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UM CONTO SOBRE A AGRESSIVIDADE: VALOR DE RECURSO, TOMADA DE DECISÃO E ADAPTAÇÕES MORFOLÓGICAS

Santa Maria, RS
2017

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Tese apresentada ao Programa de Pós-Graduação em Biodiversidade Animal, da Universidade Federal de Santa Maria (UFSM, RS), como requisito parcial para a obtenção do título de **Doutor em Biodiversidade Animal**

Orientador: Prof. Dr. Sandro Santos

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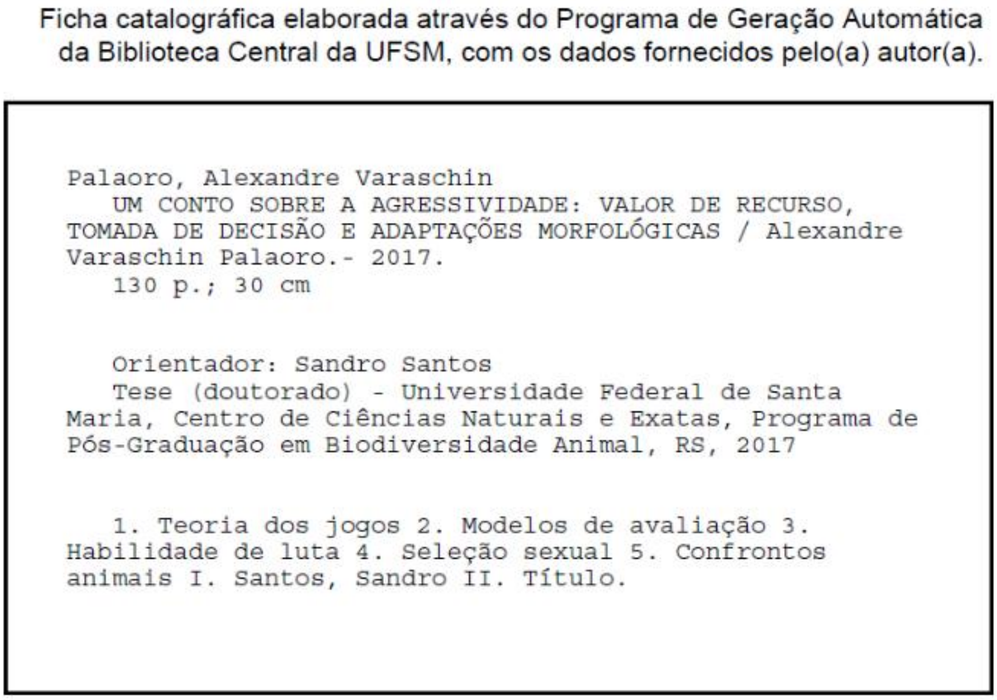

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Santa Maria, RS
2017

Oft him anhaga are gebideð, metudes miltse,
þeah þe he modcearig geond lagulade longe sceolde
hreran mid hondum hrimcealde sæ wadan wræclastas.

Wyrd bið ful aræd!

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Agradeço primeiramente a minha família: pai, mãe, irmão e cunhada (quem que agradece a cunhada?!). Não há palavra no português (e olha que o português é conhecido pelo excesso de palavras...) para expressar o quanto vocês foram, são e continuarão sendo essenciais na minha vida. Vocês sempre acreditarem em mim e me deixarem fazer o que gosto, mesmo não entendendo 100% porque alguém gostaria de passar noites e noites em claro assistindo caranguejos brigar em um laboratório - ao fazer isso me deram o mundo como presente. Nunca conseguirei agradecer o suficiente por isso. Sem vocês, toda essa caminhada não teria significado algum.

Ao Programa de Pós-Graduação em Biodiversidade Animal da Universidade Federal de Santa Maria pela infraestrutura e recursos para o desenvolvimento dessa tese. Agradeço à CAPES pela bolsa de doutorado, e pela bolsa de doutorado sanduíche. Agradeço ao secretário do PPG em Biodiversidade Animal, Sidnei Cruz, pelo auxílio prestado durante a realização do doutorado. Aos membros da banca, Dr. Paulo Enrique Cardoso Peixoto, Dra. Lilian Manica, Dr. Eduardo Santos e Dr. Kléber Del Claro por ter tirado um pouco do seu finito tempo para me auxiliar na jornada do cientista com seus conselhos e críticas. Também agradeço ao Sr. Graciano Sonego por permitir que coletássemos os animais em sua propriedade durante todos esses anos. Por último, gostaria de agradecer ao Dr. Carlos G. Jara pelo auxílio nas coletas de eglídeos chilenos.

Ao meu orientador, Dr. Sandro Santos, por ter confiado no meu trabalho e ter dado liberdade para que minha imaginação fluísse sem restrições. Essa tática nem sempre funcionou, a exemplo das várias entradas em sua sala com cara de desesperado dizendo: “Sandro, precisamos mexer no projeto”. Mas, no final, foi uma experiência extremamente enriquecedora e com certeza transformou aquele menino perdido e preguiçoso de 2007 em quem sou hoje: um jovem adulto perdido e não muito menos preguiçoso.

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Por último, mas certamente não menos importante, a todas as pessoas que me auxiliaram durante esses quatro anos de doutorado. Um doutorado é um somatório das pessoas que estão no seu entorno, então se estou vivo (?!) hoje, é graças a essas pessoas que dividiram as alegrias e tristezas comigo durante todo esse tempo. Ninguém faz um doutorado sozinho, então é com vocês que gostaria de dividir esse título, pois sem vocês ele com certeza não existiria. Muitas vezes tudo que precisei era de uma palavra amiga e um “calma, vai dar tudo certo”, e essas pessoas sempre estiveram lá, faça chuva ou sol. Por isso, meus sinceros agradecimentos por tudo, e saibam que podem contar sempre comigo! Farei algo extremamente perigoso para alguém com memória curta como a minha, vou tentar listar todas as pessoas que me auxiliaram nessa caminhada. Caso eu esqueça alguém, favor me avisar até a data da impressão da versão final porque não é nada pessoal – eu que sou esquecido mesmo. Vamos lá:

Marcelo Dalosto, Fernando Benso Lopes, Bruno Madalozzo, Victor Lipinski, Wagner Schmidt, Vanderlei Strack, Gustavo Viapiana, Douglas Donaduzzi, Fernando Geron, Pedro Bastos, Johnatan Felber – meus irmãos de álcool, digo sangue, não... pera... Há pessoas que simplesmente entram na sua vida e começam a fazer parte integral dela, seja por meio de risadas, choros, ou simplesmente por algumas piadinhas ruins. Não é necessariamente uma escolha – a amizade simplesmente acontece, de forma natural e inpensada. Por vezes a vida e o tempo acabam nos afastando - é normal - mas sempre sabemos um do outro. São essas pessoas que levamos para a vida toda. Saibam que podem sempre contar comigo, porque eu vou com certeza continuar enchendo o saco de vocês com minhas piadas ruins, cinismo escrachado e mania de controle absurda.

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Forþon ic geþencan ne mæg, geond þas woruld, for hwan modsefa,
Min ne gesweorce, þonne ic eorla lif, eal geondþence,
Hu hi færlice, flet ofgeafon, modge maguþegnas.

Wyn eal gedreas!

RESUMO

UM CONTO SOBRE A AGRESSIVIDADE: VALOR DE RECURSO, TOMADA DE DECISÃO E ADAPTAÇÕES MORFOLÓGICAS

AUTOR: Alexandre Varaschin Palaoro
ORIENTADOR: Sandro Santos

Confronto agonístico é um fenômeno ubíquo na natureza. Dada sua abrangência, entender como e o porquê ela ocorre é essencial para entendermos sua influência na evolução do comportamento. Os objetivos desta tese são: testar a influência de ciclos ambientais previsíveis nos confrontos, quais regras os crustáceos utilizam para continuar ou desistir de um confronto e as adaptações morfológicas que fazem armamentos eficientes. Duas variáveis são comumente utilizadas para determinar a motivação do animal para brigar: o valor do recurso e os custos da agressão. Apesar de bem estudadas, não há informações sobre como ciclos ambientais previsíveis influenciam essas variáveis. Por isso, no primeiro capítulo testamos a influência das marés no comportamento agressivo da anêmona do mar *Actinia equina*. Simulamos um ambiente de marés no laboratório, expondo algumas anêmonas ao fluxo de água e outras não, confrontando-os. Para aferirmos o valor do recurso, mensuramos o tempo da resposta de fuga. Nossos resultados sugerem que áreas com fluxo são mais valiosas, pois indivíduos nesses ambientes tiveram: tempo de resposta de fuga menor, maior probabilidade de vitória e confrontos mais longos. Contudo, esses indivíduos também são menos propensos a escalar o confronto, sugerindo também um aumento nos custos do confronto. Entender que tipo de regras os animais utilizam para permanecer ou desistir em um confronto são essenciais para entendermos a evolução desse comportamento. Dois modelos teóricos explicam essa decisão: um no qual o animal utiliza apenas informação sobre si mesmo; e outro que prediz que os animais comparam a própria habilidade de luta com a do oponente. Para testar isso no segundo capítulo, primeiro testamos quais variáveis morfológicas e de performance auxiliam um animal a vencer um confronto. Após, testamos qual modelo explica melhor confrontos entre machos de *Aegla longirostri*. Nossos resultados indicam que tamanho corporal e tamanho do quelípodo são importantes para determinar quem vence. Quanto à decisão de desistir do confronto, os caranguejos aparentemente utilizam uma mistura desses dois modelos, pois os confrontos corroboram tanto predições quantitativas do modelo de comparação quanto predições do modelo sem comparação. Armamentos são utilizados em confrontos para subjugar oponentes. Dado seu papel, ter um armamento eficiente pode aumentar o sucesso reprodutivo do animal. Segundo a teoria, essa eficiência tem um custo: quanto maior a eficiência menor a variabilidade de formas de um armamento quando comparado a uma estrutura mista (i.e. que é utilizada como armamento e ornamento). No terceiro capítulo, nós investigamos a relação forma com a performance do quelípodo de três espécies de *Aegla* com diferentes funções: uma apenas para lutas (*A. longirostri*), outra para lutas e sinalização (*Aegla abtao*) e outra somente para alimentação (*Aegla denticulata*). Nossos dados corroboram a teoria: quelípodos para luta são biomecanicamente eficientes, mas sua forma é pouco variável, enquanto o quelípodo misto (*A. abtao*) também é biomecanicamente eficiente, porém a forma é mais variável. Em suma, demonstramos que flutuações ambientais previsíveis são importantes para confrontos, que os modelos teóricos de briga precisam ser repensados e que a restrição biomecânica dos armamentos previne que aumentem a sua variabilidade morfológica.

Palavras-chave: Teoria dos jogos. Modelos de avaliação. Habilidade de luta. Seleção sexual. Confrontos animais.

ABSTRACT

A TALE OF AGGRESSION: RESOURCE VALUE, DECISION MAKING AND MORPHOLOGICAL ADAPTATIONS

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ADVISOR: SANDRO SANTOS

Agonistic behavior is ubiquituous in nature. Hence, understanding how and why it occurs is fundamental for unravelling its influence in the evolution of behavior. The goals of this thesis are: to test the influence of predictable environmental cycles on fighting behavior, how animals decide when to quit a fight and the morphological adaptations for efficient weaponry. Two variables are typically used to determine an individual's motivation to fight: resource value and fighting costs. Although they are well studied, there is no information on the effects of predictable environmental cycles on these variables. Hence, in the first chapter we tested the influence of tidal cycles on the motivation and contests of the sea anemone *Actinia equina*. We simulated a tidal cycle in the laboratory in which we exposed a group of anemones to it but not others. We elicited fights between these groups, also measuring their startle responses to assess territory value. Our results suggest that territories with water flow are more valuable because individuals exposed to flow had: shorter startle responses, higher winning probability and longer contests. However, these individuals are also less likely to escalate their aggression levels, suggesting that fighting costs are also higher. Following that rationale, understanding how individuals make the decision to withdraw from a contest is important to understand the evolution of such behavior. Two theoretical models explain that decision: one in which the individual uses information only about himself; and the other predicts that individuals can assess each other's fighting ability. To test this in the second chapter, first we tested which morphological and performance traits are important for an individual to win a contest. Afterwards, we tested which model explains better the decision to withdraw in fights between males of *Aegla longirostri*. Our results indicate that body size and claw height are important to settle contests. Regarding the decision to withdraw, crabs seem to use a mix of both models because contest variables corroborate with the quantitative predictions of both assessment models. Crabs' claws are regarded as weapons in these fights, and as such, are used to subjugate opponents. Given this role, having an efficient weapon can increase the individual's fitness. According to theory, this efficiency has a cost: the higher the weapon efficiency, less variable will be its shape when compared to an structure that is used both to fight and to signal. In the third chapter, we investigated the shape and performance of the claw of three *Aegla* species that use their claws differently: one species uses only for fighting (*A. longirostri*), other for fighting and signaling (*Aegla abtao*) and the last one only for feeding (*Aegla denticulata*). Our data corroborate this theory: fighting claws are biomechanically efficient but with a conserved shape, whereas the fighting and signaling claw is also biomechanically efficient, but its' shape is more variable. Overall, we demonstrated that predictable environmental cycles are important for contest behavior, that theoretical models of assessment need to be reworked and the biomechanic efficiency constrains weapon shape.

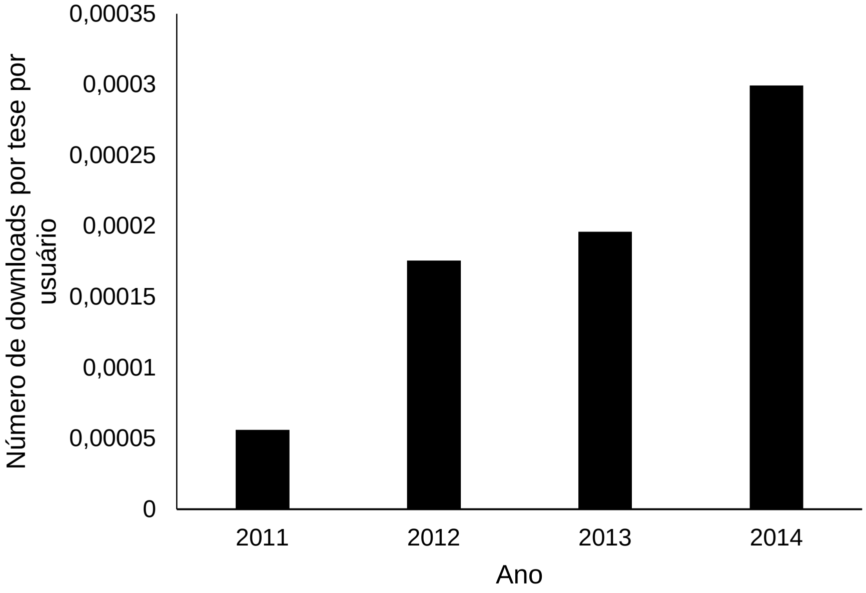
Keywords: Game theory. Assessment models. Fighting ability. Sexual selection. Animal contests.

