Animal Behaviour 139 (2018) 29–36

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

The role of exaggerated male chelicerae in male–male contests in New Zealand sheet-web spiders

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ARTICLE INFO

Article history:
Received 18 October 2017
Initial acceptance 15 November 2017
Final acceptance 8 February 2018

MS. number: 17-00838R

Keywords:
animal weaponry
Cambridgea foliata
male–male competition
self-assessment
sexual selection

Animal weaponry has long captured the imagination of researchers and these weapons are frequently exaggerated in size. Large weapons are particularly common in species in which males defend females from potential rivals and sexual selection is generally credited with driving this pattern of exaggeration. Male New Zealand sheet-web spiders, *Cambridgea foliata* (Araneae: Desidae), possess chelicerae (jaws) that are substantially larger than those of female conspecifics. To investigate whether chelicerae exaggeration is selected for in the context of male–male competition, we staged contests between males and analysed how different components of resource-holding potential influenced the outcomes and durations of contests. We found that while males with large chelicerae were more likely to win contests, body condition and body size were better predictors of contest outcome. While contest durations were highly variable, there is some evidence that males make decisions about when to retreat from contests using self-assessment. As a result, only very large males are likely to reach the most escalated phase of fighting in which they lock chelicerae with their opponent. In this way, regardless of whether extra-long chelicerae impart any advantage over similarly sized opponents, exaggerated chelicerae are only used by especially large males and are therefore of little use to small males.

Among species in which males are capable of defending females or resources important to females, exaggerated male weaponry is relatively common (Emlen, 2008). When competition is intense, these structures can reach impressive proportions and the use of exaggerated weapons in male contests is distributed across diverse taxa from crabs (Baeza, Asorey, Marine, Pierce, & Drive, 2012; Sneddon, Huntingford, & Taylor, 1997) and wasps (Longair, 2004) to lizards (Stuart-Fox, Firth, Moussalli, & Whiting, 2006) and ungulates (Coltman, Festa-Bianchet, Jorgenson, & Strobeck, 2002).

Exaggerated weapons frequently exhibit positive static allometry where large individuals possess disproportionately large weapons (Emlen & Nijhout, 2000; Kodric-Brown, Sibly, & Brown, 2006; Painting & Holwell, 2013; Petrie, 1988; but see Bonduriansky, 2007). It is suggested that positive allometry can result from net selection for trait exaggeration in the largest males if larger weapons confer greater advantages for larger individuals (Bonduriansky & Day, 2003). Alternatively, developing and bearing exaggerated weaponry may be disproportionately costly for small males which instead adopt an alternative reproductive tactic that does not require such weapons (Taborsky & Brockmann, 2010).

Yet while male weapons are clearly used in contests over females and are exaggerated in many such cases, the extent to which they contribute to a male's ability to defend a key resource (their resource-holding potential, RHP, Arnott & Elwood, 2009) is poorly understood, owing to the strong correlation between weapon size and overall body size that is implicit in cases of positive allometry. While body size is perhaps the most common predictor of contest outcomes (Bridge, Elwood, & Dick, 2000; Kotiaho et al. 1998; Macedo, Monteiro, Silveira, & Mayhew, 2013; Miyashita, 1993; Schaefer & Uhl, 2003; Schütz & Taborsky, 2011), it is more challenging to determine how even exaggerated weapons contribute to RHP, independent of body size. In a few cases, weapon size has proven a better predictor of fighting success than body size, as is the case for chelicerae length in the jumping spider, *Lyssomanes viridis* (Tedore & Johnsen, 2012), and chela length in both the hermit crab, *Diogenes nitidimanus*, and the common shore crab, *Carcinus maenas* (Sneddon et al., 1997; Yoshino, Koga, & Oki, 2011).

Such studies have used a range of different statistical methods to determine whether weapons contribute to RHP. One such method is backward elimination from a maximal model to identify the most

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https://doi.org/10.1016/j.anbehav.2018.02.020
0003-3472/

important predictors of fighting success. This has been used to determine that chelicerae length was of greater importance to RHP in the aforementioned study by Tedore and Johnsen (2012) and has been used in other studies to determine how relatedness can influence aggression (Lizé, Khidr, & Hardy, 2012). While these methods allow for significance testing, they have been criticized for producing high Type I error rates and failing to identify the most important variables (Bolker et al., 2009; Mundry & Nunn, 2009). While not without its problems, information-theoretic approaches are a promising alternative for identifying key predictors and ranking different models as it is possible to compare the explanatory power of several models at once (Briffa et al., 2013).

