the importance of the RHP traits. Our model has divided the persistence component of RHP in 2 different traits: stamina and DE. While stamina has been the focus of research for quite some time and is relatively well understood for some species (Briffa and Sneddon 2007), DE has been largely neglected. A clearer understanding of how animals develop both OC and DE should provide new insights of contests where damage is an integral part of fighting. Biomechanical studies should prove invaluable to compare either within individuals or among populations. Another aspect that could provide further insights to animal contests is the covariation between stamina and the other RHP traits. As noted above, under some circumstances, DE and stamina might covary

during development, and thus, distinguishing between them might be difficult because it is possible that both of these traits use the same pathways to increase. Therefore, studies aiming to understand this covariation are needed.

## **Conclusion**

Herein, we have shown that a slight change in the assumptions commonly used to predict contest duration (i.e., the scaling of RHP traits) can alter the predictions for decision-making in a contest. Current predictions have implicitly assumed a linear relationship between RHP traits, and we show that if a more realistic view (i.e., body size-RHP traits scale with power relationship, and that damage increases during development) is taken into account, these predictions are altered. Furthermore, we also show that RHP scales faster in larger individuals than it does in smaller individuals, highlighting the allometric nature of the RHP. Understanding the influence of this inherent variation in RHP traits related to inflicting and receiving damage, and how they influence decision-making could be central to answering a persistent question in animal contest studies: how do losers decide to give up? Our analyses show that when RHP scales nonlinearly with body size, determining how this decision is made may require adjusting our expectations of linear relationships between RHP and duration. This logic applies to contests settled by mutual-assessment and to contests settled by self-assessment, as long as opponents inflict direct costs on one another using weapons. Additionally, this logic can also be applied to contests in which the winner's RHP is the most important driver of contest outcome (i.e., opponent-only assessment). In other words, nonlinear investment in weapons (and defenses) should influence the duration of any fights where the decision to quit is driven either by the difference in RHP between winners and losers, or solely by the RHP of the winner.

## *Supplementary material*

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>.

## **References**

- Arnott G, Elwood RW. 2009. Assessment of fighting ability in animal contests. *Anim Behav.* 77:991–1004.
- Bergman DA, Moore PA. 2003. Field observations of intraspecific agonistic behavior of two crayfish species, *Orconectes rusticus* and *Orconectes virilis*, in different habitats. *Biol Bull.* 205:26–35.
- Bishop DT, Cannings C. 1978. A generalized war of attrition. *J Theor Biol.* 70:85–124.
- Briffa M, Elwood RW. 2009. Difficulties remain in distinguishing between mutual and self-assessment in animal contests. *Anim Behav.* 77:759–762.