SUMÁRIO

Apresentação geral

Estou ciente de que introduções gerais de tese geralmente discorrem extensivamente sobre o estado da arte dos tópicos que o aluno estudou durante o doutorado, sendo o principal responsável pelo volume de páginas de uma tese. Muitos pesquisadores acreditam que apresentação gerais são uma boa forma de iniciar alunos (graduação, mestrado) no estudo de determinados tópicos, principalmente por serem textos acessíveis e em português. Contudo, fugi desse formato tradicional porque sempre fui muito cético quanto a ideia de que esses textos são utilizados de forma efetiva e também por causa do termo "acreditam que são uma boa forma". Minha experiência pessoal indica que a maior parte das dissertações/teses é simplesmente jogada na biblioteca (agora virtual) e deixada lá juntando pó (ou "limbo da internet"). Essa ideia, inclusive, é explorada em um episódio do seriado de comédia Friends (temporada 7, episódio 7), no qual um dos personagens (Ross, interpretado por David Schwimmer) descobre que alunos vão para a biblioteca – especificamente na sessão na qual sua tese está – para "dar uns amassos" justamente porque ninguém nunca está lá. Como opiniões pessoais e episódios de sitcoms americanas não são base para argumentação nenhuma, acessei a página da biblioteca virtual da USP (http://www.teses.usp.br/) e baixei os seguintes dados públicos: números de teses e dissertações, número de downloads (visitantes apenas), número de usuários (total). Fiz uma razão de número de downloads por usuário por tese/dissertação e observei que, no geral, as teses possuem muito menos de um download por usuário (Fig. 1). Apesar de o número estar aumentando com os anos, para mim, ainda é um número baixíssimo de acessos.

Fig 1. Número de downloads por tese por usuário da biblioteca virtual da USP nos anos de 2011 a 2014. Somente esses anos foram utilizados por serem os únicos que possuem dados de número de usuários



Dado isso, gostaria de evitar a redação de algo longo e prolixo por natureza que dispende tempo tanto da banca quanto o meu para algo que será lido por, sendo otimista, meia dúzia de pessoas (incluindo os membros da banca). Por isso, pensei em uma maneira mais produtiva de escrever algo abrangente sobre o que estudei durante o doutorado: um texto de divulgação científica. Não há formatação definida para nenhuma revista de divulgação, a maioria só requer linguagem acessível, textos até 2000 palavras e uso de figuras e esquemas. Logo, tentei fazer exatamente isso. Ao redigir esse texto apaziguarei minha incessante relutância em produzir algo que não será utilizado por quase nenhuma esfera da sociedade, para, quem sabe, ajudar alguns curiosos a entender melhor o porquê animais brigam.

Por que e como os animais brigam? E o que isso tem a ver com nós?

Alexandre V. Palaoro

Era um dia comum de meados de setembro. Céu limpo, sol brilhando, temperaturas amenas, um pouco de rinite por causa do pólen, tudo calmo e tranquilo. Pedrinho estava sentado em sua classe escutando o professor falar sobre a segunda guerra mundial. Após uma hora e vinte minutos de aula sobre um dos maiores confrontos da história da humanidade, o professor faz aquela famigerada pergunta: “alguma dúvida pessoal?”. Ao escutar essa pergunta pela milésima vez em sua breve vida, algo muda - Pedrinho começa a pensar sobre a disciplina de história e se sente inquieto. Desde que começou a estudar história só viu coisas sobre guerra: Guerra de Troia, Guerras Médicas, Guerras Púnicas, a revolta de Spartacus, Cruzadas (todas as seis edições dela), Primeira Guerra Mundial, e agora a Segunda. As guerras parecem algo constante na história da humanidade: ideologias, jogos de poder, conquistas de espaço, países eram formados e destruídos com uma frequência estonteante. Todas essas mudanças abruptas e frequentes faziam o mundo fervilhar. Contudo, ao olhar o noticiário hoje em dia, nada disso parecia ocorrer. O mundo mudava muito pouco e parecia que as maiores disputas estavam mais no plano econômico do que no plano bélico. Ou seja, a guerra parecia ser muito mal vista hoje em dia, ou caiu em desuso porque o ser humano é pacífico agora. Todos esses pensamentos cruzaram na cabeça de Pedrinho em uma fração de segundos, fazendo a cabeça do menino girar. Pensou que ia desmaiar dado o volume de pensamentos que estava tendo, mas todas as ideias estavam girando em torno de um ponto que ele não conseguia entender: “Porque as guerras acontecem? Como elas se desenvolvem?”.

É sobre esse ponto que quero discutir hoje. Porém, ao invés de fazer um detalhamento complexo sobre cenários político-econômicos carregado de números, traições e relações de parentesco entre famílias reais no melhor estilo Guerra dos Tronos, vou tentar utilizar uma abordagem diferente: a ecologia comportamental e evolutiva. Mas porque cargas d’água eu faria isso? Por um motivo bem simples, na verdade. Animais brigam – e muito. Em alguns casos, são bem similares às humanas, com grupos de indivíduos brigando como se fossem duas nações (como hienas, formigas e outros animais com sistemas sociais). Por isso, o método científico nos possibilita testar teorias e hipóteses que são complementares e análogas as aplicadas ao estudo de guerras entre humanos (e até a uma briga mano a mano, como dizem). Portanto, espero que ao explicar o porquê os animais brigam e quais os aspectos por trás disso você, caro leitor, entenda melhor as decisões feitas nas guerras humanas.

Brigar ou não brigar, eis a questão

Antes de iniciarmos é bom ressaltar que estou definindo briga como competição entre dois animais da mesma espécie e, geralmente, do mesmo sexo. Brigas também podem ocorrer entre bandos de animais, grupos, famílias e por aí vai. Porém, como diz nosso amigo, Jack: “vamos por partes”. Portanto, começaremos com o termo mais simples de uma interação entre dois indivíduos da mesma espécie e sexo. Apesar de ser um termo bem restrito, brigas ocorrem em quase todas as espécies do reino animal, desde invertebrados sem um cérebro central (isto é, as coloridas anêmonas do mar, que apesar de sésseis brigam bastante, Figura 1) até mamíferos com sistemas sociais desenvolvidos (chimpanzés, por exemplo, Figura 1). Como é um comportamento comum em todos animais, é bem provável que os motivos para brigar também sejam comuns. Ao longo dos anos, pesquisadores perceberam que os animais disputam qualquer coisa que seja indivisível e a qual eles necessitem para sobreviver e/ou acasalar – geralmente isso significa comida, abrigo, território ou parceiros reprodutivos. Obviamente o item a ser disputado varia muito de espécie para espécie, anêmonas, por exemplo, disputam por áreas com mais fluxo de correnteza, enquanto machos de caranguejos, cervos e muitos outros animais disputam a atenção das fêmeas durante o período reprodutivo – mas, para padronizar e simplificar nossas vidas, vamos chamar todos os itens disputados de recurso.

Figura 1. Brigas em todo o reino animal: as anêmonas-do-mar no canto superior esquerdo

(foto: Alexandre V. Palaoro), artrópodos (grilos) no canto superior direito (fonte: **Kim Kyung-hoon**), cervos (canto inferior esquerdo); Fonte: https://www.youtube.com/channel/UC650u4npJNtyVbBGscP3Zfg) e animais sistemas sociais (chimpanzés, mas podiam muito bem serem formigas) no canto inferior direito (fonte: http://www.amusingtime.com/images/06/funny-fighting-monkeys-picture.jpg).

Como nada na biologia é tão simples, além de o recurso ser indivisível e necessário, ele também precisa de outras características para sabermos se uma briga vai ocorrer e como ela vai ocorrer (ou seja, a intensidade da briga). A primeira, e mais importante, dessas características é o valor do recurso. Cada recurso tem um valor intrínseco que mede o quanto ele beneficiará o animal. Pense na tabela nutricional de qualquer alimento no mercado ou em um perfil do Tinder e você terá uma boa analogia. Se cada recurso tem um valor, então é intuitivo que os animais preferirão os recursos mais valiosos. Logo, quanto mais valioso, maior é a vontade de obtê-lo e mais você estará disposto a gastar para obtê-lo (nunca vi alguém disputando o último pé de alface em um supermercado...).

Outra característica que afetará diretamente o valor do recurso é o contexto no qual ele é disputado. Para fazermos uma analogia, olhe para a figura abaixo e pense em quanto o indivíduo da figura pagaria para tomar um copo d’água (fonte: Shutterstock).

Nada? Ok. Agora olhe para a próxima figura (fonte: Barry Macey).

Quanto os dois personagens pagariam por um copo d’água nesse contexto? Provavelmente muito mais do que na primeira figura. Com isso, podemos perceber a importância do contexto no valor do recurso. Se há muito recurso disponível, não há motivo para disputa-lo, mas, conforme ele fica mais escasso e raro, a probabilidade de uma disputa ocorrer aumentará (a lei da oferta e da procura é um simulacro desse processo). Tudo isso leva a um valor subjetivo do recurso: cada animal irá perceber determinado recurso de maneira diferente, assinalando um valor diferente dependendo da sua situação. Animais com fome valorizarão um alimento muito mais do que um animal saciado, por exemplo.

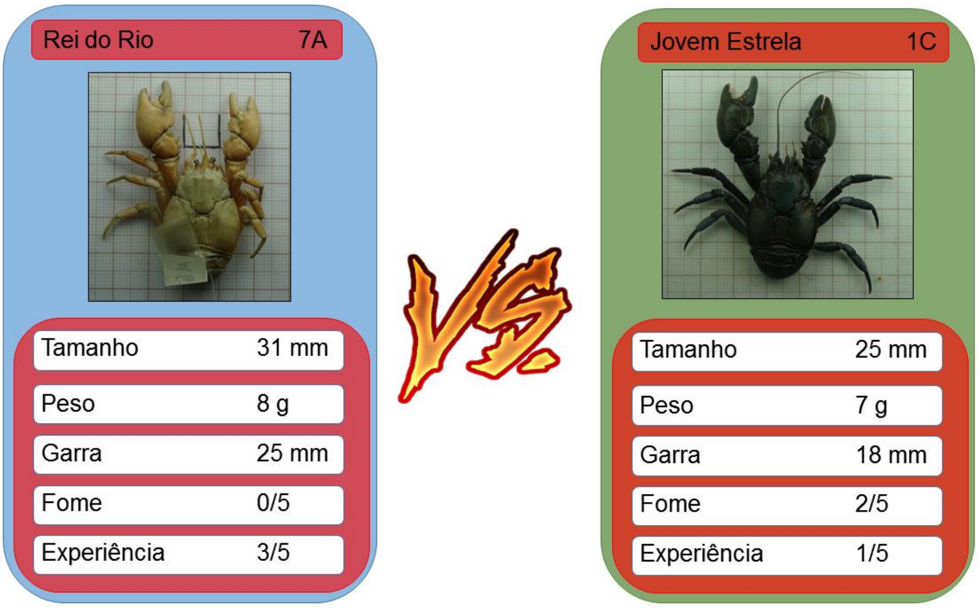
Você pode estar imaginando agora que recursos são só benefícios, que sempre valerá apena brigar por eles. Contudo, entrar em uma briga custa ao animal – e esse custo é alto. É só pararmos para olhar qualquer tipo de arte marcial para percebermos que nos últimos rounds os lutadores estão ofegantes – os gastos energéticos com uma briga são imensos. Sem falar nos riscos de sofrer qualquer tipo de dano físico (sim UFC, estou olhando para você). No reino animal, confrontos que resultam em lesões, perda de sangue, ou ossos quebrados não são comuns - tanto que toda vez que um vídeo desses cai na internet causa alvoroço (vide vídeo dos pinguins brigando, link: https://www.youtube.com/watch?v=Jupr_hLO9BQ). Esse tipo de confronto raramente ocorre porque pode resultar em morte – qualquer pata quebrada, ou sangue exposto, pode fazer com que o animal não consiga fugir ou facilite sua localização por um predador.

Ok, isso ficou bem complicado rápido demais. Vamos tentar simplificar essa história e tentar responder se vamos entrar em uma briga ou não. Imagine que você avistou um recurso, digamos, um pedaço de carne. O valor nutricional desse pedaço é de 150 calorias. Como você está com fome, essas 150 calorias são necessárias para sua sobrevivência. Ao chegar no pedaço de carne, você percebe que outra pessoa também está de olho no mesmo pedaço de carne – e ela também está com fome. Como você está com muita fome, sua motivação para competir por aquele pedaço de carne é altíssima. Mas, como você faz para calcular os custos de uma briga sem ter brigado? Existem algumas formas de isso acontecer: ou você estabelece um limite de energia para gastar e briga até chegar nesse limite, ou você estima a habilidade de luta do seu adversário (se possível) e, se essa não for muito maior que a sua, pode ser que você gaste menos energia do que o alimento vai te dar. Tudo isso é um cálculo muito complexo que não temos como pôr em números tão facilmente. Geralmente, os animais iniciariam um confronto com ações pouco custosas. Caso ninguém desista aí é porque a motivação é alta para os dois, então a intensidade da briga começa a aumentar até que alguém desista. Em suma, se o valor for maior do que os custos, vale a pena entrar na briga porque no fim das contas você ainda terá um saldo positivo. Caso o custo exceda o valor do recurso, não vale a pena brigar. Esse simples mecanismo de custos e benefícios faz com que brigas ocorram em virtualmente todas as espécies, pois sempre haverá algum tipo de recurso a ser disputado. Mas agora fica a dúvida: o que é habilidade de luta e como ela interfere na luta?

O papel do lutador

Em artes marciais definimos a habilidade de luta como o estilo e os golpes que determinador lutador usa durante um combate. No mundo animal esse conceito é diferente, pois utilizamos características físicas e fisiológicas do animal para determinar a habilidade de luta do animal. De um modo geral, animais grandes tem uma habilidade de luta maior que animais pequenos (lembrando sempre que estamos falando de dois indivíduos da mesma espécie e sexo). Uma forma simples de pensar sobre isso é pensar em uma carta do famigerado jogo de super trunfo (Figura 2) – aquele que tiver os maiores valores geralmente vence a briga. Mas o que isso tem a ver com entrar em uma briga ou não? Bom, se você percebe que seu adversário é maior que você, para que você vai tentar entrar em uma briga? Mas será que eu posso confiar nessa informação?

Figura 2. Todas as características na carta descrevem a habilidade de luta dos animais. Muitas outras características podem ser utilizadas, essas são apenas alguns dos exemplos mais comuns



Fonte: Alexandre V. Palaoro.

Obtendo informação e calculando os custos de uma guerra

Apesar de nem todos os animais conseguirem comparar os oponentes a si próprios (é um processo cognitivamente complexo que merece um texto a parte), ele é um processo equivalente as pesquisas recentes sobre guerras entre estados. Justamente por isso, focarei nesse ponto. Toda briga e guerra deve ser vista em duas frentes: uma que está interessada em obter informações, e outra que está interessada nos danos causados e obtidos durante o confronto (a parte dos custos de uma briga). Começaremos com a parte de obter informações.

