The hidden links between animal weapons, fighting style and their expression on contest resolution

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SUMMARY

1. In many species that fight over resources, individuals use specialized structures to overpower their rivals (i.e. weapons). Despite their similar roles for contest settlement (i.e. affecting the winning chances), weapons are highly diverse morphological structures across species. However, the comprehension on how this diversity evolved is still open for debate.
2. Unfortunately, most studies on how weapons are used during contests focus on size asymmetries between winners and losers. Although such information is important to understand, it does not provide much information regarding the mechanisms promoting weapon diversification. In addition, in many situations, the effect of weapon size on

contest resolution may be confounded with the effect of body size due to allometric correlations.

3. One way to decompose the relative importance of weapon and body size on contest outcome is to focus on the functional role of weapons. That is, investigate the function of the weapon during contests, and how size should affect its function.
4. We propose two hypotheses that explicitly associate how weapon function may determine the relative importance of weapon and body size in affecting rivals during contests. One based on the internal morphology of the weapon – whether muscles are within the weapon or not – and the other based on fighting style – whether the weapon is used to injure the rival or not.
5. To test our hypotheses, we developed a meta-analysis spamming 31 genera across the animal kingdom.
6. We found that internal morphology and fighting style are important to determine the relative importance of weapon and body size on contest resolution. Weapons that do not have muscles within them (e.g., horns) affect more the chance of winning than weapons that have muscles within them (e.g., claws). Similarly, weapons used to throw/push rivals away (e.g., oversized mandibles) affect more the chance of winning than those used to make the rival flee (e.g., jaws).
7. Overall, we have shown that weapon usage (i.e. weapon function) may affect weapon evolution in predictable ways: weapons without muscles and using for pushing may be selected for size, while muscled weapons used for injuring may be selected for strength.

Keywords. Animal contests, morphological evolution, animal fighting, sexual selection, weapon biomechanics

INTRODUCTION

Antlers, claws, horns, and enlarged mandibles are just a few of a much larger diversity of animal weapons we have in the animal kingdom. These weapons are used during contests to overpower rivals when individuals fight for a resource (McCullough, Miller, & Emlen, 2016). Consequently, weapons are said to influence the outcome of a contest (Palaoro & Briffa, 2017). Given that winners secure more, and better, resources than losers, fighting influences fitness of the individual (Pinto, Palaoro, & Peixoto, 2019; Vieira & Peixoto, 2013). This link between bearing weapons, winning contests, and fitness is said to explain the wide variety of weapons in the animal kingdom (Emlen, 2008; Rico-Guevara & Hurme, 2019). However, most studies focus on how weapon size asymmetries between winners and losers affects contest outcome (Pinto, Palaoro, & Peixoto, 2019; Vieira & Peixoto, 2013). However, when looking only at the size asymmetries, we lose some of the information on how the weapon is used during the contest to affect the rival (i.e. the functional role of the weapon during the contest; Eberhard et al., 2018). Without information on the functional role of the weapon, we may bias our comprehension on the magnitude of the effect of weapon size in contest outcome and on how weapons evolve and diversify across animal taxa (Eberhard et al., 2018; McCullough et al., 2016).

One of the challenges in detecting the effect of weapons on contest resolution stem from the allometric correlation between weapons and body size (Palaoro & Briffa, 2017, Pinto, Palaoro, & Peixoto, 2019; Vieira & Peixoto, 2013). Since the allometric correlation between weapon and body size is strong for most species (Voje, 2016), one may wonder that both variables should provide similar information about how individual traits affect winning probability. However, body size also affects contest outcome independent of weapon size, especially when we consider contests between species that do not bear weapons (e.g., butterflies,

dragonflies, Vieira & Peixoto, 2013). Without accurate estimations of the relative effect of weapon and body size on contest resolution, we may be unable to identify the selective pressures acting on each trait. Here, we test the impact of considering the weapon's functional role to improve our knowledge about the relative effect of weapon and body size on contest resolution. For this, we use information on weapon internal morphology and on the behaviors adopted by the rivals during contests. Below, we propose two hypotheses that merge weapon functional role and the relative effect of weapon and body size for contest resolution. First, we present the biomechanical hypothesis, in which the morphology of the weapon might reveal their overall importance in contests. Second, we present the functional hypothesis, in which how the weapon is used during contests - i.e., the fighting style - matters for their importance in contest resolution.

Biomechanical hypothesis

We propose that weapons may be separated in two major groups based on their internal morphology (hereafter referred to as "morphology" for simplicity): 1) weapons that have specific (generally internal) muscles responsible for the action of the weapon (from now on, muscled weapons) and 2) weapons that are not attached to a particular set of muscles (from now on, muscleless weapons). Muscled weapons are comprised by jaws, claws, mandibles, and legs, and they generally work by one part of the weapon closing on the rival and squeezing it or by producing an explosive movement to strike the rival (Emlen, 2008). Muscled weapons may be weakly dependent on individual body size to overpower rivals. For instance, whenever a crab closes its' claw on a rival, it requires only the action of the closer muscle of the claw; no other muscle is needed to grab the rival and win the contest (Dennenmoser & Christy, 2013; Morrell, Backwell, & Metcalfe, 2005). The same pattern is found in the mandibles of stag beetles,

in which the closing muscle closes the jaws on the rival (Goyens, Dirckx, & Aerts, 2015). The body size, in these instances, will function mainly as a stabilizer of the whole body, working as an auxiliary trait (Goyens et al., 2015; Okada, Suzaki, Okada, & Miyatake, 2011). Hence, for species that possesses muscled weapons, the differences between winners and losers should be greater for weapon size than for body size.

Muscleless weapons are mainly represented by horns and antlers (Emlen, 2008). These weapons are often used to enter in direct contact with the rival without the need to squeeze or strike. The entire body, in these cases, is responsible for overpowering the rival - the weapon is a tool by which the power of the whole body acts upon. For instance, when male deer lock antlers, the antler is used mainly as a point of contact, a lever, by which the individual transfer the power generated by their entire body. It is thus the body that is doing all the pushing (Jennings & Gammell, 2013). For species possessing muscleless weapons, the main trait used to overpower rivals is the body, while the weapon becomes the auxiliary trait. Hence, in muscleless weapons, we expect winners and losers to differ more strongly on body size than weapon size. Therefore, the biomechanical hypothesis posits that the internal morphology of the weapon (i.e., presence or absence of auxiliary muscles) can shift the relative importance of weapon and body size to win fights.