- Briffa M, Hardy IC, Gammell MP, Jennings DJ, Clarke DD, Goubault M. 2013. Analysis of animal contest data. In: Hardy ICW, Briffa M, editors. *Animal contests*. Cambridge (UK): Cambridge University Press. p. 47–85.
- Briffa M, Sneddon LU. 2007. Physiological constraints on contest behaviour. *Funct Ecol*. 21:627–637.
- Briffa M. 2008. Decisions during fights in the house cricket, *Acheta domesticus*: mutual or self-assessment of energy, weapons and size? *Anim Behav*. 75:1053–1062.
- Buzatto BA, Machado G. 2008. Resource defense polygyny shifts to female defense polygyny over the course of the reproductive season of a Neotropical harvestman. *Behav Ecol Sociobiol*. 63:85–94.
- Buzatto BA, Roberts JD, Simmons LW. 2015. Sperm competition and the evolution of precopulatory weapons: increasing male density promotes sperm competition and reduces selection on arm strength in a chorusing frog. *Evolution*. 69:2613–2624.
- Condon C, Lailvaux SP. 2016. Losing reduces maximum bite performance in house cricket contests. *Funct Ecol*. 30:1660–1664.
- Copeland DL, Levay B, Sivaraman B, Beebe-Fugloni C, Earley RL. 2011. Metabolic costs of fighting are driven by contest performance in male convict cichlid fish. *Anim Behav*. 82:271–280.
- Costa JR, Dalosto MM, Palaoro AV, Santos S. 2016. Contest duration and dynamics are affected by body size in a potentially subsocial crayfish (Crustacea: Decapoda). *Ethology*. 122:502–512.
- Dennenmoser S, Christy JH. 2013. The design of a beautiful weapon: compensation for opposing sexual selection on a trait with two functions. *Evolution*. 67:1181–1188.
- Dyson ML, Reichert MS, Halliday TR. 2013. Contests in amphibians. In: Hardy ICW, Briffa M, editors. *Animal contests*. Cambridge (UK): Cambridge University Press. p. 228–257.
- Elwood RW, Arnott G. 2012. Understanding how animals fight with Lloyd Morgan's canon. *Anim Behav*. 84:1095–1102.
- Emlen DJ, Nijhout HF. 2000. The development and evolution of exaggerated morphologies in insects. *Annu Rev Entomol*. 45:661–708.
- Emlen DJ, Warren IA, Johns A, Dworkin I, Lavine LC. 2012. A mechanism of extreme growth and reliable signaling in sexually selected ornaments and weapons. *Science*. 337:860–864.
- Emlen DJ. 2008. The evolution of animal weapons. *Ann Rev Ecol Evol Syst*. 39:387–413.
- Enquist M, Leimar O. 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. *J Theor Biol*. 102:387–410.
- Fawcett TW, Mowles SL. 2013. Assessments of fighting ability need not be cognitively complex. *Anim Behav*. 86:e1–e7.

- Garcia MJ, Murphree J, Wilson J, Earley RL. 2014. Mechanisms of decision making during contests in green anole lizards: prior experience and assessment. *Anim Behav.* 92:45–54.
- Garcia MJ, Paiva L, Lennox M, Sivaraman B, Wong SC, Earley RL. 2012. Assessment strategies and the effects of fighting experience on future contest performance in the green anole (*Anolis carolinensis*). *Ethology.* 118:821–834.
- Green PA, Patek SN. 2015. Contests with deadly weapons: telson sparring in mantis shrimp (Stomatopoda). *Biol Lett.* 11:20150558.
- Hahn DA, Denlinger DL. 2007. Meeting the energetic demands of insect diapause: nutrient storage and utilization. *J Insect Physiol.* 53:760–773.
- Hardy ICW, Briffa M. 2013. *Animal contests*. Cambridge (UK): Cambridge University Press.
- Huxley JS. 1924. Constant differential growth-ratios and their significance. *Nature.* 114:895–896.
- Jennings DJ, Carlin CM, Hayden TJ, Gammell MP. 2010. Investment in fighting in relation to body condition, age and dominance rank in the male fallow deer *Dama dama*. *Anim Behav.* 79:1293–1300.
- Jennings DJ, Elwood RW, Carlin CM, Hayden TJ, Gammell MP. 2012. Vocal rate as an assessment process during fallow deer contests. *Behav Processes.* 91:152–158.
- Johns A, Gotoh H, McCullough EL, Emlen DJ, Lavine LC. 2014. Heightened condition-dependent growth of sexually selected weapons in the rhinoceros beetle, *Trypoxylus dichotomus* (Coleoptera: Scarabaeidae). *Integr Comp Biol.* 54:614–621.
- Junior RSL, Peixoto PEC. 2013. Males of the dragonfly *Diastatops obscura* fight according to predictions from game theory models. *Anim Behav.* 85:663–669.
- Kelly CD. 2006. The relationship between resource control, association with females and male weapon size in a male dominance insect. *Ethology.* 112:362–369.
- Kokko H. 2013. Dyadic contests: modeling fights between two individuals. In: Hardy ICW, Briffa M, editors. *Animal contests*. Cambridge (UK): Cambridge University Press. p. 5–32.
- Lailvaux SP, Hathway J, Pomfret J, Knell RJ. 2005. Horn size predicts physical performance in the beetle *Euoniticellus intermedius* (Coleoptera: Scarabaeidae). *Funct Ecol.* 19:632–639.
- Lappin AK, Husak JF. 2005. Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *Am Nat.* 166:426–436.
- Lease HM, Wolf BO. 2010. Exoskeletal chitin scales isometrically with body size in terrestrial insects. *J Morphol.* 271:759–768.
- Lindstedt SL, Boyce MS. 1985. Seasonality, fasting endurance, and body size in mammals. *Am Nat.* 125:873–878.
- McCullough EL, Ledger KJ, O'Brien DM, Emlen DJ. 2015. Variation in the allometry of exaggerated rhinoceros beetle horns. *Anim Behav.* 109:133–140.