Toda briga pode ser vista como um animal tentando estimar a habilidade de luta de seu adversário através de comportamentos agressivos. Porque eles fazem isso? Ora, pelo simples fato que o seu oponente pode estar blefando sua habilidade de luta e que todo tipo de comunicação é imperfeito e erros acontecem na hora de transmitir e receber essas informações. Como exemplo temos o comportamento dos vikings dinamarqueses que penduravam seus escudos nas bordas dos navios para demonstrar quantos homens estavam naquele barco – mas o número de escudos era sempre maior que o número de soldados, ou o quanto de informação e nuances são perdidas durante uma comunicação somente por texto (é difícil perceber sarcasmo em mensagens de whatsapp, não concorda? ;-)). Portanto, toda briga é um processo de obter informações sobre o oponente, tanto sobre sua habilidade de luta quanto sua motivação. Cada vez que você realiza um ato, mais informação você tem sobre o oponente, e essa informação é atualizada a cada ato subsequente. Logo, quantos mais atos, mais informação, e maior precisão da sua estimativa sobre a habilidade do oponente. Esse raciocínio nos revela um ponto importantíssimo sobre duração de uma briga: quanto mais parecidos são os indivíduos brigando, mais tempo eles vão demorar para ter certeza de quem é o maior. Por isso, brigas entre indivíduos similares demoram mais do que quando eles são muito diferentes. Porque, afinal, você pensa que a Guerra Fria durou tanto tempo?

Mas agora você pode estar se perguntando: “ok Alexandre, mas nós, seres humanos, temos a linguagem a qual reduz todo esse nível de incerteza a quase zero.” Essa é uma excelente observação! Só que, se a linguagem reduz tanto o nível de incerteza, porque o Presidente Kennedy (EUA) não falou com o General Khruschev (USSR) durante a crise de mísseis de Cuba para parar com aquilo, já que a iminência de uma guerra nuclear era tão próxima? Como Fearon nota: “formas convencionais de comunicação diplomática podem ser inúteis”. Apesar de ser uma afirmação forte, as vezes a parte mais informativa de uma conversa diplomática são os atos simbólicos de querer sentar para negociar (motivação para terminar a luta) e de levantar no meio da conversa sem acertar nada (motivação para continuar lutando). Percebam que utilizei a palavra ‘motivação’ aqui, a mesma que utilizei anteriormente no texto quando falava sobre quanto os animais querem recursos. Essa não é apenas uma coincidência, pois as motivações dos animais para desistir ou continuar em brigas, e as motivações para desistir ou continuar em uma guerra são parecidas. Ambas formas de motivação (desistir/continuar) estão relacionados com o quanto de informação temos sobre nossos oponentes, a qual está relacionada com a última avaliação feita. Portanto, quanto mais avaliações fizermos, mais próximos esses limites estarão dos valores reais da habilidade de luta do oponente.

Quanto maior a precisão, mais fácil é saber se vai continuar ou desistir de uma luta. Isso funciona basicamente para qualquer decisão que tomamos na vida, não é verdade? Quanto maior for a diferença entre coisas que estamos escolhendo, mais fácil é de fazer a escolha: escolher entre ficar em casa ou tirar férias é muito fácil, agora escolher entre férias nos Estados Unidos ou férias na Europa pode levar algum tempo (e as vezes fazemos listas para ajudar na escolha). Em suma, as decisões tomadas em guerras entre estados utilizam um raciocínio similar aos animais em um confronto que estão se avaliando: quanto mais soubermos sobre o inimigo, melhor. A diferença crítica entre estudos de briga entre animais e de guerras humanas é que nos animais nós tentamos entender porque eles não se lançam sempre em brigas mortais, enquanto que nas guerras tentamos entender porque é a que guerreamos.

Os danos causados e obtidos durante uma guerra também são similares ao que observamos em animais: uma nação pode causar danos físicos ao oponente (exemplo, bombardeios) e ao mesmo tempo terá gastos econômicos com armamento bélico (similar a gastos fisiológicos). Portanto, em última instância, esse acúmulo de danos dirá muito sobre a persistência de uma nação, o que estará relacionada diretamente com a sua habilidade de luta e ao valor que está sendo dado ao recurso disputado. Agora chegamos ao ponto crítico do texto – se animais brigam quando o benefício de obter um recurso é maior do que seu custo, o que é um recurso para o ser humano? Em primeira instância podemos mencionar alguns fatores como: terras (exemplo, invasões vikings), poder monetário (exemplo, Guerras Púnicas), poder político (Guerra Fria), soberania ideológica (Segunda Guerra Mundial), soberania religiosa (Cruzadas), e mais uma miríade de fatores. Infelizmente, essa é uma análise que merece mais detalhamentos históricos do que posso dar nesse texto. Além disso, como diz George Orwell: “a história é escrita pelos vencedores”, então o verdadeiro motivo da maioria das guerras até a Idade Média pode estar levemente alterado (haviam poucos historiadores e os poucos registros eram facilmente alterados/queimados). Contudo, as brigas entre animais e as guerras humanas são parecidas, pois obedecem a regras similares e são jogadas de forma também similar: confrontos, sejam eles brigas ou guerras, seguem a regra básica do benefício do recurso sendo disputado, os custos que serão necessários para obter esse recurso e contra quem estamos lutando. Não somos tão diferentes dos animais, afinal de contas....

Objetivos

Objetivo geral

O objetivo desta tese é estudar os seguintes aspectos da agressividade: (1) a influência da dinâmica do ambiente no valor do recurso e nos custos de lutar; (2) quais são as variáveis morfológicas e de performance que influenciam a probabilidade de vitória em um confronto; (3) que tipo de informação os caranguejos do gênero Aegla estão utilizando quando decidem desistir de um confronto; (4) quais são as adaptações morfológicas necessárias para transformar o quelípodo em um armamento biomecanimanete eficiente.

Objetivos específicos

Capítulo 1:

Testar a influência de um ambiente dinâmico e variável no comportamento agressivo da anêmona do mar *Actinia equina*. Por muito tempo é utilizado o valor do recurso e os custos de uma luta para investigar a motivação dos animais para brigar. Apesar de muitos avanços terem sido feitos, ainda há pouquíssimos estudos sobre a variabilidade ambiental e agressão. Como o comportamento agressivo evoluiu em um ambiente variável, é de suma importância que saibamos o quanto esse ambiente está influenciando a agressão para entendermos a agressão em seu aspecto evolutivo. Com isso, nosso objetivo foi testar se anêmonas que foram expostas a um ambiente simulando as marés de um costão rochoso tem uma motivação maior para defender seu território do que anêmonas que não foram expostas ao fluxo de água. Nossa hipótese é que se o fluxo aumentar o valor do território, as anêmonas expostas ao fluxo terão uma resposta de fuga mais rápida, uma maior probabilidade de vencer o confronto e terão confrontos mais longos do que anêmonas que não foram expostas ao fluxo. Caso o fluxo intenso aumente os custos de uma luta, encontraremos as respostas contrárias.

Capítulo 2:

Investigar quais características morfológicas e de performance influenciam a probabilidade de vitórias em confrontos de machos de *Aegla longirostri*, e que tipo de informação eles utilizam para tomar a decisão de desistir do confronto. Nossa hipótese é que o tamanho corporal e a força do quelípodo sejam importantes para decidir confrontos, dado que ambos indicam que o animal é mais velho e tem mais experiência em confrontos, além de ser mais forte e ter uma performance corporal maior. Quanto à informação para desistir do confronto, nossa hipótese é que os caranguejos utilizem informações do oponente, uma vez que crustáceos utilizam comunicação química durante os confrontos.

Capítulo 3:

Investigar quais são as modificações na forma e na performance que transformam o quelípodo em um traço morfológico de alimentação em um armamento biomecanicamente eficiente, além de testar se armamentos possuem constrições biomecânicas na sua forma comparando-os com traços de duas utilidades (i.e. que são utilizados como armamento e ornamento). Todos os testes serão realizados utilizando três espécies do gênero *Aegla*. *Aegla longirostri* será a espécie de armamento puro, i.e. não utiliza nenhum tipo de sinalização. *Aegla abtao* será a espécie com quelípodo de duas utilidades, i.e. armamento e ornamento. *Aegla denticulata* será a espécie que utiliza o quelípodo apenas para alimentação. Nossa hipótese é que o armamento puro será biomecanimente eficiente e terá uma forma pouco elaborada, enquanto que o traço de duas utilidades será menos eficiente que o armamento puro, mas terá uma forma muito mais elaborada, enquanto que o quelípodo para alimentação não será biomecanicamente eficiente para confrontos e a forma do traço será intermediária aos dois outros tipos de quelípodos.

ARTIGO 1: HOW DOES ENVIRONMENT INFLUENCE FIGHTING ABILITY? THE EFFECTS OF TIDAL FLOW ON RESOURCE VALUE AND FIGHTING COSTS IN SEA ANEMONES

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How does environment influence fighting? The effects of tidal flow on resource value and fighting costs in sea anemones

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ABSTRACT

An animal's decision to enter into a fight depends on the interaction between perceived resource value (V) and fighting costs (C). Both could be altered by predictable environmental fluctuations. For intertidal marine animals, such as the sea anemone *Actinia equina*, exposure to high flow during the tidal cycle may increase V by bringing more food. It may also increase C via energy expenditure needed to attach to the substrate. We asked whether simulated tidal cycles would alter decisions in fighting *A. equina*. We exposed some individuals to still water and others to simulated tidal cycles. To gain insights into V, we measured their startle responses before and after exposure to the treatments, before staging dyadic fights. Individuals exposed to flow present shorter startle responses, suggesting that flowing water indicates high V compared to still water. A higher probability of winning against no flow individuals and longer contests between flow individuals, suggests that increased V increases persistence. However, encounters between flow individuals were less likely to escalate, suggesting that C is not directly related to V. Therefore, predictable environmental cycles alter V and C, but in complex ways.

Keywords. Animal contests, contest costs, environmental cues, resource value

1. INTRODUCTION

The initial Hawk-Dove model [1] and its subsequent developments (e.g. [2,3]) use two key variables to explain why animals might choose to fight; the cost of fighting (C) and the value placed on the contested resource (V). Thus, there has been substantial empirical focus on the effects of C and V on strategic decisions during contests. Most tests of contest theory involve staged encounters under stable laboratory environments. In contrast, information on how environmental conditions might influence C and V are lacking [4]. Given that fighting behaviour has evolved in fluctuating natural environments, rather than under stable laboratory conditions, this is an important omission. Therefore, studies focussing on the effects of fluctuating abiotic features of the environment could give new insights into the functions of agonistic behaviour.

There are several routes through which environmental conditions could influence animal contests by altering C and V. Weather stability may affect V by constraining or relaxing the reproductive period, thus affecting the value of territories [5]. Weather may also play a role in aerial contests: wind velocity can increase C through drag or convective cooling effects [6], and sunlight may increase territory V [7]. Furthermore, lunar cycles are known to alter mammal activity, and may thus cause fluctuations in prey's perceived predation risk, affecting C [8]. On heterogeneous rocky shores, structural features of the shore mean that the strength of currents varies across the same shore. Strong currents could increase the risk of dislodgement such that animals need to allocate more energy to tenacity. This could increase the relative C if more energy is needed to maintain attachment to the rocky surface, both during routine activity and during fights. If animals have to pay more to stay attached, then less energy will left over for aggressive behaviours and, equally, any energy expended on fighting will be lost to tenacity [9]. However, intertidal currents could also alter V. For sedentary animals, tidal currents bring food particles into their capture space. Fighting animals might therefore place greater value on territories that are associated with high flow and hence high rates of food supply. Thus, variation in tidal currents could influence both V and C for fighting anemones, potentially in opposite directions.

The effects on V and C can be investigated by probing their effects on motivational state [10] and contest dynamics [11,12]. If perceived V is higher for one opponent, this individual should have an increased chance of victory. When V is high for both opponents we should see lengthier and more aggressive contests. In contrast, high costs should have the opposite effect: reduce the chance of victory for the individual with higher C, while also reducing contest duration and escalation. V and C might thus interact. To disentangle this interaction, we need to manipulate the environmental variable of interest independently for each individual in the contest. Beadlet sea anemones, *Actinia equina*, show startle responses, which can be used to probe V, and readily fighting for territories on the rocky intertidal [13]. They use their specialised fighting tentacles, the acrorhagi, to damage their opponents during fights [14], but some fights are resolved without stinging (maybe due to self-inflicted damage [15]), which may increase C. Thus, *A. equina* is an ideal system for studying the influence of environmental fluctuations on fighting.

Here, we use an orthogonal design to investigate contests between pairs of focal and opponent anemones that have been exposed to either still or flowing seawater (with flow pattern arranged to mimic the tidal cycle). We first use startle response duration to assess the effect of flow rate on V. If high flow increases the perceived value of territory, anemones held under this condition should show shorter startle responses (prior to staged fights) than those held in still water. In subsequent fights, if high flow only increases V, individuals that experienced this should then be more likely to defeat individuals held in still water, and contest duration and intensity should increase when both individuals have experienced flowing seawater. If high flow only increases C, individuals that experienced high flow should be less likely to defeat individuals held in still water, and contest duration and intensity should decrease when both individuals have experienced flowing seawater. Thus, the effects of flow regime on V and C can be inferred by the interaction between the prior experiences of flow regime of focal and opponent anemones.

2. METHODS

(a) Collection, experimental treatment and startle responses

We collected 140 *A. equina* on the upper shore of Portwrinkle beach, Cornwall, U.K. and transported them to the lab. We housed all anemones within a large circular aquarium (diameter = 100 cm) filled with aerated seawater. Within this aquarium, we kept anemones individually in rectangular enclosures (36 cm^2) made with mesh (0.325 cm^2) to allow water flow during the entire experiment. We subdivided the circular aquarium (Fig. S1a) into two parts - an outer zone and an inner zone – by a solid PVC wall. This wall ensured that flow in the outer zone would not affect the water in the inner zone. We acclimated the anemones for three days before we started the experiment. Feeding schedules can be seen in Fig. S1b.

We simulated tidal cycles for the individuals in the outer zone only. We attached five reef pumps to the side of the aquarium equidistantly (flow speed: 7.8 ± 1.4 cm/s, Fig. S1a). We left the water flowing for 5 hours (incoming tide), turned them off for two hours (slack water), reversed the direction of the pumps and left the pumps on for five hours (outgoing tide; Fig. S1c). We repeated this process, simulating a full day of the tidal cycle. The individuals in the inner zone of the aquarium spent the same period in still water.

We then recorded the time the anemone took to recover from a startling stimulus as an index of perceived V [10]. These 'startle response' durations should, on average, reflect underlying motivational states driven by variation in V (longer startle responses reflect lower V [10]). We thus elicited the startle responses of all individuals before (control, or startle response 1) and after exposure to flowing or still seawater (startle response 2; Fig. S1b).

(b) Fighting and morphological measurements

We staged fights between pairs of anemones where one individual was designated as the 'focal' and the other as the 'opponent'. We used four treatments determined by the prior experiences of flowing or still seawater: flow vs. flow (N = 20), no flow vs. no flow (N = 20), flow vs. no flow (N = 15) and no flow vs. flow (N = 15). We visually size-matched focals and opponents and we used a new rectangular aquarium (filled with seawater) for fights. After 1h of acclimation we moved the two anemones to the centre of the aquarium until they had contact with each other's tentacles (starting point of the fight). We considered the fight over when one anemone had moved one pedal disk diameter away (estimated visually) or retracted their tentacles for 10 min [14]. Following fights, we took samples from unused acrorhagi to measure nematocyst length (mm) [10] and then measured the dry weight of anemones (g) [14].