Functional hypothesis

We suggest that the importance of the weapon to win contests should be correlated to how the weapon is used during a fight - the fighting style of the species (Eberhard et al., 2018; McCullough et al., 2016). Broadly speaking, weapons can are used in contests in two ways: 1) weapons mainly used to grasp, kick, strike, pierce or squeeze until the loser decides to back away from the winner (from now on, biting weapons) and 2) weapons used to forcefully

remove the loser from the resource without (necessarily) causing direct injuries (from now on, pushing weapons). Biting weapons make the rival flee based on the injuries caused by a direct strike of the weapon (Green & Patek, 2018; Palaoro & Briffa, 2017). For instance, mantis shrimp strike their rivals using their high-performance raptorial appendages that are able to crack the shells of molluscs and crabs (Green & Patek, 2015). When individuals are contesting a burrow, the loser withdraws from a fight after being hit by the rival's powerful strike - typically leaving the contest before any major injuries are done (Green & Patek, 2018). Leaf-footed bugs follow a similar pattern, but with a different weapon. The individuals squeeze each other using their enlarged hind legs until the eventual loser decides to back away from the contested resource (Nolen, Allen, & Miller, 2017). In both cases, the rival is deciding to retreat after receiving direct strikes of the weapon. Therefore, for biting weapons, we expect that the weapon should be more important to settle the contest than the body size of the individual.

Pushing weapons are used, for example, by some beetle species that contest burrows or tree saps. In such species, the winner uses its horns, enlarged mandibles, or hind legs, to push the loser away from the burrow or dislodge the loser from the female/tree branch (McCullough & Simmons, 2016; O'Brien, Katsuki, & Emlen, 2017; Rink, Altwegg, Edwards, Bowie, & Colville, 2019). That is especially true for stag beetles, which use their enlarged mandibles to lift the rival and throw him away from the resource - they do not use their mandibles to bite the rival into submission (Goyens et al., 2015). Therefore, although such mandibles have specific muscles attached to them, they are not used to injury the rival. A similar pattern occurs in cervid fights, in which individuals are mainly pushed away from the resource (Jennings & Gammell, 2013). Due to the emphasis in pushing or shoving rivals away, the trait that should enable individuals to dislodge rivals is the body, rather than the weapon; the weapon is only transmitting the power generated by the body. Therefore, in injury fights the main factor affecting contest

resolution should be the biting weapon and its' ability to cause injuries, whereas in pushing fights the main factor determining victory should be the body and its' ability to push the rival away.

Despite the existence of marked differences in weapon morphology and fighting style, and on the growing theoretical interest in how these two aspects can influence weapon evolution (Eberhard et al., 2018; McCullough et al., 2016), there is no evaluation of how weapon morphology and fighting style might affect the relative importance of body and weapon traits in animal contests. Thus, by focusing on the weapon functional role during the contest (according to our categorization of weapons based on morphology and fighting style), we may be able to provide ways to disentangle how agonistic interactions affect the evolution of body size and weapon morphology. However, weapons are frequently used during contests regardless of morphology and fighting style. Because of their frequent use, it might be that the overall effect of weapons on winning chances is always higher than body size. For this reason, we used a meta-analytical approach to first test the common prediction that weapons are more important than body size for contest resolution (Palaoro & Briffa, 2017). Next, we evaluated the biomechanical hypothesis that posits that muscled weapons (i.e., weapons that have muscles attached to them) should be more important than body size, whereas muscleless weapons (i.e., weapons that do not have muscles attached) should be less (or equally) important than body size in determining the winner. Lastly, we evaluated the functional hypothesis, which posits that weapons with the main function of injuring rivals (i.e., biting weapons) should be more important than body size, whereas weapons that dislodge rivals from the resource (i.e., pushing weapons) should be less (or equally) important than body size in determining the winner. To measure the importance of each trait in contest resolution, we used a standardized measure (Hedges' *g*) of the mean difference between winners and losers for that trait (Vieira & Peixoto,

2013). Based on this measure, we expect larger differences between winners and losers in traits that should be more important to resolve fights.