- McCullough EL. 2014. Mechanical limits to maximum weapon size in a giant rhinoceros beetle. *P Roy Soc Lond B Bio.* 281:20140696.
- McGinley RH, Prenter J, Taylor PW. 2015. Assessment strategies and decision making in male-male contests of *Servaea incana* jumping spiders. *Anim Behav.* 101:89–95.
- McLean CA, Stuart-Fox D. 2015. Rival assessment and comparison of morphological and performance-based predictors of fighting ability in Lake Eyre dragon lizards, *Ctenophorus maculosus*. *Behav Ecol Sociobiol.* 69:523–531.
- Mesterton-Gibbons M, Heap SM. 2014. Variation between self- and mutual assessment in animal contests. *Am Nat.* 183:199–213.
- Morris JS, Carrier DR. 2016. Sexual selection on skeletal shape in Carnivora. *Evolution.* 70:767–780.
- Nijhout HF, Emlen DJ. 1998. Competition among body parts in the development and evolution of insect morphology. *Proc Natl Acad Sci USA.* 95:3685–3689.
- Nilsson GE, Ostlund-Nilsson S. 2008. Does size matter for hypoxia tolerance in fish? *Biol Rev Camb Philos Soc.* 83:173–189.
- Palaoro AV, Dalosto MM, Costa JC, Santos S. 2014. Freshwater decapod (*Aegla longirostri*) uses a mixed assessment strategy to resolve contests. *Anim Behav.* 95:71–79.
- Palaoro AV, Briffa M. 2016. Data from: weaponry and defenses in fighting animals: how allometry can alter predictions from contest theory. Dryad Digital Repository. <http://10.5061/dryad.19r0c>.
- Parker GA. 1974. Assessment strategy and the evolution of fighting behaviour. *J Theor Biol.* 47:223–243.
- Payne RJH, Pagel M. 1997. Why do animals repeat displays? *Anim Behav.* 54:109–119.
- Payne RJH. 1998. Gradually escalating fights and displays: the cumulative assessment model. *Anim Behav.* 56:651–662.
- Peixoto PEC, Benson WW. 2012. Influence of previous residency and body mass in the territorial contests of the butterfly *Hermeuptychia fallax*. *J Ethol.* 30:61–68.
- Pélabon C, Firmat C, Bolstad GH, Voje KL, Houle D, Cassara J, Rouzic AL, Hansen TF. 2014. Evolution of morphological allometry. *Ann NY Acad Sci.* 1320:58–75.
- Prenter J, Taylor PW, Elwood RW. 2008. Large body size for winning and large swords for winning quickly in swordtail males, *Xiphophorus helleri*. *Anim Behav.* 75:1981–1987.
- R Development Core Team. 2015. R: a language and environment for statistical computing. Version 3.1.1. Vienna (Austria): R Foundation for Statistical Computing.
- Reddon AR, Voisin MR, Menon N, Marsh-Rollo SE, Wong MYL, Balshine S. 2011. Rules of engagement for resource contests in a social fish. *Anim Behav.* 82:93–99.
- Rillich J, Schildberger K, Stevenson PA. 2007. Assessment strategy of fighting crickets revealed by manipulating information exchange. *Anim Behav.* 74:823–836.