(c) Statistical methods

To test if flow individuals perceive V higher than no-flow individuals, we used an ANCOVA with startle response 2 as our response variable, startle response 1 was a co-variate and treatment was a category (flow or no flow). We used logistic regressions with (a) the outcome for focal individuals (win or lose) and (b) whether fights escalated (stings or no stings) as our response variables, and treatment of focals and opponents as our categories. Startle responses, dry weight and nematocyst lengths are known to influence fighting ability in *A. equina* [14], and hence we used the absolute values of both focals and opponents as covariates in our model. We $\log_{10}$-transformed, centred and scaled them before adding to the model [16]. Lastly, to test the effects of V on duration, we used a linear model to determine the effects of the predictors mentioned above on the contest duration ($\log_{10}$ transformed). All analyses were made in R v. 3.3.1 [17].

3. RESULTS

Anemones that were exposed to flow had a shorter startle response than individuals exposed to still water ($F_{3,138} = 3.5$, $P = 0.017$, $R^2 = 0.07$, Fig. 1a). There was a non-significant trend for focals to be more likely to lose to opponents that had been exposed to flow ($\chi^2_{1,60} = 3.6$, $P = 0.058$; Fig. 1b). Contests were more likely to escalate when opponents were large ($\chi^2_{1,60} = 5.6$, $P = 0.017$). An interaction between focal and opponent treatment indicates that escalation was more likely when each anemone had experienced different pre-fight conditions and least likely when both had been exposed to flowing seawater before fights ($\chi^2_{1,60} = 6.27$, $P = 0.012$; Fig. 1c). Contests were longer when focal anemones were larger ($F_{1,60} = 4.1$, $P = 0.047$) and when opponents had been exposed to flowing seawater ($F_{1,60} = 4.3$, $P = 0.042$). A near significant interaction effect indicates that the longest fights occurred when both opponents had been exposed to flowing seawater ($F_{1,60} = 3.9$, $P = 0.053$; Fig. 1d). For full details of the analyses including non-significant effects, see tables S1-S3.

4. DISCUSSION

Shorter startle response durations in anemones held in simulated tidal flow indicate that they are more highly motivated to return to their ongoing feeding behaviour and therefore perceived their territory as being of greater value (V). Chance of victory only seemed to decrease when no flow individuals fought opponents exposed to flow but this may be an artefact of randomly choosing focal individuals. First, flow individuals won 21 out of 30 fights against no flow individuals (70%). Second, when we re–allocated focals and opponents, the proportion of fights won by focals on the flow treatment consistently vary between 60% and 80% (Fig. S2). Therefore, flow rate appears to influence persistence in a fight and hence the chance of victory.

Nevertheless, for anemones that were in flowing seawater, contests were less intense than contests involving individuals that were exposed to still water. Fewer than 10% of fights involving stinging when both opponents had been exposed to flowing water. Individuals may be more cautious to escalate when opponents show a similar V to avoid high levels of damage. Stinging results not only in damage to the opponent (e.g. skin necrosis, loss of feeding opportunities [14]), but in self-inflicted damage as well. The acrorhagial epithelium is ‘peeled’ away from the aggressor, which needs to be regenerated afterwards [15]. The focal might thus be cautious when the opponent has the same probability of stinging back. Fights between individuals of different treatments reinforce this idea because flow and no flow individuals were equally likely to initiate stinging, but flow individuals won more fights nonetheless. These results suggest that although more valuable resources might lead to greater persistence, high V does not necessarily lead to a high willingness to accept elevated chances of injury. Thus, V seems to be influencing decisions about persistence and injuries - both related to C - in different ways. If true, then longer fights between high V individuals are not unexpected. Since dyads are avoiding costly behaviours, contests take longer to resolve because C is accumulated only with persistence, and not with injuries.

Flowing seawater influences the perceived value of the territories but anemones only seem to accept greater persistence costs, and not greater injury costs, because of this increase in V. What is clear is that decisions to escalate can be altered by the abiotic environment. The costs and benefits of animal contests are typically investigated under stable conditions but aggression has evolved under natural conditions that show spatial and temporal variation. Thus, fighting behaviour may be considered a spatial-temporal mosaic in which the costs and benefits vary, sometimes due to predictable cycles (e.g. tidal, weather [6] stability [5]). Here we have shown how fighting animals can adjust the strategic (whether to give up) and tactical (whether to escalate) decisions frequently modelled by evolutionary theory based on fluctuating environmental cues.

Ethics. This work was performed on invertebrates not covered by the Use of Animals (Scientific Procedures) Act. Thus, there is no requirement for ethical approval within the university that deals with animals used in this experiment. However, experiments were conducted following the ASAB/ABS guidelines on the use of animals in education and research.

Data accessibility. Data used can be found in Dryad: http://dx.doi.org/10.5061/dryad.526g0 [18]

Authors' contributions. AVP and MB designed the study; AVP and MV performed the study; AVP, MV, SS and MB performed the statistical analyses; AVP, MB and SS wrote the manuscript; MV, SS and MB revised the manuscript. All authors approved the version to be published. All authors agree to be accountable for all aspects of the research.

Competing interests. We declare we have no competing interests.

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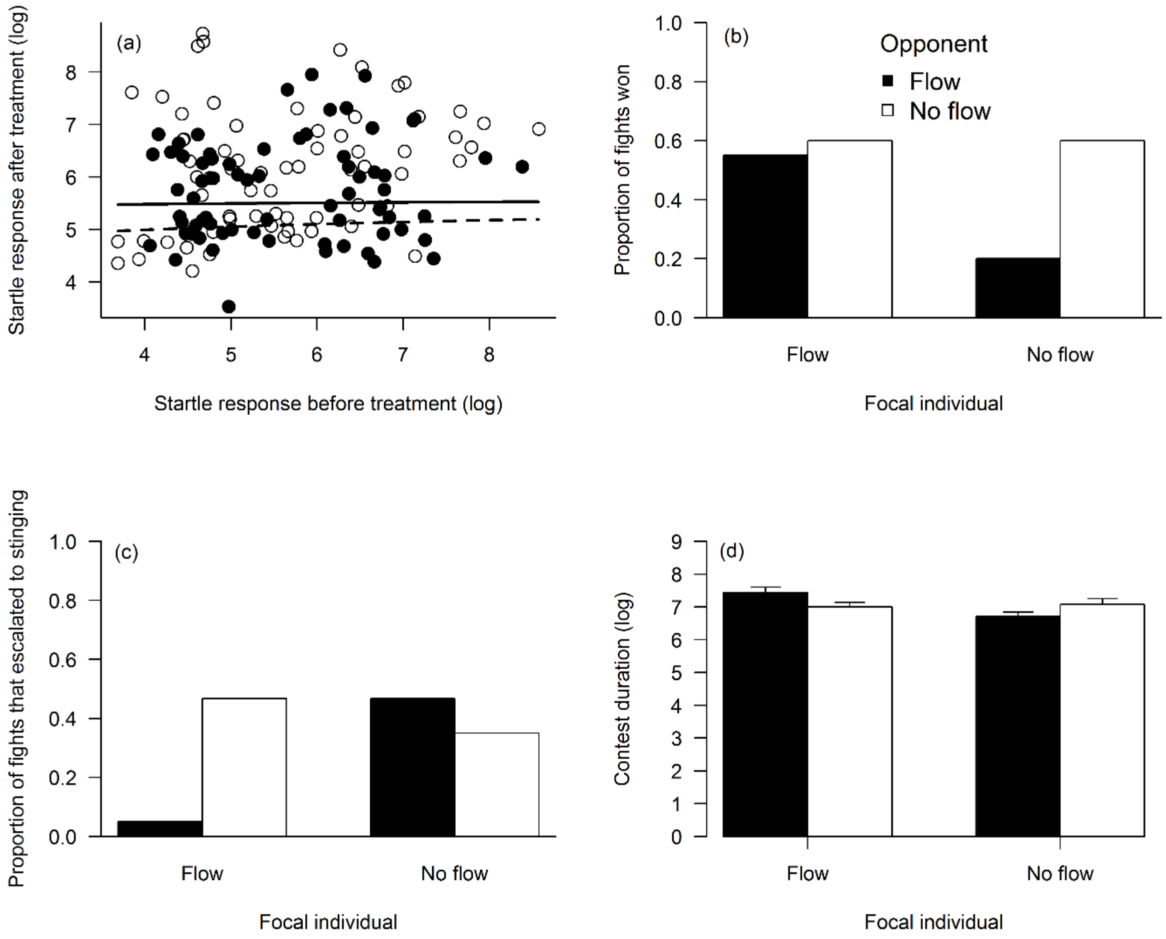

Fig 1. (a) Duration of the startle response of individuals that were exposed to a simulated tidal cycle (dashed line) were on average lower than the duration of the startle response of individuals that were not exposed to flow (solid line), even when we consider the duration of startle responses before treatment was applied (x-axis). (b) Proportion of fights won by a randomly chosen focal against his opponent following an 2x2 factorial experimental design. (c) Proportion of fights that escalated to highly aggressive and costly behaviours (i.e. stinging) regardless of whom performed the behaviour. (d) Duration of contests between focals and opponents of *A. actina* anemones (mean + SE).

SUPPLEMENTARY FILES

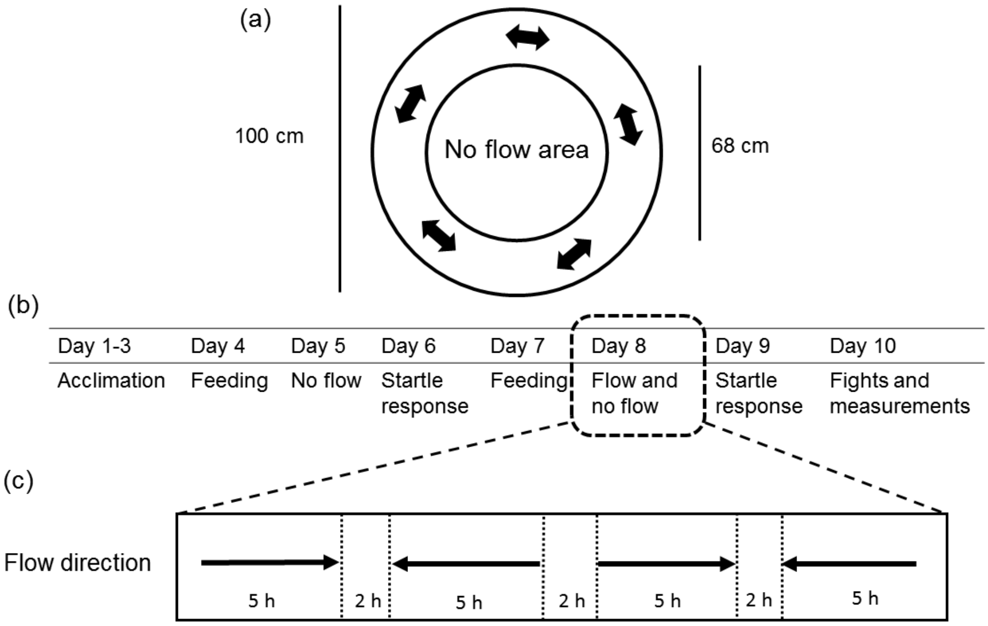

Fig S1. (a) Schematic representation of the experimental aquarium. Individuals were accommodated on both parts – the outer circle and the inner circle – but only individuals on the outer circle received flow on day 8. Arrows indicate where the reef pumps were positioned and that water flowed on both directions to simulate the tidal cycle. (b) Experimental design with and inset for the simulation of the tidal cycles, (c) in which arrows indicate the flow direction and the numbers indicate how many hours in each stage. Dotted lines indicate resting periods in which the pumps were turned off and inverted the direction.

Table S1. Significance test from the logistic model to examine to effect of environmental cues and RHP-traits on contest outcome. All effects were $\log_{10}$-transformed, centred and scaled prior to being used in the model. Marginally significant effects are printed in italics.

Effect	χ^2	df	P-value
Focal treatment	1.433	1	0.231
Opponent treatment	*3.603*	*1*	*0.058*
Focal startle response 2	*3.460*	*1*	*0.063*
Opponent startle response 2	1.030	1	0.310
Focal dry weight	1.175	1	0.278
Opponent dry weight	1.916	1	0.166
Focal nematocyst length	1.058	1	0.303

Opponent nematocyst length	0.526	1	0.468
Focal treatment * Opponent treatment	1.002	1	0.317
Residuals	81.836	60	-

df: degrees of freedom

Table S2. Significance test from the logistic model to examine to effect of environmental cues and RHP-traits on contest escalation. All effects were $\log_{10}$-transformed, centred and scaled prior to being used in the model. Significant effects are printed in bold.

Effect	χ^2	df	P-value
Focal treatment	2.409	1	0.121
Opponent treatment	1.860	1	0.172
Focal startle response 2	0.407	1	0.523
Opponent startle response 2	0.879	1	0.348
Focal dry weight	2.770	1	0.096
Opponent dry weight	**5.652**	**1**	**0.017**
Focal nematocyst length	0.331	1	0.565
Opponent nematocyst length	0.090	1	0.763
Focal treatment * Opponent treatment	**6.268**	**1**	**0.012**
Residuals	66.479	60	-

df: degrees of freedom

Table S3. Significance test from the linear model built to examine to effect of environmental cues and RHP-traits on contest duration. All effects were $\log_{10}$-transformed, centred and scaled prior to being used in the model. Significant effects are printed in bold and marginally significant are printed in italics.