METHODS

Literature search and eligibility criteria

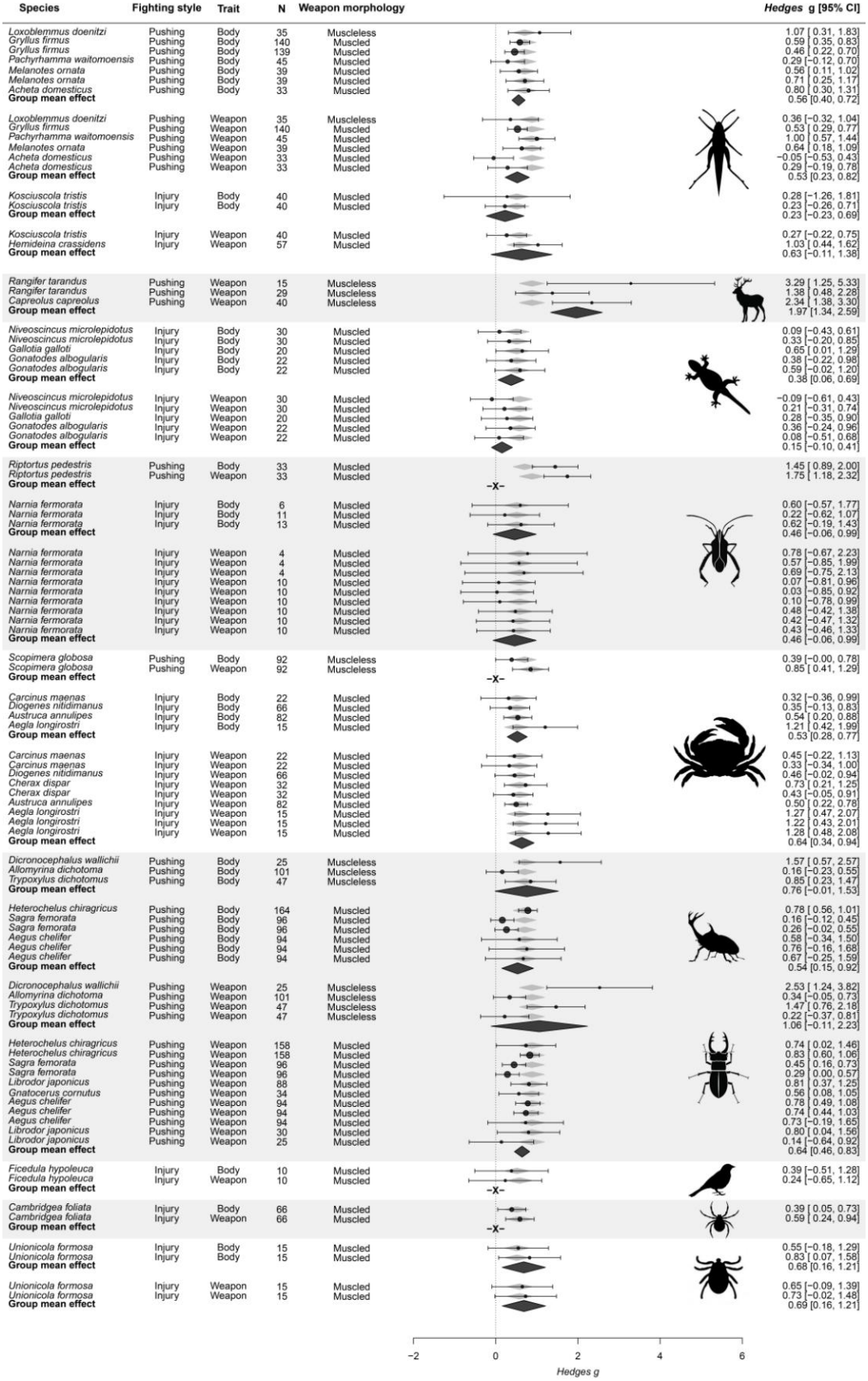
We searched for articles using the Web of Science (https://www.webofknowledge.com) and Scopus (https://scopus.com) databases. For both searches we used the search strings shown in the Supplementary file. We obtained a total of 1108 papers through those searches and we also added 12 relevant papers cited in reviews that we did not find in our primary searches (Emlen, 2008; Pinto et al., 2019; Rico-Guevara & Hurme, 2019; Vieira & Peixoto, 2013). We excluded all studies in which the species did not bear a weapon (i.e., specialized morphology used to gain mechanical advantage on the rival, *sensu* (Eberhard et al., 2018)). Since we had to classify species according to their fighting style, we excluded all species in which the behaviours adopted during the fights were undescribed. For the selected studies, we searched for information about mean trait values (and their corresponding variation) for winners and losers of contests. Therefore, we also excluded any study that reported only the mean trait size without distinguishing winners and losers. Within each study, we searched for the pairing method used by researchers. If individuals with similar body or weapon sizes were paired, we excluded that study from our analysis because pairing influences the relative importance of fighting ability on fight outcome (Palaoro & Briffa, 2017). Another source of confounding effect might come from resource value (*sensu* (Arnott & Elwood, 2008)): individuals that value more a resource often fight harder regardless of their fighting ability (e.g., (Palaoro, Velasque, Santos, & Briffa, 2017)). To avoid any bias, we only included the treatments in which there was no

evidence that individuals had different motivations to fight. Lastly, we only included replicates in which there is a clear winner and loser – we excluded fights that ended in a tie.

Categorizing weapon internal morphology and fighting style

We categorized weapon morphology based on the position of the muscle relative to the weapon (Fig. 1). For each selected species, we considered that a given structure was a weapon if there was a clear description that the structure was used in the fight to overcome rivals (Eberhard et al., 2018). We considered claws, jaws, mandibles and legs as muscled weapons because all move independently of the body and are attached to specific muscles nearby. For example, individuals with claws need to grasp their rivals and grasping strength depend on the muscles inside the claw (Dennenmoser & Christy, 2013). In contrast, we considered horns and antlers as muscleless weapons because they are unable to perform moves independent of the body (or any movement).

To categorize fighting style, we searched for a description of how the individuals use the weapon during fights and of how the decision to withdrawal occurs (McCullough et al., 2016; Rico-Guevara & Hurme, 2019). If individuals used their weapons to push, shove, or dislodge the rival from the resource and if most fights were terminated by excluding the rival from the resource, we classified as 'pushing weapons'. If the weapons were used to grab, bite, kick, pierce or squeeze the rival and if most fights were terminated by the loser retreating from the resource without being throwed away, we classified them as 'biting weapons'. All classifications and more detailed justifications can be found in Table S1.