- Rojas R, Morales MC, Rivadeneira MM, Thiel M. 2012. Male morphotypes in the Andean river shrimp *Cryphiops caementarius* (Decapoda: Caridea): morphology, coloration and injuries. *J Zool.* 288:21–32.
- Rudin FS, Briffa M. 2011. The logical polyp: assessments and decisions during contests in the beadlet anemone *Actinia equina*. *Behav Ecol.* 22:1278–1285.
- Schultz ET, Conover DO. 1999. The allometry of energy reserve depletion: test of a mechanism for size-dependent winter mortality. *Oecologia.* 119:474–483.
- Sneddon LU, Huntingford FA, Taylor AC, Orr JF. 2000. Weapon strength and competitive success in the fights of shore crabs (*Carcinus maenas*). *J Zool.* 250:397–403.
- Swanson BO, George MN, Anderson SP, Christy JH. 2013. Evolutionary variation in the mechanics of fiddler crab claws. *BMC Evol Biol.* 13:137.
- Taylor PW, Elwood RW. 2003. The mismeasure of animal contests. *Anim Behav.* 65:1195–1202.
- Vieira MC, Peixoto PEC. 2013. Winners and losers: a meta-analysis of functional determinants of fighting ability in arthropod contests. *Funct Ecol.* 27:305–313.
- Voje KL. 2016. Scaling of morphological characters across trait type, sex, and environment. *Am Nat.* 187:89–98.
- Wofford SJ, Earley RL, Moore PA. 2015. Evidence for assessment disappears in mixed-sex contests of the crayfish, *Orconectes virilis*. *Behaviour.* 152:995–1018.



Table 1: Predictions of the assessment models and our model regarding RHP and contest duration between RHP-matched opponents

	EWOA	CAM	SAM	Self-assessment with Power Law
Relation between body size and contest duration	Positive	Positive	No relation	Depends on the allometric scaling of the RHP traits: small OC—positive; large OC—positive, but decreasing after a given body size
Relation between size and RHP	No prediction	No prediction	No prediction	RHP is more dissimilar in paired large individuals than in paired small individuals

Table 2: Results of the 2-way Anova we performed to test if the difference in OC between a focal individuals and its' opponents differs between scaling method (i.e., linear and power scaling of RHP with body size) and pairing method (i.e., size-matching small individuals or size-matching large individuals)

	df	Sum of squares	Fvalue	P
(a) OC = 1.1				
Scaling	1	1255	186.41	<0.0001
Pairing method	1	11664	1731.9	<0.0001
Scaling:Pairing method	1	600	89.06	<0.0001
Residuals	116	781		
(b) OC = 1.12				
Scaling	1	2044	259.4	<0.0001
Pairing method	1	13555	1720.9	<0.0001
Scaling:Pairing method	1	986	125.2	<0.0001
Residuals	116	914		
(c) OC = 1.2				
Scaling	1	9316	602.9	<0.0001
Pairing method	1	25345	1646.1	<0.0001
Scaling:Pairing method	1	4676	302.6	<0.0001
Residuals	116	1792		

df = degrees of freedom.