Effect	Sum of squares	F-value	df	P-value
Focal treatment	0.124	0.284	1	0.596
Opponent treatment	**1.877**	**4.299**	**1**	**0.042**
Focal startle response 2	0.612	1.402	1	0.241
Opponent startle response 2	0.129	0.295	1	0.589

Focal dry weight	**1.786**	**4.090**	**1**	**0.047**
Opponent dry weight	0.103	0.236	1	0.629
Focal nematocyst length	0.032	0.072	1	0.788
Opponent nematocyst length	*1.725*	*3.952*	*1*	*0.051*
*Focal treatment * Opponent treatment*	*1.697*	*3.886*	*1*	*0.053*
Residuals	26.195	-	60	-

df: degrees of freedom

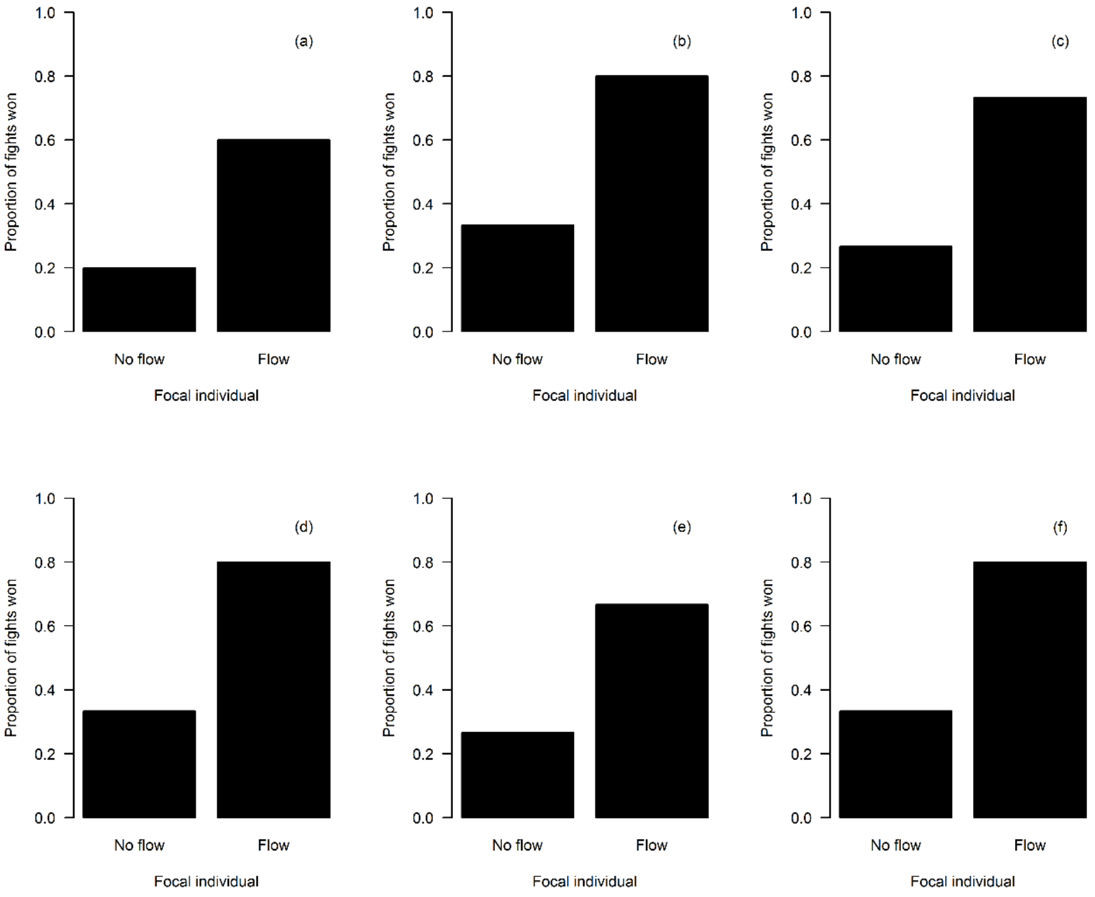

Fig S2. The main point is to show that flow individuals win more fights against no flow individuals than expected by chance, while also discarding any effect of randomly choosing who is the focal individual. We randomly reallocated whom was chosen as the focal individual only between in fights that had individuals facing different treatment opponents six times. In other words, we reallocated the focal individuals only in the flow vs. no flow and no flow vs. flow pairs and we only show these results here. Therefore, the focal individual in the graph fought an opponent of a different treatment that it was exposed to (e.g. a focal that was not exposed to flow fought an individual that was exposed to flow). We wanted to assess the effects of the randomization process on contest outcome. Since we predicted that high V individuals would have a higher chance to win against low V individuals, we only used treatments in which the dyad differed in the perceived V. The first graph (a) is the one used in all analyses in the manuscript, the rest (b, c, d, e, f) are shown here to demonstrate the effect of reallocation on our data. Note that flow focals consistently win ≥ 0.6 of the fights against no flow opponents, whereas no flow focals won ~ 0.35 of the fights against flow opponents.

ARTIGO 2: FRESHWATER DECAPOD (*AEGLA LONGIROSTRI*) USES A MIXED ASSESSMENT STRATEGY TO RESOLVE CONTESTS

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Freshwater decapod (*Aegla longirostri*) uses a mixed assessment strategy to resolve contests

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ABSTRACT

How animals decide to withdraw from a contest has puzzled researchers for years. Currently, four models try to explain how this decision is made: war of attrition (WOA); cumulative assessment (CAM); opponent-only assessment (OOA); and sequential mutual assessment (SAM). Although their predictions differ, they must be simultaneously tested to infer which model best describes contests. Herein, we identified the traits related to the resource-holding potential (RHP) in the decapod *Aegla longirostri*, and used these traits to test the predictions of each model. We identified which morphological/performance traits affect contest outcome, related these traits to the contest duration of male dyads, and tested the differences in aggressive acts (claw grabs). We tested the models using pairs of random and RHP-matched opponents. Additionally, we performed contests where RHP-matched opponents could communicate before the contest ('previewed'), and contests where the focal animal would only communicate with one individual and fight another unseen individual afterwards ('unseen'). In comparing these groups we tested whether information was being exchanged. The best predictor of contest outcome included a combination of cephalothorax length and claw height, and claw grabs increased with opponent similarity. Contest duration increased with loser's cephalothorax length and decreased with winner's cephalothorax length in random pairs, and winners spent more time in claw grab than losers. These findings refute WOA and OOA. In RHP-matched pairs, no relation was found and contests with previewed opponents were shorter than contests with unseen opponents, both results suggest SAM. However, the time spent in claw grab did not differ between previewed and unseen opponents. We argue that SAM is cognitively complex, and mutual assessment without comparison of RHP could be a better explanation. Furthermore, claw grab is important in contest resolution. Thus, the costs inflicted may suggest a mixed assessment strategy for *A. longirostri*'s contests.

Keywords:

aggressive behaviour

agonistic interaction

animal contest

assessment model

crab

fighting ability

freshwater crustacean

game theory

resource-holding potential

RHP

INTRODUCTION

Animals use agonistic behaviours during contests to secure access to limited resources (e.g. food, mates, shelter; Hardy & Briffa, 2013). Theory dictates that, as resource becomes more valuable (e.g. scarcer; Grant, Gaboury, & Levitt, 2000), contests get longer and more intense (Maynard Smith & Price, 1973). However, even intense contests rarely result in severe injuries and/or death (Maynard Smith, 1976). Most contests are settled by a decision of one of the contestants to withdraw from the contest (i.e. the loser). This decision is based on the benefits and costs of persisting in the contest (Kokko, 2013). The benefits are related to resource value (e.g. Doake & Elwood, 2011), whilst the costs are related to increased predation risk, energy and/or injuries accrued during the contest (Briffa & Sneddon, 2010). Thus, contest duration and increasing escalation can be seen as the interaction between the willingness to pay the costs (e.g. the resource value) and the ability to pay the costs (i.e. fighting ability, energy reserves; Elwood & Arnott, 2012).

When contestants perceive the resource equally, the individual with the highest fighting ability (resource-holding potential, RHP; Parker, 1974) usually wins the contest. The RHP is often associated with body size, in which large animals are stronger and better at inflicting injuries (Archer, 1988). Other traits can also be considered as correlates of RHP (reviewed in Arnott & Elwood, 2009), but weapon size and/or strength can be particularly influential in affecting the chances of winning a contest among taxa with developed weaponry (vertebrates: Clutton-Brock, Albon, Gibson, & Guinness, 1979; Lailvaux, Herrel, Vanhooydonck, Meyers, & Ircshick, 2004; arthropods: Pomfret & Knell, 2005; Seebacher & Wilson, 2006, 2007; Sneddon, Huntingford, Taylor, & Orr, 2000). Weapons can be used to inflict injury in the opponent (Lailvaux et al., 2004) and/or can signal the RHP of the bearer (Hoffmann & Schildberger, 2001; Hughes, 1996). Alternatively, weapons can affect contest outcome by being energetically demanding to wield (Matsumata & Murai, 2005). Therefore, weaponry has to be accounted for when investigating which traits relate to the RHP.

Understanding how animals decide to retreat from a contest is the goal of assessment models. Currently, assessment models can be classified into three main groups based on the relationship between RHP and the withdrawal decision: self-assessment (SA), opponent-only assessment (OOA) and mutual assessment (sequential mutual assessment, SAM) (Elwood & Arnott, 2012). The SA models dictate that animals do not (or cannot) assess their opponents RHP, and thus, the decision to give up is based solely on their own RHP. The SA is further subdivided in war of attrition models (WOA; Mesterton-Gibbons, Mardens, & Dugatkin, 1996; Payne & Pagel, 1996, 1997) and the cumulative assessment model (CAM; Payne, 1998). These models make different predictions regarding how costs are accrued during a contest (Kokko, 2013). The WOA models assumes that costs accrue because of the animal's own actions (e.g. energy spent, time invested; Mesterton-Gibbons et al., 1996), whereas CAM assumes that, alongside with the costs of the animal's own actions, costs are also accrued through the opponents' actions (e.g. injuries), and that with a higher RHP, animals inflict costs at a higher rate (Payne, 1998).

The OOA represents the opposite of the SA models, and predicts that the decision to give up is based solely on the opponent's RHP (Elwood & Arnott, 2012). However, OOA is not a theoretical model, and it is considered very unlikely to occur (for a discussion see Elwood & Arnott, 2013). Nevertheless, since there is evidence for OOA (e.g. Reddon et al., 2011), we considered it during data analysis. Lastly, the SAM model assumes that animals assess their opponents' RHP and their own, basing their decision to withdraw on both RHPs (Enquist & Leimar, 1983).

Despite the predictions of the assessment, models having been tested in a wide range of species (see Hardy & Briffa, 2013); these have rarely been fully supported by empirical data (Arnott & Elwood, 2009; Briffa & Elwood, 2009). This has two explanations: (1) difficulty in identifying RHP traits (Stuart-Fox, 2006); (2) the exclusion of one model does not corroborate the other models (Junior & Peixoto, 2013). Thus, all models have to be tested simultaneously. Taylor and Elwood (2003) showed that the relationship between contest duration and the RHP of both opponents can be used to discriminate between the assessment models, since they make different predictions regarding the relation between contest duration and RHP (Table 1). Alternatively, contest dynamics and structure can be used to differentiate WOA from CAM/SAM: WOA predicts that the behaviours of both contestants are matched in type, frequency and intensity, whereas CAM and SAM predict that behaviours are unmatched between contestants (Payne, 1998). Thus, by analysing the differences in the behavioural acts performed by winners and losers, we could provide more evidence to distinguish between WOA and CAM/SAM models.

Although SAM and CAM models suggest two distinct forms of assessment, they make the same predictions when opponents are not matched for their RHP (Briffa & Elwood, 2009). The best way to distinguish between SAM and CAM is using data from contests between RHP-matched opponents. In this scenario, SAM and CAM make contrasting predictions (Fawcett & Mowles, 2013). Still, the evidence for SAM in RHP-matched pairs is based on a nonsignificant relation between contest duration and RHP, which reduces inference power (Table 1; Arnott & Elwood, 2009). Alternatively, performing contests between RHP-matched opponents that have interacted using chemical/visual/mechanical cues (previewed opponent), and comparing to contests between RHP-matched opponents that have not interacted in any way (unseen opponent), can be a solution for this issue (Arnott & Elwood, 2009). Since SAM predicts that there is information exchange between the opponents and CAM does not, different predictions are made (Table 1). Because of information exchange, we can also expect that individuals would use less aggressive acts during the contests with previewed opponents than with unseen opponents. By comparing contests duration and aggressive acts between these two conditions, inference can be made with two sources of evidence, thus allowing more robust inference (Briffa & Elwood, 2009; Table 1).

Decapod crustaceans are excellent models to study animal contests. They fight readily in laboratory conditions even in the absence of obvious resources (Ayres-Peres, Araújo, & Santos, 2011), and their interactions in controlled environments reflect their interactions in natural environment (Bergman & Moore, 2003; Fero & Moore, 2008; Parra, Barria, & Jara, 2011). In addition, decapods have been shown to use extensive chemical signalling in aggressive contexts (Breithaupt, 2011; Briffa, 2013), and contests tend to be longer and more intense in the absence of chemical cues (Katoh, Johnson, & Breithaupt, 2008). Such extensive use of chemical communication suggests that some sort of information is being exchanged during the contest (i.e. SAM). Conversely, the ubiquitous use of their highly developed claws during contests (Sneddon et al., 2000) suggests that injuries are being inflicted on their opponents (Figure S1 in Dennennmoser & Christy, 2012), which suggests CAM. Through empirical testing, Smallegange, Sabelis, and van der Meer (2007) investigated the assessment models in shore crabs (*Carcinus maenas*), but their results could not distinguish between SAM and CAM. Lastly, Briffa (2013) states that swimming crab contests do not fully fit SAM predictions regarding contest structure, since there is no clear pattern of escalating phases. These contrasting evidences highlight the need for more studies on decapod contests.

The goals of our study were (1) to determine which traits relate to the RHP of the freshwater decapod *Aegla longirostri* (Anomura) and (2) to test the predictions from WOA, CAM, SAM and OOA models by analysing data from random contests, RHP-matched pairs, previewed and unseen opponent contests, thus assessing whether one of the models explains how *A. longirostri* decides to withdraw from a contest.

METHODS

Study Organism, Capture, Housing and Measuring

Aegla longirostri has a marked sexual dimorphism, with males having larger bodies and larger claws than females (Colpo, Ribeiro, & Santos, 2005). During contests, males use mostly their left claw for grabbing, striking and pulling (Ayres-Peres et al., 2011), since it is larger than the right claw (Colpo et al., 2005). The use of chemical cues has already been reported during sexual interactions (Palaoro, Ayres-Peres, & Santos, 2013) similar to what has been found for crayfish (Breithaupt, 2011). Thus, the use of chemical cues during contests is thought to be important because of the ecological/behavioural similarity aeglids share with crayfish (Burress, Gangloff, & Siefferman, 2013), a more thoroughly studied group (Breithaupt, 2011).

We captured 115 adult males of *A. longirostri* in two first-order streams (29º40′13″S; 53º45′44″W and 29º39′49″S; 53º44′34″W) in southern Brazil, and transported them to the laboratory. We accommodated all aeglids in individual aquaria (2 litres) for 1 week prior to experimentation to eliminate the effect of prior experiences (Moore, 2007). All aquaria had constant aeration, 2 cm of gravel, and ad libitum food composed of decaying leaves taken from the stream (Cogo & Santos, 2013). We measured all individuals according to their cephalothorax length (Fig. 1a), claw length (Fig. 1b), claw height (Fig. 1b), height of the dactyl (Fig. 1b) and distance between the fulcrum and the tubercle (Fig. 1b), using a digital calliper (precision: 0.01 mm), and apodeme area (Fig. 1b). We used the height of the dactyl, the distance between the fulcrum and the tubercle, and apodeme area to calculate the index of closing force.

The index of closing force is a measure of the claw's strength (Dennennmoser & Christy, 2012). The claw closing force is determined by the mechanical advantage of the claw's dactyl and the cross-sectional area of the muscle that moves the dactyl. This muscle is attached to a flat cuticular apodeme, which is attached to the dactyl and longitudinally bisects the manus (proximal area of the claw; Fig. 1b; Dennennmoser & Christy, 2012). To calculate the mechanical advantage, the height of the dactyl is divided by the distance between the fulcrum (i.e. point where the dactyl flexes; Fig. 1b) and the first tubercle in the dactyl (Dennennmoser & Christy, 2012; Fig. 1b). The muscle cross-sectional area is calculated as the area of the apodeme, which is highly correlated with the muscle cross-sectional area (Warner & Jones, 1976; Fig. 1b). By multiplying the values for mechanical advantage and muscle cross-sectional area, we get the index of closing force of that claw, which is correlated to the force produced by the claw (Levinton, Judge, & Kurdziel, 1995). Since calculating the muscle cross-sectional area requires euthanizing the individuals (or at least removing both claws), we chose a more parsimonious protocol. We used 20 individuals that perished during pilot studies of this and other experiments (i.e. were already available in the scientific collection of the laboratory, voucher number UFSM-C 248) to calculate the muscle cross-sectional area. We then regressed their muscle cross-sectional area with their claw height. The correlation was high for the left claw ($R^2 = 0.9623$; Fig. 2). Thus, we used the equation from that regression ($y = -0.3701 + 0.0804 \times x$) to calculate the muscle cross-sectional area of the left claw of all the individuals used in our experiment. With the extrapolated muscle cross-sectional area, we multiplied it by the individual's mechanical advantage to get the index of closing force of the left claw. We did not perform the same procedure for the right claw because of its low use during contests (Ayres-Peres et al., 2011) and the low correlational value ($R^2 = 0.7974$), which could lead to spurious results. Therefore, we used cephalothorax length, claw length, claw height and the index of closing force as the morphological and performance traits possibly related to the RHP (see below).