Species
Fighting style
Trait
N
Weapon morphology
Hedges g [95% CI]
Loxoblemmus doenitzi Pushing Body 35 Muscleless 1.07 [0.31, 1.83]
Gryllus firmus Pushing Body 140 Muscled 0.59 [0.35, 0.83]
Gryllus firmus Pushing Body 139 Muscled 0.46 [0.22, 0.70]
Pachyrhamma waitomoensis Pushing Body 45 Muscled 0.29 [−0.12, 0.70]
Melanotes ornata Pushing Body 39 Muscled 0.56 [0.11, 1.02]
Melanotes ornata Pushing Body 39 Muscled 0.71 [0.25, 1.17]
Acheta domesticus Pushing Body 33 Muscled 0.80 [0.30, 1.31]
Group mean effect 0.56 [0.40, 0.72]
Loxoblemmus doenitzi Pushing Weapon 35 Muscleless 0.36 [−0.32, 1.04]
Gryllus firmus Pushing Weapon 140 Muscled 0.53 [0.29, 0.77]
Pachyrhamma waitomoensis Pushing Weapon 45 Muscled 1.00 [0.57, 1.44]
Melanotes ornata Pushing Weapon 39 Muscled 0.64 [0.18, 1.09]
Acheta domesticus Pushing Weapon 33 Muscled −0.05 [−0.53, 0.43]
Acheta domesticus Pushing Weapon 33 Muscled 0.29 [−0.19, 0.78]
Group mean effect 0.53 [0.23, 0.82]
Kosciuscola tristis Injury Body 40 Muscled 0.28 [−1.26, 1.81]
Kosciuscola tristis Injury Body 40 Muscled 0.23 [−0.26, 0.71]
Group mean effect 0.23 [−0.23, 0.69]
Kosciuscola tristis Injury Weapon 40 Muscled 0.27 [−0.22, 0.75]
Hemideina crassidens Injury Weapon 57 Muscled 1.03 [0.44, 1.62]
Group mean effect 0.63 [−0.11, 1.38]
Rangifer tarandus Pushing Weapon 15 Muscleless 3.29 [1.25, 5.33]
Rangifer tarandus Pushing Weapon 29 Muscleless 1.38 [0.48, 2.28]
Capreolus capreolus Pushing Weapon 40 Muscleless 2.34 [1.38, 3.30]
Group mean effect 1.97 [1.34, 2.59]
Niveoscincus microlepidotus Injury Body 30 Muscled 0.09 [−0.43, 0.61]
Niveoscincus microlepidotus Injury Body 30 Muscled 0.33 [−0.20, 0.85]
Gallotia galloti Injury Body 20 Muscled 0.65 [0.01, 1.29]
Gonatodes albogularis Injury Body 22 Muscled 0.38 [−0.22, 0.98]
Gonatodes albogularis Injury Body 22 Muscled 0.59 [−0.02, 1.20]
Group mean effect 0.38 [0.06, 0.69]
Niveoscincus microlepidotus Injury Weapon 30 Muscled −0.09 [−0.61, 0.43]
Niveoscincus microlepidotus Injury Weapon 30 Muscled 0.21 [−0.31, 0.74]
Gallotia galloti Injury Weapon 20 Muscled 0.28 [−0.35, 0.90]
Gonatodes albogularis Injury Weapon 22 Muscled 0.36 [−0.24, 0.96]
Gonatodes albogularis Injury Weapon 22 Muscled 0.08 [−0.51, 0.68]
Group mean effect 0.15 [−0.10, 0.41]
Riptortus pedestris Pushing Body 33 Muscled 1.45 [0.89, 2.00]
Riptortus pedestris Pushing Weapon 33 Muscled 1.75 [1.18, 2.32]
Group mean effect
Narnia fermorata Injury Body 6 Muscled 0.60 [−0.57, 1.77]
Narnia fermorata Injury Body 11 Muscled 0.22 [−0.62, 1.07]
Narnia fermorata Injury Body 13 Muscled 0.62 [−0.19, 1.43]
Group mean effect 0.46 [−0.06, 0.99]
Narnia fermorata Injury Weapon 4 Muscled 0.78 [−0.67, 2.23]
Narnia fermorata Injury Weapon 4 Muscled 0.57 [−0.85, 1.99]
Narnia fermorata Injury Weapon 4 Muscled 0.69 [−0.75, 2.13]
Narnia fermorata Injury Weapon 10 Muscled 0.07 [−0.81, 0.96]
Narnia fermorata Injury Weapon 10 Muscled 0.03 [−0.85, 0.92]
Narnia fermorata Injury Weapon 10 Muscled 0.10 [−0.78, 0.99]
Narnia fermorata Injury Weapon 10 Muscled 0.48 [−0.42, 1.38]
Narnia fermorata Injury Weapon 10 Muscled 0.42 [−0.47, 1.32]
Narnia fermorata Injury Weapon 10 Muscled 0.43 [−0.46, 1.33]
Group mean effect 0.46 [−0.06, 0.99]
Scopimera globosa Pushing Body 92 Muscleless 0.39 [−0.00, 0.78]
Scopimera globosa Pushing Weapon 92 Muscleless 0.85 [0.41, 1.29]
Group mean effect
Carcinus maenas Injury Body 22 Muscled 0.32 [−0.36, 0.99]
Diogenes nitidimanus Injury Body 66 Muscled 0.35 [−0.13, 0.83]
Austruca annulipes Injury Body 82 Muscled 0.54 [0.20, 0.88]
Aegla longirostri Injury Body 15 Muscled 1.21 [0.42, 1.99]
Group mean effect 0.53 [0.28, 0.77]
Carcinus maenas Injury Weapon 22 Muscled 0.45 [−0.22, 1.13]
Carcinus maenas Injury Weapon 22 Muscled 0.33 [−0.34, 1.00]
Diogenes nitidimanus Injury Weapon 66 Muscled 0.46 [−0.02, 0.94]
Cherax dispar Injury Weapon 32 Muscled 0.73 [0.21, 1.25]
Cherax dispar Injury Weapon 32 Muscled 0.43 [−0.05, 0.91]
Austruca annulipes Injury Weapon 82 Muscled 0.50 [0.22, 0.78]
Aegla longirostri Injury Weapon 15 Muscled 1.27 [0.47, 2.07]
Aegla longirostri Injury Weapon 15 Muscled 1.22 [0.43, 2.01]
Aegla longirostri Injury Weapon 15 Muscled 1.28 [0.48, 2.08]
Group mean effect 0.64 [0.34, 0.94]
Dicronocephalus wallichii Pushing Body 25 Muscleless 1.57 [0.57, 2.57]
Allomyrina dichotoma Pushing Body 101 Muscleless 0.16 [−0.23, 0.55]
Trypoxylus dichotomus Pushing Body 47 Muscleless 0.85 [0.23, 1.47]
Group mean effect 0.76 [−0.01, 1.53]
Heterochelus chiragricus Pushing Body 164 Muscled 0.78 [0.56, 1.01]
Sagra femorata Pushing Body 96 Muscled 0.16 [−0.12, 0.45]
Sagra femorata Pushing Body 96 Muscled 0.26 [−0.02, 0.55]
Aegus chelifer Pushing Body 94 Muscled 0.58 [−0.34, 1.50]
Aegus chelifer Pushing Body 94 Muscled 0.76 [−0.16, 1.68]
Aegus chelifer Pushing Body 94 Muscled 0.67 [−0.25, 1.59]
Group mean effect 0.54 [0.15, 0.92]
Dicronocephalus wallichii Pushing Weapon 25 Muscleless 2.53 [1.24, 3.82]
Allomyrina dichotoma Pushing Weapon 101 Muscleless 0.34 [−0.05, 0.73]
Trypoxylus dichotomus Pushing Weapon 47 Muscleless 1.47 [0.76, 2.18]
Trypoxylus dichotomus Pushing Weapon 47 Muscleless 0.22 [−0.37, 0.81]
Group mean effect 1.06 [−0.11, 2.23]
Heterochelus chiragricus Pushing Weapon 158 Muscled 0.74 [0.02, 1.46]
Heterochelus chiragricus Pushing Weapon 158 Muscled 0.83 [0.60, 1.06]
Sagra femorata Pushing Weapon 96 Muscled 0.45 [0.16, 0.73]
Sagra femorata Pushing Weapon 96 Muscled 0.29 [0.00, 0.57]
Librodor japonicus Pushing Weapon 88 Muscled 0.81 [0.37, 1.25]
Gnatocerus cornutus Pushing Weapon 34 Muscled 0.56 [0.08, 1.05]
Aegus chelifer Pushing Weapon 94 Muscled 0.78 [0.49, 1.08]
Aegus chelifer Pushing Weapon 94 Muscled 0.74 [0.44, 1.03]
Aegus chelifer Pushing Weapon 94 Muscled 0.73 [−0.19, 1.65]
Librodor japonicus Pushing Weapon 30 Muscled 0.80 [0.04, 1.56]
Librodor japonicus Pushing Weapon 25 Muscled 0.14 [−0.64, 0.92]
Group mean effect 0.64 [0.46, 0.83]
Ficedula hypoleuca Injury Body 10 Muscled 0.39 [−0.51, 1.28]
Ficedula hypoleuca Injury Weapon 10 Muscled 0.24 [−0.65, 1.12]
Group mean effect
Cambridgea foliata Injury Body 66 Muscled 0.39 [0.05, 0.73]
Cambridgea foliata Injury Weapon 66 Muscled 0.59 [0.24, 0.94]
Group mean effect
Unionicola formosa Injury Body 15 Muscled 0.55 [−0.18, 1.29]
Unionicola formosa Injury Body 15 Muscled 0.83 [0.07, 1.58]
Group mean effect 0.68 [0.16, 1.21]
Unionicola formosa Injury Weapon 15 Muscled 0.65 [−0.09, 1.39]
Unionicola formosa Injury Weapon 15 Muscled 0.73 [−0.02, 1.48]
Group mean effect 0.69 [0.16, 1.21]
−2
0
2
4
6
Hedges g