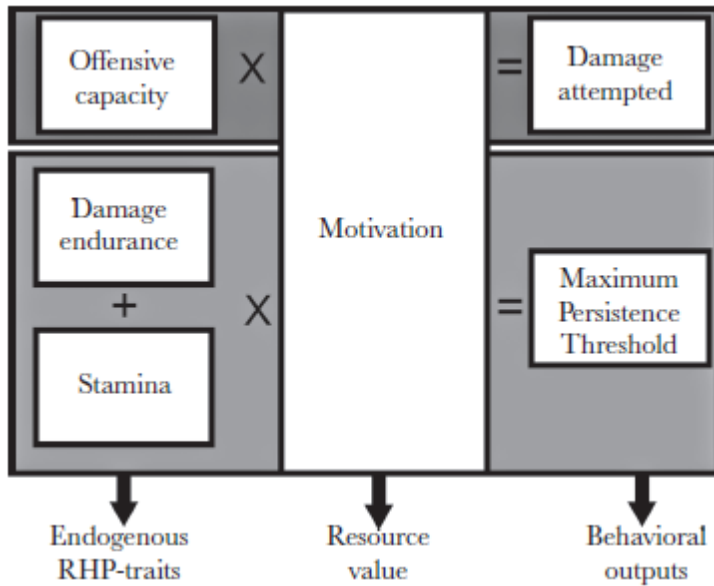


Figure 1: Factors contributing to RHP and their behavioral outputs. First, RHP traits that depend on the animal's morphology or physiology are endogenous RHP traits, and they are subdivided into 2 types of traits: offensive (dark grey), and defensive RHP traits (light grey). Offensive capacity (OC) is how much damage an animal causes to its opponent given its ability (e.g., weapon size). The defensive RHP traits are subdivided into damage endurance (DE), which is how much damage from the opponent the individual can take, and stamina, which is how long the individual can sustain demanding activity (e.g., perform costly acts during a contest). Second, motivation is defined loosely as extrinsic and intrinsic factors that can influence the motivation of the individual to fight (i.e., resource value). This must have a value between 0 and 1, because motivational state cannot increase an individual's maximum persistence threshold or damage attempted. Rather it will determine the proportion of this maximum that an individual is prepared to allocate to a contest. Lastly, the behavioral outputs are the variables we can measure in a fight. For instance, damage attempted could be the number of strikes, and the maximum persistence threshold could be the contest duration. Our model deals mainly with how DE and OC interact to determine how long it takes to exceed the maximum persistence threshold.