Experimental Set-up

We assigned the individuals to four different treatments. First, we paired 28 individuals randomly (*N* = 14 pairs; random treatment). Second, we paired 32 individuals according to the RHP traits, with a maximum difference of 10% between the individuals (*N* = 16 pairs; RHP-matched treatment). Third, we paired 18 individuals using the same criteria as the RHP-matched treatment, but allowed the opponents to interact visually and chemically during the acclimation period (see below; *N* = 9 pairs; previewed opponent treatment). Finally, we arranged 27 individuals in triads according to their RHP traits. In this treatment, the focal animal could interact visually and chemically with one individual during acclimation, and perform the contest with the other individual that was not seen during the acclimation (see below; *N* = 9 triads; unseen opponent treatment).

We performed all interactions in an aquarium (21 × 15 × 13 cm) divided in three sections using removable dividers. Both dividers were opaque and nonperforated in the random treatment and in the RHP-matched treatment. The previewed opponent treatment had both translucent and perforated dividers to allow chemical/visual communication between the opponents during acclimation. Lastly, the unseen opponent treatment had one opaque and nonperforated divider (i.e. the real opponent could not be seen or smelled during acclimation), and one translucent and perforated divider (i.e. the opponent that could interact visually/chemically with the focal individual during the acclimation period). Therefore, in the unseen opponent treatment, the focal individual would be accommodated in the middle, and the opponents in the extremities behind the dividers. We accommodated the individuals in the aquarium, and left them to acclimate to the new conditions for 20 min. Afterwards, we lifted the dividers (and removed the extra individual in the unseen opponent treatment) and left the individuals to interact for an additional 20 min. The contests were recorded at night with a Sony Handycam HDR-CX560® positioned 30 cm vertically above the aquarium, and four incandescent red light bulbs (40 W) positioned equidistantly around the aquarium. We used red lights because crustaceans have low sensitivity for this wavelength (Turra & Denadai, 2003). After the contest, we returned the individuals to their previous individual aquaria, and observed them for 1 week prior to returning them to the natural environment. In case any animal died or moulted, we excluded them from the analysis to avoid biasing the results (Moore, 2007). Ten of the 115 captured individuals died, and we discarded them from the analysis. This mortality rate can be explained by the high metabolic demand of aeglids compared with other decapods (Dalosto & Santos, 2011). Thus, some individuals brought to the laboratory might be stressed due to the environmental conditions during collection (e.g. mild droughts, highly fluctuating temperatures) and may die during acclimation. However, aeglids can rapidly recuperate their high population densities (Bueno et al., 2014), and thus, our field samplings do not impact the population significantly. No individuals were injured during the interactions.

To calculate contest duration, we summed the duration of the first three bouts. A bout was initiated when one individual approached to within one body length of the opponent and the opponent did not flee. The bout was deemed finished when the individuals did not interact for 5 s after they had backed away or fled from each other (Goessmann, Hemelrijk, & Huber, 2000). We did not use a minimum aggressive level to determine a bout, since that could bias the results through analysing fights rather than contests (Elwood & Arnott, 2013). We used only the first three bouts because fight durations are longer when individuals have limited space to flee, such as in an aquarium (Bergman & Moore, 2003). Therefore, contest duration could be overestimated if we had used all bouts. Besides, aeglids may not form a clear dominance relationship (winner–loser) in only one bout (Ayres-Peres et al., 2011; Palaoro et al., 2013). Hence, using only the first bout could have affected our analysis of which traits are associated with the RHP due to the lack of clear dominance. The winner was deemed the individual that did not flee in the majority of the three bouts, whereas the one that fled was deemed the loser. To analyse aggressive acts, we counted the number of claw grabs and the time spent in claw grabs performed by both winners and losers. We used only claw grabs as a proxy for aggressiveness due to their conspicuous and ubiquitous use in aeglid contests (Ayres-Peres et al., 2011). In addition, noncontact and contact phases of aeglid contests are not distinguished, and the individuals do not perform any visual display. Since only contact behaviours are conspicuous enough to be accurately assessed (Ayres-Peres et al., 2011), we evaluated only the claw grabs to avoid biasing the results.

Determination of Traits Associated with RHP

To test which traits are associated with the probability of winning a contest, we performed logistic regressions using cephalothorax length, claw length, claw height and the index of closing force as explanatory variables and winner/loser (i.e. 1 or 0) status as the response variable. Prior to testing, we performed a data modification (e.g. Kemp, 2000; Junior & Peixoto, 2013) to avoid pseudoreplication. First, since the claw is positively correlated with body size (Colpo et al., 2005), we performed three linear regressions using each claw variable separately (claw length, claw height, index of closing force; response variables) with cephalothorax length as an explanatory variable to obtain values of claw morphology and performance regardless of body size. Thus, we extracted the standardized residuals from each analysis, and used the residuals values throughout the study. Second, we randomly selected focal males from all four treatments. If the focal male won the contest, we assigned him a value of 1, and if he lost, we assigned a value of 0 (*N* = 48 focal males). Third, we calculated the difference in cephalothorax length, residual claw length, residual claw height and residual index of closing force between focal males and their opponents. By doing this, we expected that focal winners would have higher values than focal losers.

More than one trait can be related to the probability of winning a contest (Briffa et al., 2013). Thus, we used the Akaike's Information Criterion corrected for small samples (AICc) to select the most parsimonious hypotheses of which traits are related to the RHP (see Results, Table 2). Using all available hypotheses can be considered only an explorative analysis (Symonds & Moussali, 2011), and would need further confirmatory analysis (Dochtermann & Jenkins, 2011). Therefore, we tested only nine hypotheses (Table 2). Since we have a priori knowledge to generate meaningful hypotheses, we were able to use this evidence for inference rather than only generating further hypothesis (Symonds & Moussali, 2011).

Four of our hypotheses related each trait alone with the probability of winning a contest (i.e. 1 or 0), since there is evidence that these traits (cephalothorax length, claw length, claw height and index of closing force) alone can affect contest outcome (Table 2; Moore, 2007). Our next three hypotheses combined cephalothorax length with one of the claw measurements (claw length, claw height and index of closing force), since the claw morphology/performance may only be important when body size is matched (Table 2; Sneddon, Huntingford, & Taylor, 1997). Next, we tested whether only the claw was important using all claw traits and their interactions without considering the cephalothorax length (Table 2). In our last hypothesis, we tested whether all traits are important using the full model (i.e. cephalothorax length and all claw traits; Table 2). We did not test hypotheses with only two claw traits because it would be difficult to provide arguments that only two dimensions are important without isolating the other experimentally. We used the cut off rule of $\Delta \leq 2$ to distinguish between the most parsimonious candidates (Burnham & Anderson, 2002), and used the traits contained in these models in the remainder analyses. In addition, to test the importance of claw grabs during contests, we performed a generalized linear model with a quasi-Poisson error structure and a log link. We used the number of claw grabs performed by the winner as the response variable and the difference in the traits identified in the previous analysis (|winner – loser|) as the explanatory covariables.

Distinguishing among WOA, OOA and SAM/CAM Models

We performed a multiple linear regression following Taylor and Elwood's (2003) suggestion, using the data from the random treatment. We used contest duration as the response variable and each morphological/performance trait identified in the previous analysis of both winners and losers as explanatory covariables. Afterwards, we compared our results to the predictions of each model (Table 1). We performed a two-tailed permutation paired *t* test to test whether the behaviours of the opponents were matched. We tested the difference between the time spent in claw grab by winners and losers using the data from RHP-matched treatment. We did not use the data from the random pairs because of an excessive number of zeros.

Distinguishing between SAM and CAM Models

We performed three different tests to distinguish between these two models. First, we used the data from the RHP-matched treatment to perform a multiple linear regression using contest duration as the response variable, and each morphological/performance trait identified in the RHP analysis of both winners and losers as explanatory co-variables. We then compared our results to the predictions of each model (Table 1).

Next, we used the data from the previewed opponent treatment and the unseen opponent treatment. We compared the contest duration of these two treatments using a two-tailed permutation *t* test. Finally, we compared the time spent in claw grab by winners with a two-tailed permutation *t* test using the same treatments from the prior analysis. We did not perform tests with losers because of an excessive number of zeroes, which would bias the analysis. We performed all analyses in the R environment (R Development Core Team, 2013). For the AIC analysis, we used the 'bbmle' package (Bolker & R Development Core Team, 2013).

Ethical Note

All individuals were sampled, maintained and returned to the natural environment under license from IBAMA (Instituto Brasileiro do Meio Ambiente), number 14180–1, granted on 4 December 2007 and according to the applicable statutes (Federal law number 5197, of 3 January 1967; Resolutions: number 16 of 4 March 1994 and number 332 of 13 March 1990).

RESULTS

Summary of the Contests

All contests resulted in physical contact between the opponents. All individuals fought using the same body posture during the contests, with the right claw bent downwards (i.e. the tip of claw pointed towards the substrate of the contest aquarium) and the left claw extended forward trying to grasp the opponent.

Traits Related to the RHP

The model that considered cephalothorax length and claw height was the most parsimonious model. The model that considered only cephalothorax length was the second most parsimonious (Table 2). Thus, we adopted cephalothorax length and residual claw height as proxies of RHP in our study. The number of claw grabs decreased as the difference in cephalothorax length increased (GLM: $\chi^2_{1,28} = 16.56$, $P = 0.012$; Fig. 3) but did not increase/decrease significantly as the difference in residual claw height increased (GLM: $\chi^2_{1,27} = 0.034$, $P = 0.9$).

Distinguishing between WOA, OOA and SAM/CAM Models

In random pairings, contest duration increased significantly with loser's cephalothorax length (Fig. 4a, Table 3) and decreased significantly with winner's cephalothorax length (Fig. 4a, Table 3). Residual claw height was not significantly correlated with contest duration for losers (Fig. 4b, Table 3) or winners (Fig. 4b, Table 3). Additionally, winners spent significantly more time in claw grab than losers (permutation paired *t* test: $t_{15} = -2.705$, $P = 0.02$; Fig. 5).

Distinguishing between SAM and CAM Models

In RHP-matched pairings, contest duration was not significantly correlated with cephalothorax length or residual claw height for losers or winners (Fig. 6a, b, Table 3). Contests were significantly shorter in the previewed opponent treatment than in the unseen opponent treatment (two-tailed permutation *t* test: $t_{14} = -2.005$, $P = 0.046$; Fig. 7). However, the time spent in claw grab by winners did not differ between the treatments (two-tailed permutation *t* test: $t_{12} = 0.4$, $P = 0.69$).

DISCUSSION

Herein, we show how *A. longirostri* make decisions during contests using four sources of information. First, we found that body size and weaponry can influence contest outcome. The effect of body size on contest outcome is well known and studied across several taxa (reviewed in Arnott & Elwood, 2009; Briffa & Sneddon, 2010), where large body size is related to dominance. However, the effect of weaponry may vary depending on the type of contest. Contests divided in noncontact and contact phases may show different relations between weaponry and contest outcome depending on which part is being analysed. Rudin and Briffa (2011) showed in the beadlet anemone, *Actinia equina*, that weaponry (acrorhagi) was only important when the contest escalated to physical contact. On the other hand, decapods use their claws in almost all contests, whether by displaying them in the noncontact phase or using them to grab opponents (Briffa, 2013). Most of our analyses did not demonstrate a relatively high importance of the claw (i.e. no significant correlations with contest duration) in *A. longirostri*'s contest. Nevertheless, we found that as similarity between opponents increased, more claw grabs were performed by the winner (Fig. 3). In addition, even in shorter contests (i.e. previewed opponents), the claw grabs were necessary to resolve the contest. Therefore, weaponry is important in defining contests in *A. longirostri*, especially when individuals are size matched.

Sneddon et al. (1997) showed that claw length is a better predictor of winning a contest than is body size. In our analysis, claw height, not length, was a better predictor of contest outcome when combined with body size. This peculiarity may be related to different uses of the claw. The species studied by Sneddon et al. (1997), *C. maenas*, uses its claws for both visual displays (i.e. meral spread) and for grabbing other crabs (Sneddon et al., 1997), whereas *A. longirostri* only uses its claw for grabbing and striking opponents (Ayres-Peres et al., 2011). The use of a claw to display a signal may favour longer fingers and a smaller manus (Fig. 1b), whereas the use as a weapon favours shorter fingers and a larger manus. This occurs because shorter fingers would increase the mechanical advantage of the claw, and the larger manus would have more space for the closing muscle, resulting in increased closing force (Dennenmoser & Christy, 2012). Crabs would then have claws that favour both signalling and fighting (i.e. a mix between the two claw shapes), and aeglids would have claws that favour fighting only. Therefore, claw height may be a better predictor of contest outcome than claw length in species that use their claws mainly as weapons rather than for signalling.

In the subsequent analyses, we investigated the relationships of contest duration and RHP traits to discriminate whether *A. longirostri* losers decided to withdraw based on SA, SAM or OOA. We also analysed differences in aggressive levels to further increase the robustness of our inferences. In random pairs, the contest duration increased with loser's RHP and decreased with winner's RHP. This refutes WOA and OOA as possible explanation models for contests in *A. longirostri* (Table 1). In addition, there was no behavioural matching between winners and losers (Fig. 3), which provides further evidence for refuting WOA as a possible explanation model. The remaining two models, SAM and CAM, were analysed using three approaches. In the first approach, using RHP-matched pairs, we showed that neither the loser's RHP nor the winner's RHP correlated with the contest duration. This evidence suggests SAM. However, it is difficult to infer using nonsignificance as an argument (Briffa & Elwood, 2009). An alternative analysis, therefore, would be to examine the contest duration between previewed and unseen opponents.

In our second approach, we found that contests with previewed opponents were shorter than contests with unseen opponents. Since in both treatments the individuals could interact with an opponent during acclimation, this strongly suggests that information from the opponent was used in the decision to withdraw. In our third approach, we expected that the individuals would need less aggressive acts to define the contests due to the information exchange with previewed opponents. However, the time spent in claw grabs did not differ between previewed or unseen opponents. Although this finding was the opposite of what we expected, it supports both SAM and CAM models. These models differ only in their interpretation of the claw grab meaning. Under SAM assumptions, the claw grab can be interpreted as conveying information regarding the RHP of the individual. Under CAM assumptions, the claw grab conveys costs to the opponent. Thus, individuals exchange information (i.e. contests between previewed opponents were indeed shorter), but ultimately rely on the claw grab to resolve contests.