213

Fig 1. Summary of Hedges' *g* (and corresponding confidence intervals) for species, fighting style, weapon morphology, type of trait, and the number of winners in the study. The grey polygon behind each Hedges' *g* is the fitted value of each study on the complete model. The width of the polygon denotes the credibility interval limits of that study. The darker polygon is the group mean effect calculated through a meta-analytic model with no moderators. The width of the polygon denotes the 95% confidence interval of that estimate.

Data extraction and effect sizes

To calculate Hedges' g, we used the mean trait values and their standard deviations for body size and weapon size measures of winners and losers of each selected study. Hedges' *g* is a standardized dimensionless measure and, for this reason, allows comparisons among different types of measurements and species (Koricheva, Gurevitch, & Mengersen, 2013). Since we always calculated the Hedges' *g* as the difference between winner and loser traits, values greater than zero indicate that winners, on average, have a larger trait than losers, while values smaller than zero indicate that losers have, on average, a larger trait than winners. Unfortunately, mean values and standard deviations were not always available on papers. In those cases, we gathered results from statistical tests comparing winners and losers (e.g., ^{2} values, F values, Wilcoxon values, degrees of freedom, p-values, and sample sizes) to transform the statistical results into Hedges' *g* values using the package "*compute.es*" in R (Del-Re, 2013, p.). Whenever the mean and standard deviations were displayed on graphs, we used the *webplotdigitizer* software to extract the values directly from the figures (Rohatgi, 2019). If none of those options were available, we contacted the corresponding author to request the data. We retained the signs of all original statistics before transforming into Hedges' *g* values.

Since body size and weapon size are allometrically correlated (Voje, 2016), we needed to ensure that this correlation would not bias our estimates (Weaver, Santos, Tucker, Wilson, & Hill, 2018). Thus, we gathered the Pearson's correlation coefficient of the body size and weapon size measures from the papers in which we retrieved the data to calculate the Hedges' *g* values. Whenever the study did not provide the correlation coefficient, but the authors sent us the dataset, we calculated the Pearson correlation coefficient from their data. However, when neither the study provided the coefficient, nor we had the dataset, we searched the literature for another study from the same species that had the allometric coefficient. These studies can be found in Supplementary Table S2.

Data analyses

Our first prediction was that weapons, regardless of morphology and fighting style, would have higher Hedges' *g* values than body size. To test this, we used a mixed-effects model in the R package '*metafor*' (Viechtbauer, 2010). We considered Hedges' *g* values as the response variable, the inverse of the variance of Hedges' *g* as a weight, and the type of trait (i.e., body or weapon) measured in the original study as our moderator. In this analysis, we included five different random variables. First, we used study ID because sometimes we extracted more than one effect size per study (e.g., one effect size for body size and one for weapon size). Given the allometric correlation between body size and weapon, the effect sizes retrieved for the same species will have a higher likelihood of being similar than we would expect by chance. To account for this effect, we built a correlation matrix using the Pearson's correlation coefficient between body size and the weapon, and used this matrix to account for the effect of allometry in our analyses. For the three studies that we did not find the correlation coefficients, we used the mean of all correlation coefficients in our sample (we also substituted the mean values for

261 0.5 as a correlation coefficient, but the results did not change - data not shown, but present in
262 github).

263 For our second random variable, we categorized how each trait was measured. For
264 instance, some studies use body weight as a proxy for body size, while others use body length;
265 and whether traits scale according to weight or length might bias our estimates (Houle, Pélabon,
266 Wagner, & Hansen, 2011). Hence, we used 'type of proxy' as a random variable to account for
267 any variation that may come from the type of measurement used. Thirdly, we used species ID
268 to account for effect sizes that came from the same species, but different studies. Fourth, we
269 used the environment in which the original study was performed (i.e., laboratory or wild).
270 Finally, we used a matrix containing the phylogenetic relatedness among species. We used the
271 same random variables in all analyses.

272 We estimated phylogenetic relatedness based on a phylogeny constructed for the 31
273 species used in our study (see Results) with the Interactive Tree of Life online tree generator
274 (iTOL; https://itol.embl.de/, Fig. S1). Since we did not have two species of the same genus in
275 our analyses, we used the genus as the tips of our tree. After generating the tree, we estimated
276 branch length using a Brownian motion model of evolution to simulate an ultrametric
277 phylogenetic tree (Paradis, Claude, & Strimmer, 2004). We then imputed the ultrametric tree as
278 a variance-covariance matrix of our phylogenetic random variable. We made these analyses
279 using the packages "*rtol*" (Michonneau, Brown, & Winter, 2016) and "*ape*" in R (Paradis et al.,
280 2004).