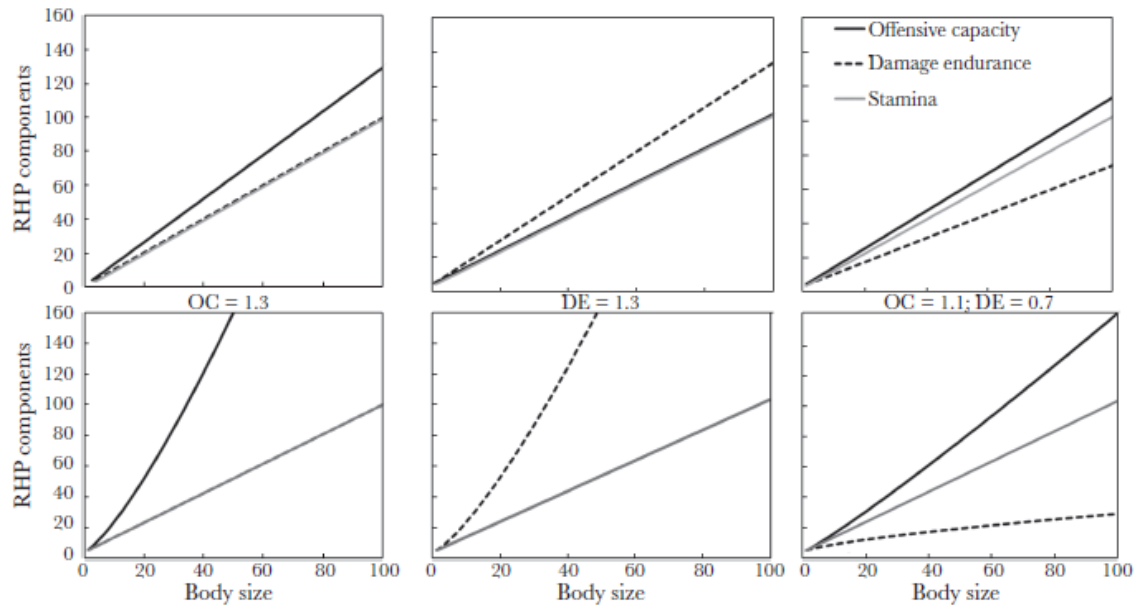


Figure 2: Scaling of RHP traits according to 2 different relationships between the variables and 3 scenarios. The top row illustrates linear relationships and the bottom row illustrates power laws. The upper and lower panels on the left show when OC increases with a slope or scaling exponent larger than 1 but DE is fixed at 1. The middle panels illustrate the opposite—DE varies and OC is fixed at 1. The upper and lower panels on the right indicate offensive capacities increasing superlinearly (slope or scaling exponent  $> 1$ ), and sublinear increases for DE (slope or scaling exponent  $< 1$ ). In each case the distance between lines for offensive and defensive RHP represents the amount of damage that an offensive act would inflict on the recipient for a pair of size matched individuals. If DE is larger than OC, than the individual is sustaining no damage at all thus highlighting the role of stamina in terminating a contest. Values between panels indicate the slope or scaling exponents parameters ( $b$  or  $a$ —see Equations 1 and 2) used to generate the curves.