Two of our three sources provided evidence for SAM as the best model to explain decision making in *A. longirostri*. The extensive use of chemical cues during decapod contests may provide information regarding the sender, whether intentionally or not. Indeed, performing aggressive acts enhances the probability of urine release, which is the main pathway used for chemical communication in decapods (Breithaupt & Eger, 2002). In addition, aggressive acts are known to alter their opponent's behaviour only when coupled with urine release (Breithaupt & Eger, 2002). Lastly, contests without urine release tend to be longer and more intense than contests with urine release (Katoh et al., 2008). Thus, it is safe to conclude that individuals are using information from their opponents. However, 'true' mutual assessment would require the individual to compare both RHPs to make a decision, and that is a cognitively complex process (Elwood & Arnott, 2012). Crustaceans are used as models in neurobiology because of their lower neuronal complexity (Herberholz, 2007). Perhaps, a more parsimonious explanation would be that the chemical cues may affect the motivational state of the opponent. This would not require the comparison of RHPs, but rather, information about the opponent would reduce the motivation to persist in the contest (Elwood & Arnott, 2012). This process was called 'mutual assessment without comparison' by Elwood and Arnott (2012), and is less cognitively demanding than the 'true' SAM. Evidence for this comes from crayfish, where future winners release more urine than losers during contests (Breithaupt & Eger, 2002). By releasing more urine, winners could be reducing the motivation of the loser, thus reducing contest duration.

Although individuals conveyed information to their opponent, claw grabs were still necessary to resolve contests. Thus, information conveyed through chemical cues may be limited. Individuals may use claw grabs for two reasons: (1) as a social mechanism to ensure the honesty of the individual's RHP; (2) to inflict costs on the opponent. Using claw strength as a social mechanism has been shown in other decapods. For instance, the crayfish *Cherax destructor* has a high variability in force production (Walter, van Uitregt, & Wilson, 2011), which means claw size is not a reliable indicator of strength. This species uses visual displays of the claw to resolve some contests. However, to avoid losing to a larger but weaker opponent, males of *C. destructor* enter in physical contact in the majority of the contests to verify the opponent is not bluffing its RHP (Walter et al., 2011). These trials of force are also used in another crayfish species (*Procambarus clarkii*), in which individuals interlock their claws and start pushing each other. The claw interlock phase has been shown to be important in contest resolution in this species (Ueno & Nagayama, 2012). Nevertheless, we must consider that both of these species use visual displays of the claw (i.e. the meral spread), whereas aeglids do not. Furthermore, at least in *C. destructor*, claw size is not a reliable indicator of strength, which is the opposite of aeglids. The apodeme area was tightly correlated with claw height (Fig. 2), meaning that claw height is indeed a good predictor of claw strength. Therefore, aeglids may not need to use their claw grabs as a social mechanism to ensure RHP's honesty, but rather to inflict costs on their opponents.

In the light of this evidence, we hypothesize that chemical cues released with urine lowers the motivation of the loser to persist in the contest (i.e. lowers the threshold of the cost that the loser is prepared to pay; Elwood and Arnott's (2012) motivational model), and that claw strength may be needed to inflict costs on the opponents when individuals have similar RHPs. Future studies should try to decouple urine release and the costs inflicted by the claw. This can be done by blocking the decapod's urine release (Breithaupt & Eger, 2002) and altering the costs inflicted by the claw, perhaps by attaching rubber to the outer surface of the claw, which would lower the force of the claw grab felt by the focal individual, similar to what has been done to hermit crab shells (Briffa & Elwood, 2000).

In summary, we provide evidence that body size and claw strength alter contest outcome in *A. longirostri*. We also provide two sources of evidence suggesting that SAM is the best explanation model for *A. longirostri* contests. However, since SAM is cognitively complex, and decapods have a relatively simple nervous system (Herberholz, 2007), we suggest that chemical signalling may be lowering the loser's motivation to persist in a contest through 'mutual assessment without comparison'. In addition, we highlight the importance of the claw during decapod contests and suggest a possible mixed strategy including both chemical cues and the costs inflicted by claw grabbing. In this scenario, the loser would withdraw based on the information regarding the winner and his ability to inflict costs.

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Table 1

Predictions of the assessments models*

	War of attrition	Cumulative assessment	Sequential mutual assessment	Opponent-only assessment
Relation between RHP and contest duration in random pairings	Loser–Positive relation Winner–Weak positive or no relation	Loser–Positive relation Winner–Negative relation	Loser–Positive relation Winner–Negative relation	Loser–No relation Winner–Negative relation
Relation between RHP and contest duration in RHP-matched pairings	Positive	Positive	No relation	Negative
Difference in contest duration between previewed and unseen opponent	No difference	No difference	Shorter contests with previewed opponents	Shorter contests with previewed opponents

RHP: resource-holding potential.
*Adapted from Arnott and Elwood (2009).

Table 2

Model comparisons using AICc scores from logistic models to examine RHP-related traits in *Aegla longirostri*

Model	AICc	Δ_i	*df*	w_i
Cephalothorax length + residual claw height [b]	58.1	0	3	0.443
Cephalothorax length [a]	58.9	0.8	2	0.2981
Cephalothorax length + residual index of closing force [b]	60.6	2.4	3	0.1329
Cephalothorax length + residual claw length [b]	60.6	2.6	3	0.1217
Cephalothorax length + residual claw length*Residual claw height*residual index of closing force [c]	67.6	10.2	9	0.0027
Residual claw length [a]	71.3	13.3	2	<0.001
Residual claw height [a]	71.5	13.6	2	<0.001
Residual index of closing force [a]	72	14.1	2	<0.001
Residual claw length*residual claw height*residual index of closing force [d]	74.2	16.9	8	<0.001

AICc: Akaike's Information criterion value corrected for small samples; Δ_i: difference in the AICc value between of the most parsimonious model and model *i*; w_i: Akaike weight of model *i*. These models are based on the difference of each trait between a focal male (chosen randomly) and his opponent regressed with the probability of winning a contest ($N = 48$).

The numbers in the models are only used for reference in the text.

[a] Model tested the importance of each trait alone.

[b] Model tested the importance of cephalothorax length and one claw measurement.

[c] Model tested the importance of the claw (using all claw traits and their interactions) without considering cephalothorax length.

[d] Model tested the importance of all traits using the full model.

Table 3

Multiple linear regression results using contest duration as response variable and cephalothorax length and residual claw height of both winners and losers as explanatory covariables in *Aegla longirostri*

Treatment	Effect	Slope	*df*	*F*	*P*
Random pairings	Winner cephalothorax length	-17.696	1	5.387	0.045
	Winner residual claw height	-55.908	1	2.759	0.131
	Loser cephalothorax length	32.783	1	11.41	0.008
	Loser residual claw height	63.802	1	0.699	0.424
	Residual	—	9		
RHP-matched pairings	Winner cephalothorax length	1.268	1	0.002	0.964
	Winner residual claw height	18.289	1	0.127	0.728
	Loser cephalothorax length	-10.958	1	0.141	0.715
	Loser residual claw height	54.315	1	1.175	0.312
	Residual	—	11		

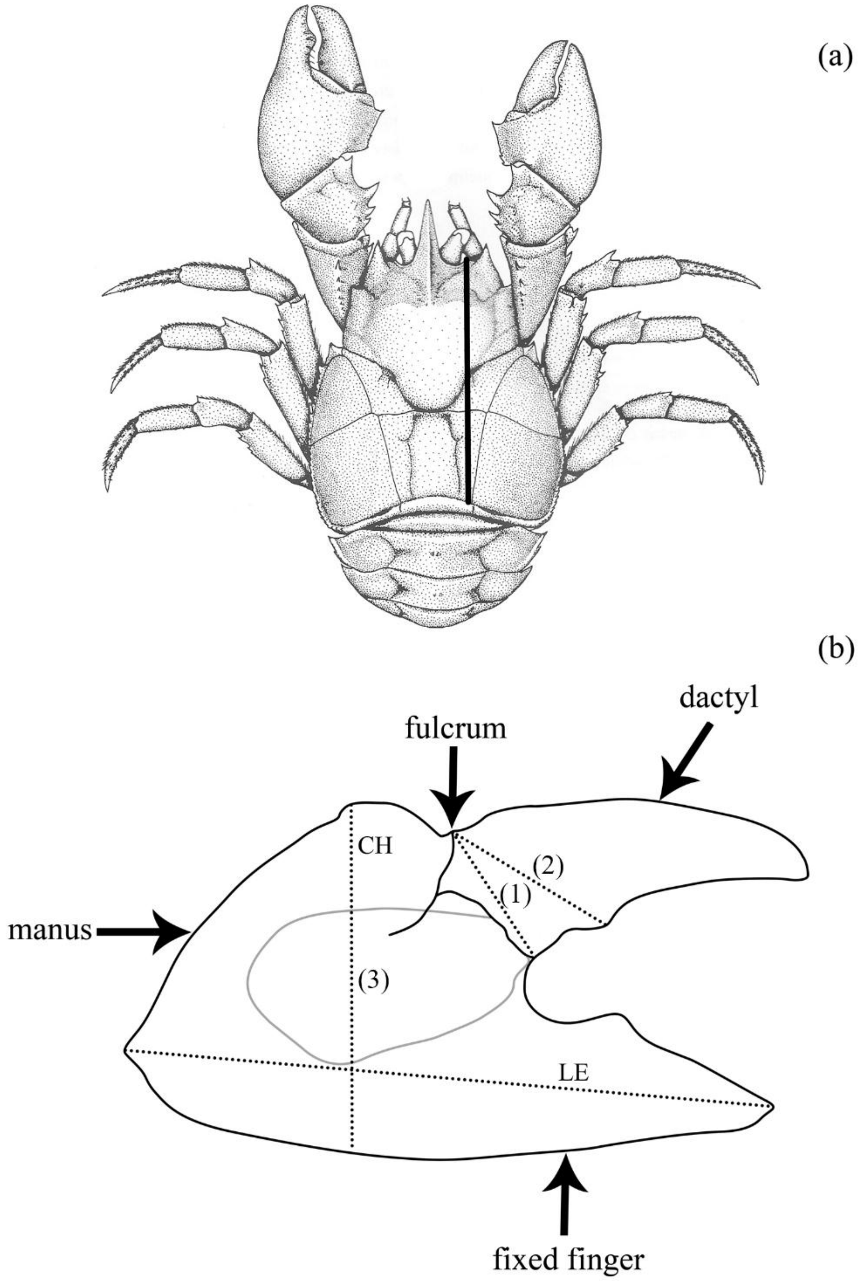

Figure 1. (a) Representation of a male *Aegla longirostri* adapted from Bond-Buckup (2003). Line denotes cephalothorax length. (b) Schematic representation of the left claw of *A. longirostri*. LE: claw length; CH: claw height; (1): dactyl height; (2): distance from the fulcrum to the first tubercle; (3): apodeme.

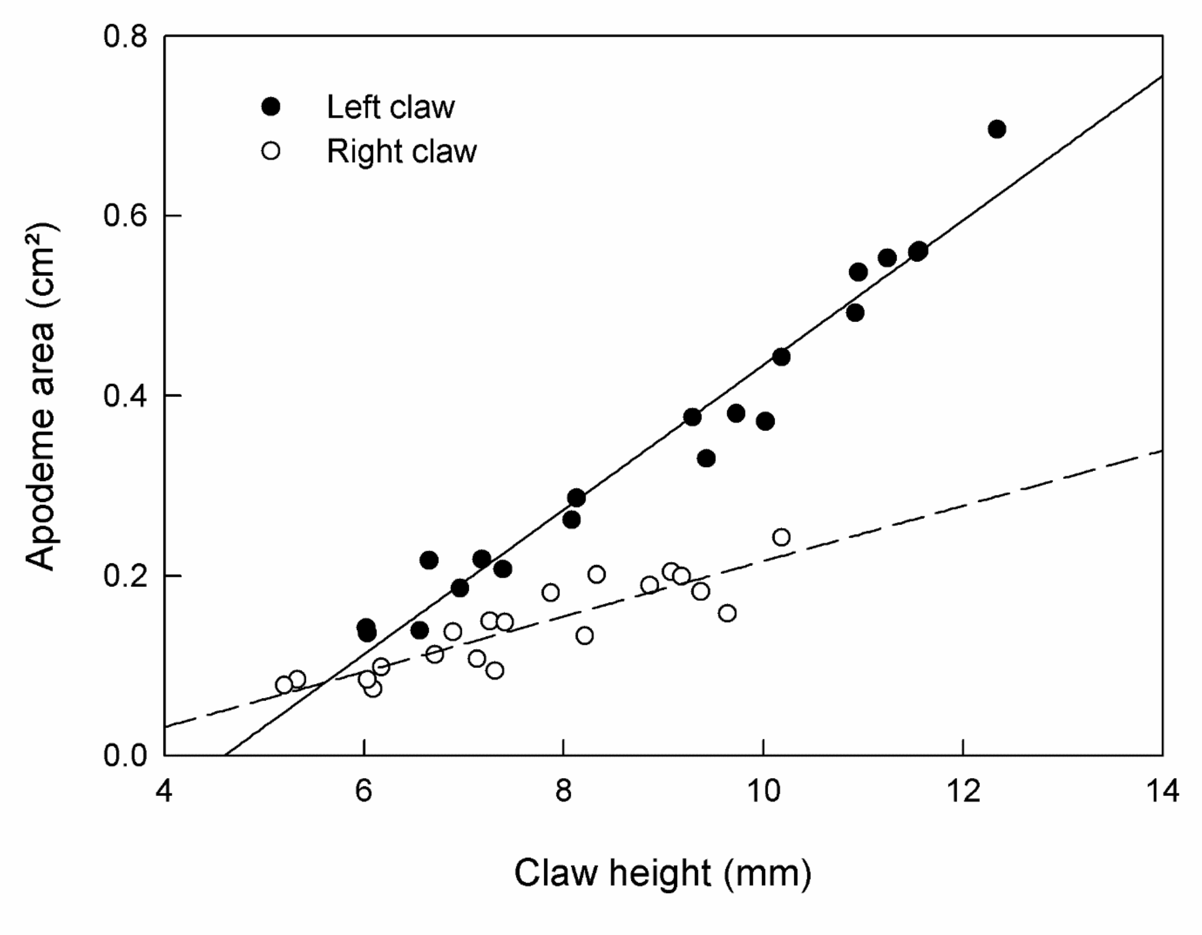

Figure 2. Relation between claw height and the apodeme area for the left claw (black circles) and the right claw (open circles). The straight line represents the regression line for the left claw (*R^2* = 0.9623), and the dashed line represents the regression for the right claw (*R^2* = 0.7974).