281 To estimate heterogeneity and biases in our models, we used two approaches. First, we
282 calculated the ratio of true heterogeneity to the total variation observed across effect estimates
283 in multivariate studies (I^2, (Borenstein, 2009)). We also partitioned the I^2 into the contribution of
284 each random variable (Nakagawa & Santos, 2012). Thus, we had estimations of the within-

studies variance (I^2_{study}, similar to most mixed models), the between measurements variance ($I^2_{measurement}$), the between environments variance ($I^2_{environment}$), the phylogenetic variance ($I^2_{phylogeny}$), and the species ID variance ($I^2_{species}$). The sum of these different I^2 are equal to the total variance observed (I^2_{total}). To estimate the phylogenetic signal in the effect size, we also calculated the phylogenetic heritability index, H^2, which is similar to the Pagel's λ (Nakagawa & Santos, 2012). Finally, to test for publication bias, we conducted a modified version of the Egger's test, in which we used the residuals of our meta-analytic model as the response variable and the variance of the effect sizes as our predictor variable (Egger, Smith, Schneider, & Minder, 1997). If the intercept of this regression is not different from zero, then there is little evidence for publication bias (Nakagawa & Santos, 2012).

According to the biomechanical hypothesis, body size will have a higher Hedges' *g* value than weapon size for muscleless weapons, while the opposite pattern would occur for muscled weapons. We also used a mixed-effects model to test this prediction (Viechtbauer, 2010). Again, we considered Hedges' *g* values as the response variable, the inverse of the variance of Hedges' *g* as a weight, but included as moderators: the morphological category (i.e., muscled or muscleless), the type of trait (i.e., body or weapon), and their interaction. We used the same random variables as in the previous analyses: study ID, type of proxy, environment, phylogeny, and species ID.

Lastly, the functional hypothesis predicts that body size would have a higher Hedges' *g* value than weapon size for pushing fights, and the opposite pattern for injury fights. To test the prediction of this hypothesis, we followed a similar procedure as described before, but our moderators were: the fighting style (i.e., pushing or injury), the type of trait (i.e., body or weapon), and their interaction. As in the other analyses, we added study ID, type of proxy,

environment, phylogeny, and species ID as random variables. We performed all analyses in the R software (R Core Team, 2018).

RESULTS

We gathered 92 effect sizes, of which 55 were related to weapon size and 36 were related to the body size (Fig. 1). Our search spanned 31 genera, comprising both vertebrate (mainly lizards) and invertebrate species (mainly arthropods, Fig. S1). Considering the 55 weapon effect sizes, 46 (83.6%) were categorized as muscled weapons and 9 (16.3%) as muscleless weapons, while 29 (52.7%) were included in injury fights and 26 (47.2%) in pushing fights. We had 17 muscled weapons that were categorized in pushing fights (32.9%) while the remainder 29 were categorized as injury fights (67.4%). All muscleless weapons were categorized in pushing fights (Fig. 1, Table S1).

Winners had larger weapons and larger bodies than losers ($QM_2 = 48.51$, $p < 0.0001$, Fig. 2), but the Hedges' *g* estimates for weapon size were similar to body size estimates ($QM_1 = 0.5$, $p = 0.47$, Fig. 2). The dataset showed medium heterogeneity across studies (as measured by I^2, Table 1), with heterogeneity within studies explaining the largest part of the heterogeneity in our sample (Table 1). We also found evidence for publication bias (Egger's test; intercept -0.259, 95% CI: -0.39, -0.12, $t = -3.87$, $p < 0.0001$).

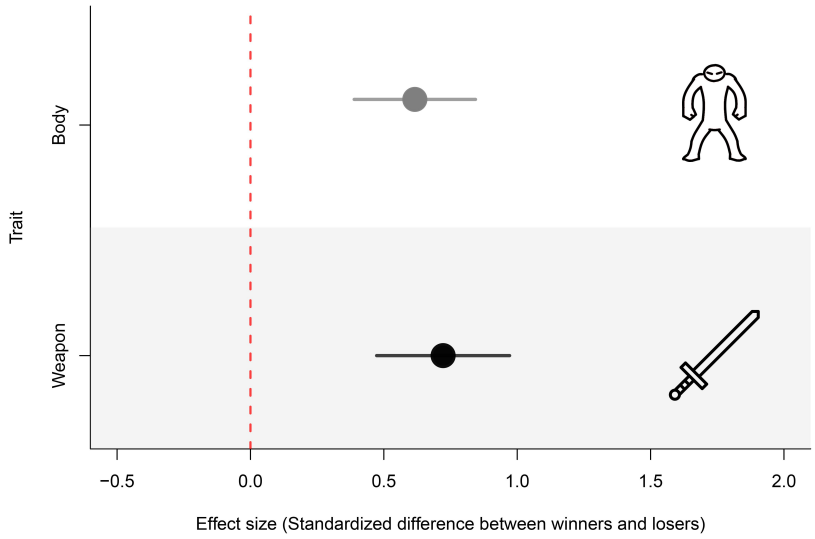


Fig. 2. Winners had larger bodies and bore larger weapons than losers, but body size and weapon size have a similar importance in contest resolution. Mean effect size (Hedges' *g*) expressing trait differences between winners and losers of 31 species. The red dotted line denotes the threshold in which winners and losers have similar mean trait values. Whiskers represent the corresponding 95% confidence intervals of the estimated Hedges' *g*.

Biomechanical hypothesis

Although winners had larger bodies and larger weapons than losers, the difference between winners and losers in body and weapon size estimations were similar for both muscled (QM_1 = 0.28, p = 0.59, Fig. 3) and muscleless (QM_1 = 1.27, p = 0.25) weapons. However, the differences between winners and losers in weapon size were smaller for muscled muscleless weapons (QM_1 = 5.25, p = 0.021, Fig. 3), while the difference in body sizes between winners and losers did not differ between species (QM_1 = 1.71, p = 0.19, Fig. 3). The model showed medium heterogeneity across studies (Table 1). Similar to the results for the overall effect size, the heterogeneity within studies explained the largest part of the heterogeneity in our sample (Table 1). We also found

evidence for publication bias (Egger's test; intercept -0.225, 95% CI: -0.34, -0.103, t = -3.66, p = 0.0004).