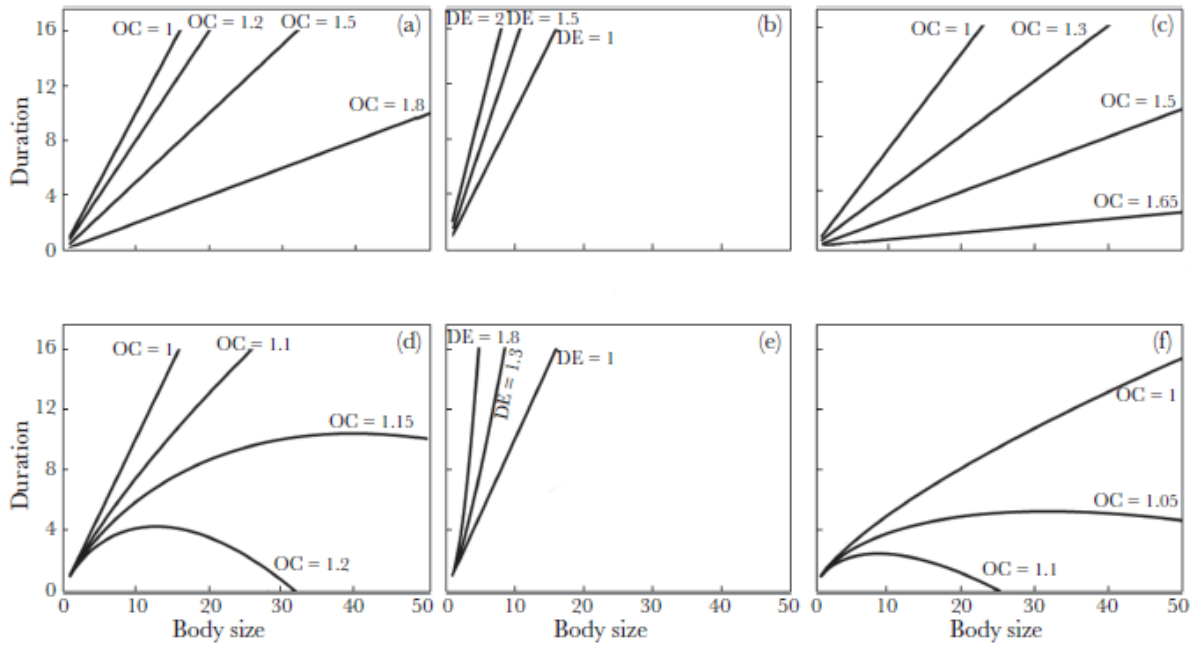


Figure 3: The top row (a–c) shows the expected contest duration between RHP-matched individuals in a model that the different components of RHP (see Figure 2) are scaling linearly with body size (see Equation 1), as assumed by current animal contest theory. In contrast, the bottom row (d– f) shows the expected contest duration between RHP-matched individuals in a model that the different components of RHP are scaling with power relationships with body size (see Equation 2). The left panels (a and d) demonstrate the predictions when OC has a slope (a) or scaling exponent (d) larger than 1 and DE is fixed at 1. The middle panels (b and e) illustrate the opposite scenario: DE increases with a slope (b) or scaling exponent (e) larger than 1 and OC is fixed at 1. The right panels (c and f) illustrate a more realistic scenario in which OC increases with a slope (c) or scaling exponent (f), and DE increases with a slope or scaling exponent of 0.5. Values indicate the slope parameters (b) or scaling exponents (a) used to generate the curves.

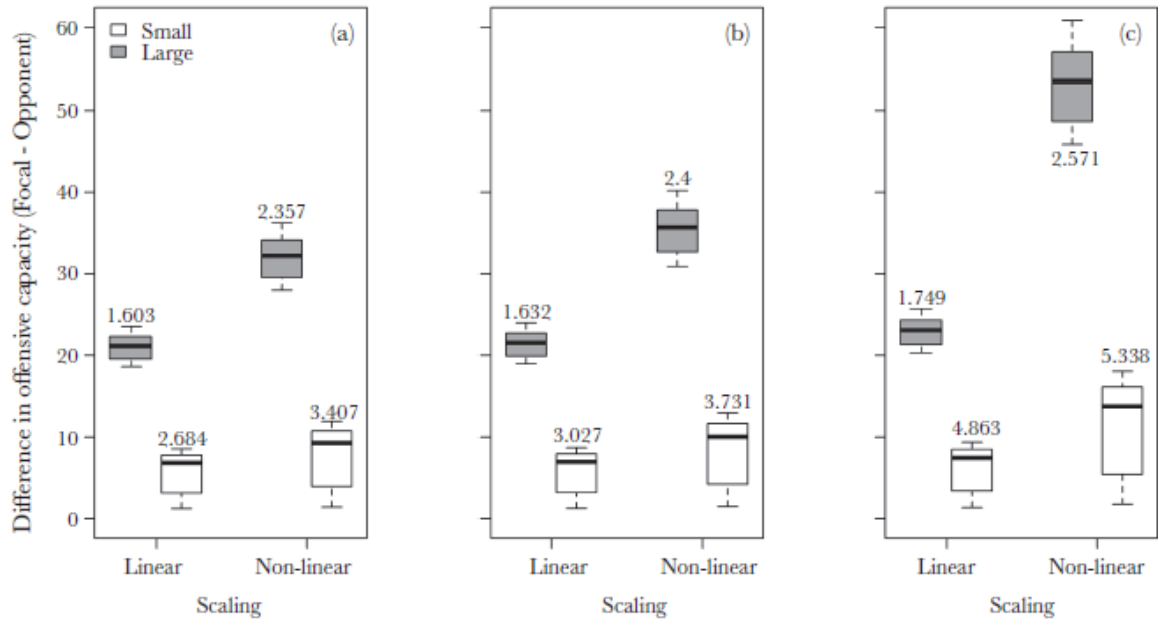


Figure 4: Difference in OC between RHP-matched (15% of difference) individuals. Large pairs (gray boxes) indicate pairs that were formed between the 60 largest individuals of a random population, and Small pairs (white boxes) indicate pairs formed between the 60 smallest individuals. (a) OC scaling exponent (nonlinear scaling) or slope (linear scaling) set at 1.1; (b) OC set at 1.12; (c) OC set at 1.2. Values above or below the boxes indicate variance.