When contests escalate to physical fighting, combatants can incur significant costs. For this reason, contests between males are frequently ritualized, with clear phases of mutual display and contact. These interactions allow males to assess their chances of winning without the risk of being injured or killed, and how these decisions are made could have important implications for the value of weaponry (Keil & Watson, 2010; Maynard Smith & Price, 1973). To better understand how combatants decide whether to persist in or retreat from a contest, game-theoretical contest models have been developed, representing one of the first and longest-running applications of game theory to animal behaviour (Arnott & Elwood, 2009; Leimar, Austad, & Enquist, 1991; Maynard Smith & Price, 1973). There are three broad groups of contest models: (1) mutual assessment models where contestants are able to assess both their rival's and their own RHP. In the context of exaggerated weaponry, we would expect opponents to interpret each other's large weapons as an index of RHP (sequential assessment model: Enquist & Leimar, 1987). In (2) 'pure' self-assessment models combatants only take their own RHP into account and simply invest in a fight up to a certain internal threshold (energetic war of attrition, Payne & Pagel, 1996; or war of attrition without assessment, Mesterton-Gibbons, Marden, & Dugatkin, 1996). Under self-assesment, larger weapons should only increase the threshold to which males are willing to fight with no impact on the other male. Finally, under (3) the cumulative assessment model (CAM), combatants invest in a fight up to a threshold defined by their own RHP, but may sustain costs as a result of their opponent's attacks (Payne, 1998). In this case, the rate at which costs accumulate will depend on the opponent's RHP and in this way the duration of the contest depends on both combatants' RHP regardless of an individual's capacity to make comparisons. In this scenario, weapon size, as an index for ability to inflict costs on an opponent, would be an important component of RHP.

Delineating between pure self-assessment and mutual/cumulative assessment involves comparing the degree of investment in a contest by both rivals (contest duration or intensity) against the RHP of the winner and loser separately (Arnott & Elwood, 2009; Taylor & Elwood, 2003). For pure self-assessment, we expect to see a strong positive correlation between the loser's RHP and contest duration/intensity, and a weaker positive correlation between the winner's RHP and contest duration/intensity. For both mutual and cumulative assessment, the relationship between loser RHP and contest duration/intensity is still expected to be positive but the winner's RHP should also be negatively correlated to contest duration/intensity.

We examined the interplay between weapon exaggeration and contest behaviour using New Zealand sheet-web spiders, *Cambridgea foliata* (Desidae), a nocturnal species common throughout the North Island of New Zealand (Forster & Wilton, 1973). Female *C. foliata* produce large sheet-webs (1.0 m^2) and in the summer, mature males wander the forest floor at night in search of females' webs. When they find one, they can cohabit, sharing the female's silk retreat during the day (L. A. Walker & G. I. Holwell, personal observation). Male *C. foliata* possess chelicerae that are substantially longer than those of females (Fig. 1) and contests that use these exaggerated chelicerae can occur when a male enters a web already inhabited by another male.

To determine how male–male competition might have driven weapon exaggeration in *C. foliata*, we conducted a series of investigations of morphology and behaviour. First, to determine whether male chelicerae are positively allometric, as we would expect given their exaggeration, we investigated the relationship between cephalothorax width (our measure for body size) and chelicerae length for both males and females. Second, we staged contests between randomly selected males in an established laboratory population and generated models predicting contest outcomes based on male characteristics including chelicerae size, male condition and body size. We then used Akaike's information criterion (AIC) model selection methods to assess their relative predictive power, with the specific aim of disentangling the influences of weapon and body size on competitive success. Finally, to further understand how males make the decision to retreat from contests, we examined the relationship between winner, loser and relative size, and both the escalation and duration of contests. We analysed these relationships separately for precontact and postcontact phases, along with the total duration of contests. Based on studies of other taxa, we expected that male chelicerae would be very likely to be positively allometric. As an explanation for this, we would then expect chelicerae length to contribute to RHP in that males with longer chelicerae should be more likely to win fights. Determining then which assessment model best describes male behaviour should indicate whether the advantages of longer chelicerae are limited only to how they help the bearer to continue fighting or whether they also communicate RHP to the bearer's opponent. Following the predictions of Arnott and Elwood (2009), we predicted a negative correlation between winner RHP and contest duration or intensity if rival males use mutual/cumulative assessment. By contrast, if rivals use self-assessment, there should be a weakly positive correlation between winner RHP and contest duration or intensity. Should our data indicate mutual or cumulative assessment, we would then expect fights between similarly sized individuals to be longer as the average size of combatants increased in the case of cumulative assessment but not mutual assessment. In all scenarios we expected loser RHP to correlate positively with contest duration/intensity.

METHODS

Morphology

We collected and measured male and female *C. foliata* from the Auckland region across two successive summers (October 2014–February 2015, December 2015–March 2016). The majority were collected from Matuku Forest and Bird reserve in West Auckland (36° 51′ 48.3″S 174° 28′ 47.7″E). We also measured museum specimens from Lincoln University (LUNZ), the Museum of New Zealand Te Papa Tongarewa, Wellington (MONZ), the New Zealand Arthropod Collection (NZAC), Auckland Museum (AMNZ) and Otago museum (OMNZ). Using digital callipers (accurate to 0.01 mm) we measured chelicerae length and cephalothorax width, our proxy for body size. We measured 101 males and 60 females.

Behavioural Observations

We returned to Matuku reserve to collect juvenile *C. foliata* for a laboratory population. In this way, when females matured, we could be certain of their reproductive history. As it was difficult to keep males alive, we collected males as both adults and subadults.