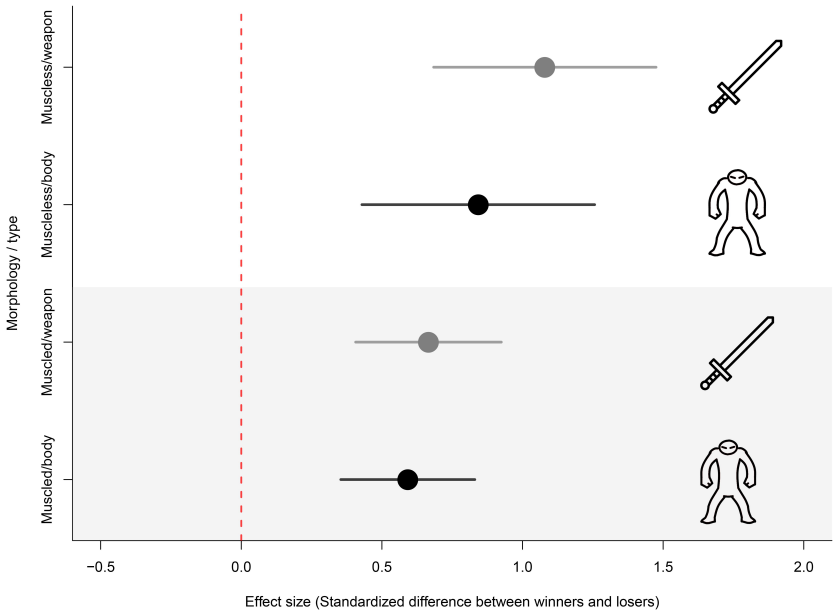


Fig. 3. Winners with muscleless weapons (i.e., no muscles attached to the weapon) have mean larger weapons than winners with muscled weapons (i.e., muscles attached to the weapon). Winners are also larger than losers regardless of trait and weapon morphology. Estimated mean effect (Hedges' *g*) for trait measures between winners and losers of species that show different weapon morphologies. For each weapon morphology, results are shown for estimated body sizes and estimates weapon sizes. The red dotted line denotes the threshold in which winners and losers have similar trait measures and the whiskers around the estimated mean values represent the 95% confidence interval.

Functional hypothesis

The difference between winners and losers in weapon size were greater for species involved in pushing fights than species that exhibit injury fights (QM_1 = 4.71, p = 0.03, Fig. 4). However, the

mean difference in body size between winners and losers did not differ between fighting styles (QM_1 = 1.65, p = 0.19, Fig. 4). Once again, despite winners being overall larger than losers in all categories, estimations of weapon size difference were not larger than the body size difference neither in pushing (QM_1 = 1.02, p = 0.31) nor in injury fights (QM_1 = 0.13, p = 0.71). The model showed medium heterogeneity across studies (Table 1). Once again, heterogeneity within studies explained the largest part of the heterogeneity in our sample. We also found evidence for publication bias (Egger's test; intercept -0.272, 95% CI: -0.39, -0.15, t = -4.46, p <0.001).

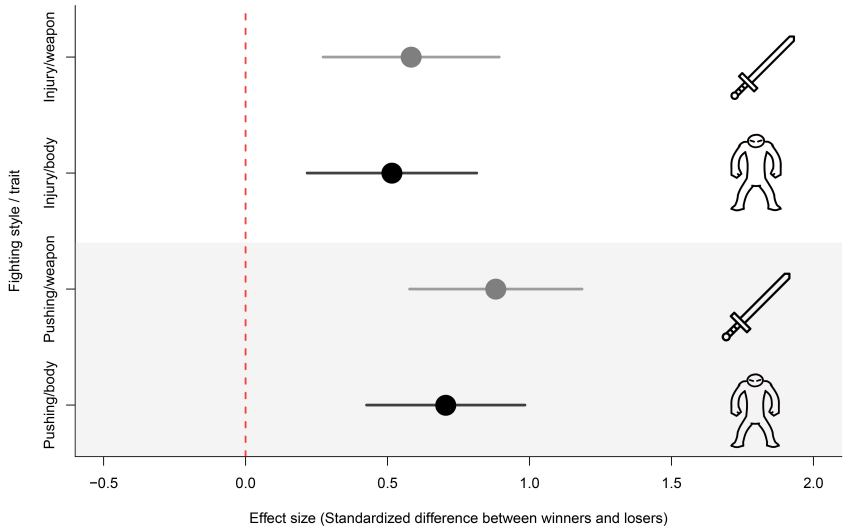


Fig. 4. Winners of pushing fights have mean larger weapons than winners of damage fights. Winners are also larger than losers regardless of trait and fighting style. Estimated mean effect (Hedges' *g*) for trait differences between winners and losers of species that show different fighting styles: pushing fights (fights in which weapons are used to push or throw rivals) and damage fights (fights in which weapons are used to cause injuries on rivals). For each fighting style, results are shown for estimated body sizes and estimates weapon sizes. The red dotted line denotes the threshold in which winners and losers have similar traits and the whiskers around the estimated mean values represent the 95% confidence interval.

DISCUSSION

Here, we evaluated if one aspect of weapon morphology (weapons associated with muscles responsible for their movement independent of the boy or not) and fighting style (weapons used to injure rivals or weapons used to push rivals) would impact the relative effect of weapon and body size on contest resolution. Our results indicated that winners are larger than losers for both body and weapon size, and that both were similarly important for contest resolution. Surprisingly, only weapon size differences differed between categories – body size differences were similar regardless of weapon morphology and fighting style. For weapon size, the difference between winners and losers is greater in species that bear muscleless weapons and fight by pushing than in species that bear muscled weapons and fight by injury. We also covered species belonging to a wide taxonomic range, spanning both vertebrate and invertebrate groups, and, given the small phylogenetic signal in our sample (Table 1), our results should be applicable to any animal that bear weapons. Hence, as predicted, weapon morphology and fighting style are important for predicting the evolution of animal weapons. However, the differences found were not in the direction we originally expected.

The similar effect of body and weapon sizes on contest resolution indicate that, independent of weapon morphology and fighting style, both traits are similarly important for winning. Although the correlation between body and weapon sizes is typically used to explain this similar effect (Vieira & Peixoto, 2013), we accounted for that correlation in all our models. Thus, we raise an alternative explanation: weapons might need a certain proportionality to body size to function properly (Eberhard et al., 2018; Irschick, Meyers, Husak, & Galliard, 2008; Lailvaux & Irschick, 2006, 2007). Perhaps other traits such as weapon shape and body shape

may have to match weapon characteristics and body size to maximize the winning chances (McCullough, Tobalske, & Emlen, 2014). For example, males of the stag beetle *Cyclommatus metallifer* grab rivals using their jaws and lift them up. To perform this movement, the individual needs a minimum body stability to prevent falling to either side while holding the rival up in the air. When body and weapon size are mismatched in any direction, body stability may decrease and even individuals with bigger weapons may have a lower probability of winning fights (Goyens et al., 2015). Hence, selection may not act solely on the weapon or on the body, but may also act on how the body functions as a unit - the whole-body performance (Irschick et al., 2008; Lailvaux & Irschick, 2006, 2007) – and on the covariation between both traits. Therefore, when several types of weapons are considered simultaneously, whole-body performance may be the main trait under selection to win fights.

For our surprise, the winners of species with muscleless weapons and pushing fights presented relatively larger weapons than losers when compared to species with muscled weapons and injury fights. Two alternative mechanisms might explain this unexpected pattern. First, given that species with muscled weapons and injury fights face injuries more frequently, we can expect that each successful hit on the rival increases the amount of injuries accrued and the likelihood of the rival withdrawing from a fight (Palaoro & Briffa, 2017). If the ability to cause injuries is sufficiently high, then it is likely that some individuals with smaller weapons (and body sizes) sometimes might win contests because they were able to hit their rivals first or more efficiently (Briffa & Lane, 2017; Palaoro & Briffa, 2017). For instance, gladiator frogs typically use their prepollex spines during contests. These prepollex are a muscleless weapon that leave deep gashes on rivals (Candaten, Possenti, Mainardi, da Rocha, & Palaoro, 2020) - some even report frogs blinded or deafened during contests (Dyson, Richert, & Halliday, 2013).

422 If the smaller rival sometimes wins contests, then the mean difference between winners and
423 losers will decrease. A similar rationale can be applied to *Anolis* lizards, a group which bear
424 muscled weapons (their jaws) and enter in injurious contests (Lailvaux & Irschick, 2007). Since
425 jaw strength is correlated to fighting (and reproductive) success (Husak, Lappin, & Van Den
426 Bussche, 2009), smaller individuals might win some contests because they bit the larger rival
427 first or bit in sensible body regions. Therefore, being able to hit first or more efficiently during
428 the contest may increase the chances to win injury fights. If this is true, it may be that individual
429 skill or personality traits, such as being highly aggressive or more consistent in striking the rival,
430 may be more important in species with muscled weapons and injury fights than species with
431 muscleless weapons and pushing fights (Briffa & Lane, 2017; Camerlink, Turner, Farish, &
432 Arnott, 2017).

433 Second, most weapon effect sizes were calculated using weapon size rather than weapon
434 strength (Fig. 1, Table S1). If weapon strength is more important than weapon size in inflicting
435 injuries on the rival, then we can expect differences between winners and losers to be more
436 variable among studies. Ultimately, this would decrease the mean difference between winners
437 and losers in injury fights and muscled weapons. For example, in species where bluffing occurs
438 (e.g., crayfish, fiddler crabs), individuals with strong claws frequently engage in physical
439 contact with rivals to avoid losing to bluffers (Bywater & Wilson, 2012; Wilson, James, Bywater,
440 & Seebacher, 2009). If individuals pinch one another, winning might be affected more strongly
441 by the size of the muscles inside the weapon than weapon size *per se*. Any effect of weapon size
442 on victory might be because of the correlation between weapon size and weapon muscles. On
443 the other hand, males of flower beetles (*Dicronocephalus wallichii*) needs to get their horned
444 heads beneath rivals to be able to lift them up and win a fight (Kojima & Lin, 2017). The farther

445 the individual is from the rival the better - it might win a fight without entering the rival's reach
446 and without endangering itself from being toppled. In these fights, then, horn length might be a
447 better predictor of winning than any measure of strength. Therefore, if most studies investigate
448 only weapon size (as is the case), then we might be missing important information to
449 understand weapon evolution, when other associated traits (such as the amount of muscles) are
450 the main responsible for determining individual fighting capacity.

451 In conclusion, we showed that the effect of weapon size on contest resolution is as
452 important as the effect of body size. This is surprising, since we expected that in species that
453 bear weapons, the role of the weapon in distinguishing winners and losers should be more
454 prevalent than the role of body size. In addition, the similar effect of weapon and body size in
455 determining the winner occurred independently of weapon morphology and the fighting style.
456 However, by looking more carefully into weapon morphology and fighting style, we were able
457 to discover a hidden pattern that indicated greater differences between winners and losers for
458 weapons that are mainly used to remove rivals from a given resource in comparison to weapons
459 that are mainly used to cause injuries. This could be caused by the lack of performance
460 measures of weapons that are primarily selected by their performance. But it also can be that the
461 selective pressure and the evolutionary pathways associated to the evolution of weapons with
462 distinct functional roles (such as causing injuries vs expelling rivals) associated to the fighting
463 behaviours may differ in predictable ways.

464

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601 **Table 1.** Heterogeneity estimates obtained from the models.

a) Overall effect of weapon size and body size

	I^2 (95% CI)	σ^2 (95% CI)
Study ID	3.86 (1.94, 5.79)	0.0149 (0.00, 0.22)
Measurement	3.75 (1.83, 5.67)	0.014 (0.00, >0.014)
Environment	<0.0001 (0.00, 1.92)	0.000 (0.00, 0.49)
Phylogeny	<0.0001 (0.00, 1.92)	0.000 (0.00, 0.11)
Species ID	21.73 (19.81, 23.65)	0.083 (0.00, 0.22)
Total	29.631 (27.44, 31.28)	-
H^2	<0.00001 (0.00, 1.92)	-

b) Weapon morphology hypothesis

	I^2 (95% CI)	σ^2 (95% CI)
Study ID	4.33 (2.41, 6.25)	0.016 (0.00, 0.21)
Measurement	3.71 (1.78, 5.62)	0.014 (0.00, 0.92)
Environment	<0.001 (0.00, 1.92)	0.00 (0.00, 0.55)
Phylogeny	<0.001 (0.00, 1.92)	0.00 (0.00, 0.09)
Species ID	21.44 (19.52, 23.36)	0.082 (0.00, 0.22)
Total	29.48 (27.56, 31.41)	-
H^2	<0.00001 (0.00, 1.92)	-

c) Fighting style hypothesis

	I^2 (95% CI)	σ^2 (95% CI)
Study ID	0.51 (0.00, 2.42)	0.002 (0.00, 0.20)
Measurement	5.24 (3.32, 7.16)	0.02 (0.00, 1.61)

Environment	<0.001 (0.00, 1.92)	0.00 (0.00, 0.48)
Phylogeny	<0.001 (0.00, 1.92)	0.00 (0.00, 0.36)
Species ID	23.72 (21.79, 25.64)	0.091 (0.00, 0.21)
Total	29.47 (27.55, 31.39)	-
H^2	<0.00001 (0.00, 1.92)	-

602