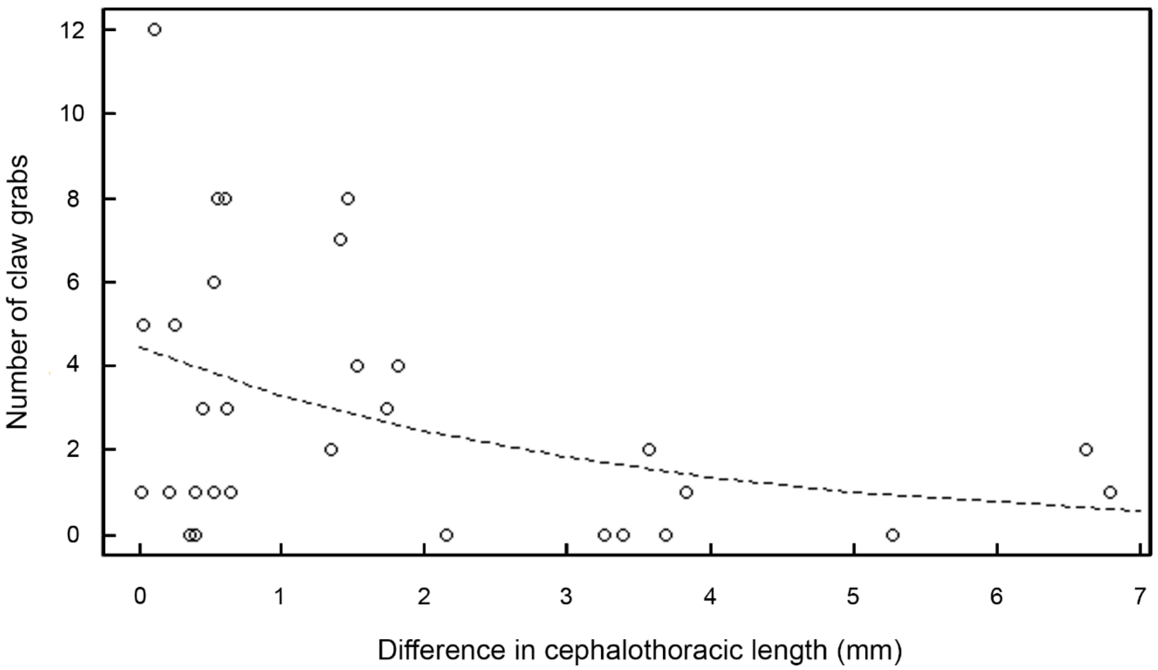

Figure 3. Relation between the difference of cephalothorax length (winner – loser) and the number of claw grabs performed by winners in contests of *Aegla longirostri* ($\chi^2_{1,28}$ = 16.56, *P* = 0.012). The dashed line represents the generalized linear model with quasi-Poisson error structure and a log link.

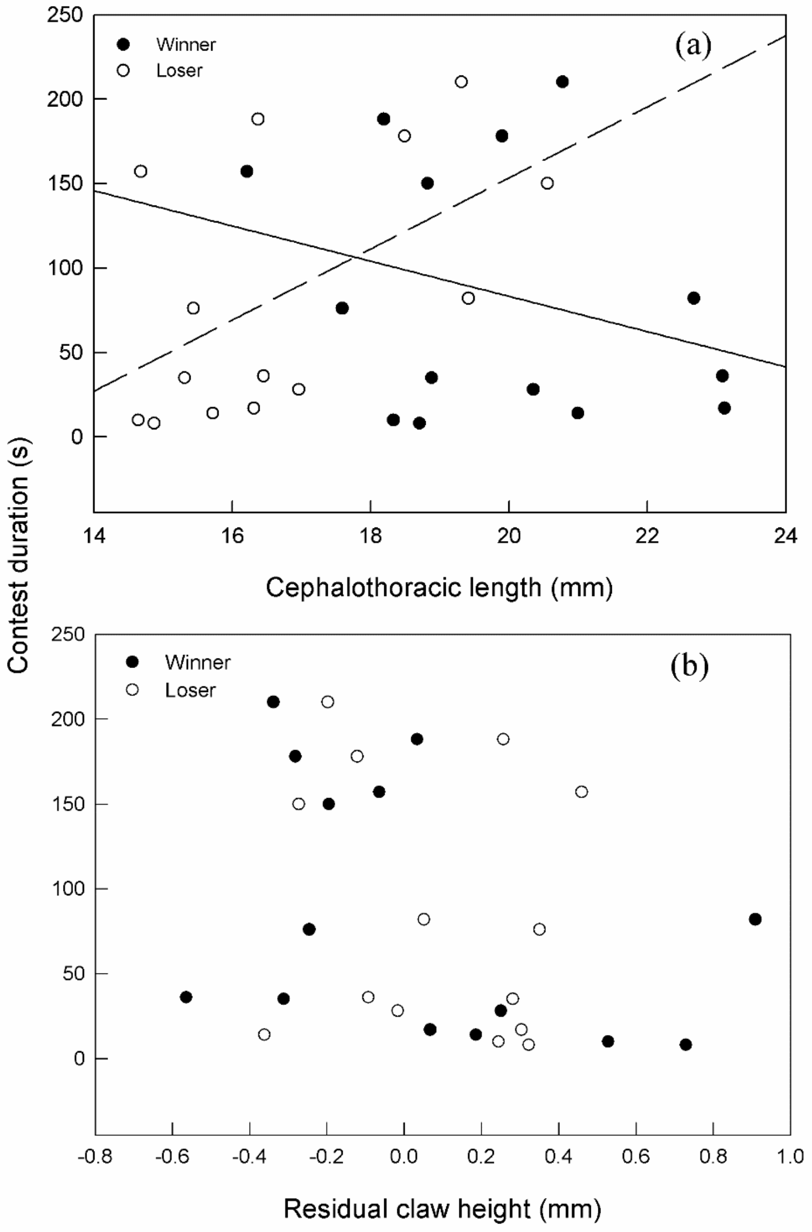

Figure 4. Relation between contest duration and (a) cephalothorax length and (b) residual claw height for random pairings. Straight line represents the regression for winners (black circles), and the dashed line represents the regression for losers (white circles). The regression lines are depicted only when the relationship was significant.

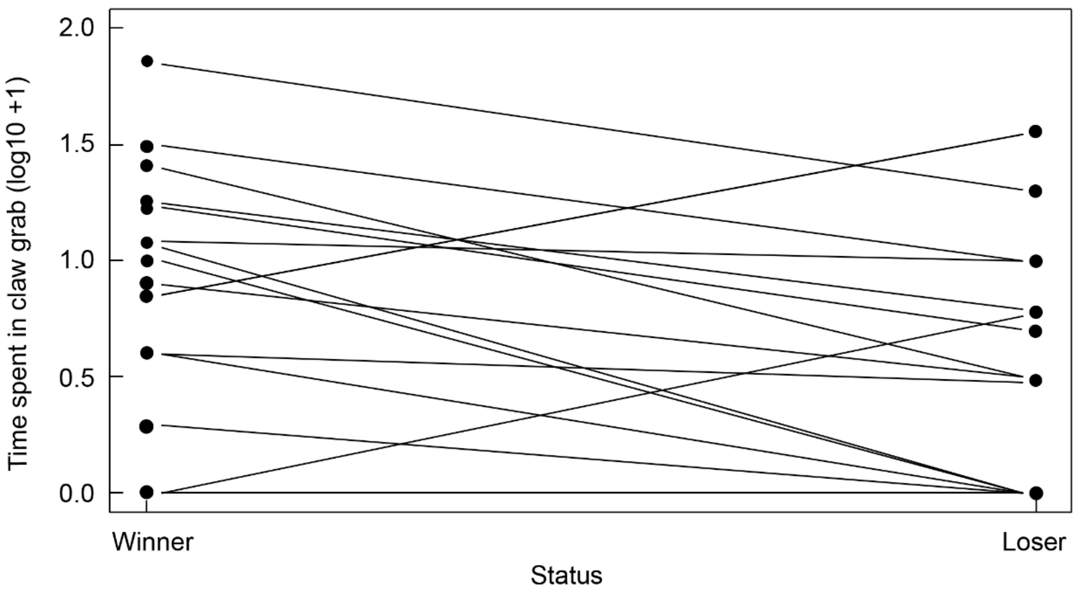

Figure 5. Time spent by winners and loser in claw grab (log *x* + 1). A permutation paired *t* test showed that winners spent more time in claw grab than losers (t_{15} = -2.705, *P* = 0.02). Lines connect the individuals of each pair.

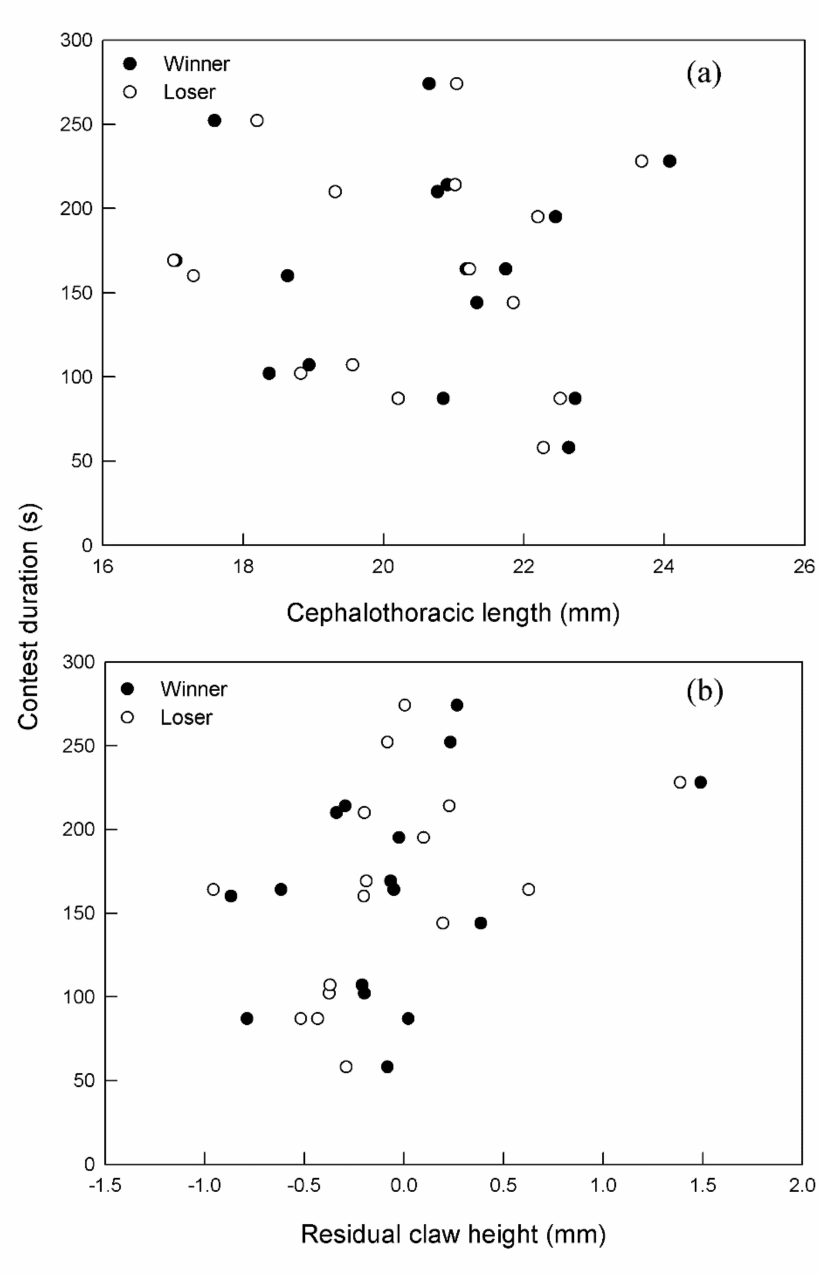

Figure 6. Relation between contest duration and (a) cephalothorax length, and (b) residual claw height for both winners (black circles) and losers (white circles) for RHP-matched pairings. The regression lines were not plotted due to non-significance.

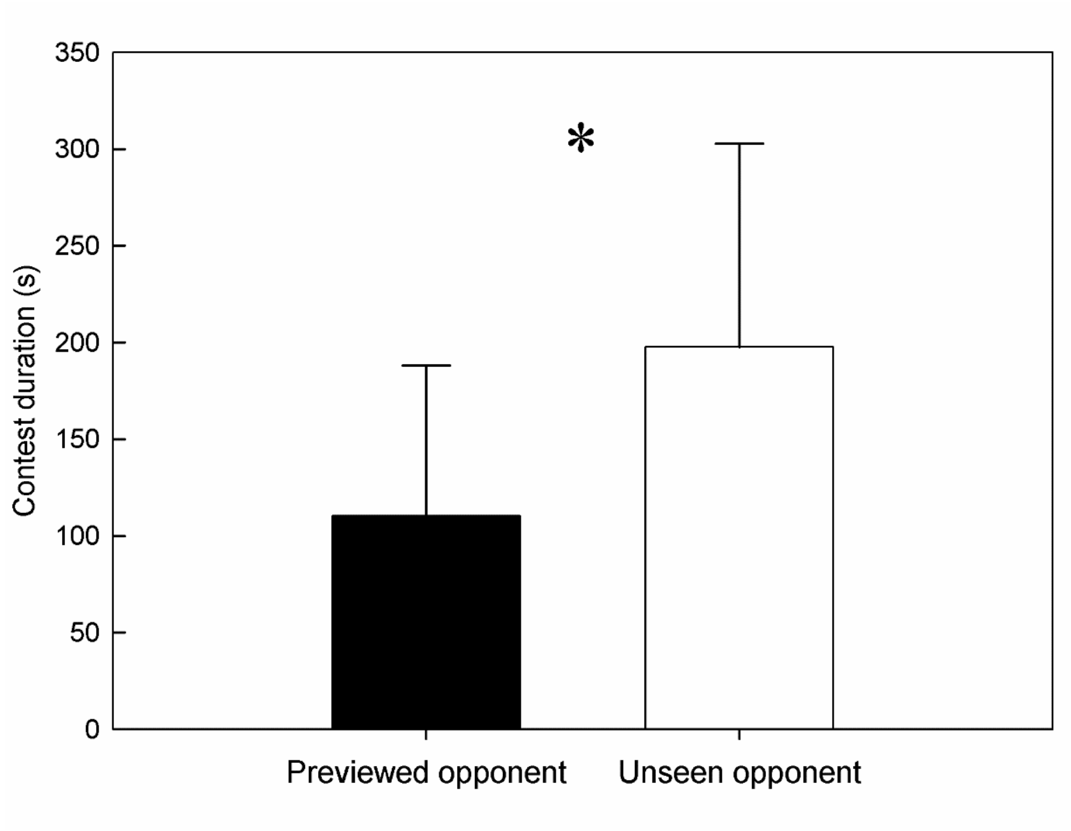

Figure 7. Mean contest duration (± S.D.). Black bar denotes the previewed opponent treatment (focal individual could interact visually/chemically with the opponent during acclimation). White bar denotes the unseen opponent treatment (focal individual would interact visually/chemically with one individual during the acclimation, and interact physically with other individual afterwards). Asterisk (*) denotes significant difference between the treatments (two-tailed permutation *t*-test; $t_{14} = -2.005$; $P = 0.046$).

ARTIGO 3: HOW WEAPONS ARE FORGED – SHAPE AND BIOMECHANICS INTERACT TO IMPROVE THE PERFORMANCE OF A SEXUALLY SELECTED TRAIT

Artigo submetido para The American Naturalist.

How weapons are forged – shape and biomechanics interact to improve the performance of a sexually selected trait

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Abstract

Weapons can be used to subjugate opponents, to display fighting prowess or both – thus different selective pressures can occur. On one hand, the pure mechanistic use of a weapon should select for strong and mechanically efficient traits; on the other, the display function should select for conspicuous, complex traits. Not only should we expect biomechanical differences, but we should also expect shape differences – pure weapons should be under strong biomechanical constraints, while signals should not. Therefore, pure weapons should have less labile shapes than signals. Herein, we used the enlarged claws of males and females of three species of freshwater crustaceans (*Aegla*) to test that idea using biomechanical variables (i.e. muscle size and mechanical advantage) and geometric morphometric analyses to assess shape variation. We show that the pure weapon is stronger and is less labile than the intermediate weapon, but it is not more efficient. When size-shape allometry is removed, the pure weapon's shape becomes sexually monomorphic and similar to a feeding claw, while the intermediate weapon differs from all. Our results thus demonstrate that while size and biomechanics can be under directional selection, weapon shape may not be – highlighting that the same trait can be under different selective pressures.

Introduction

Throughout the animal kingdom, sexually selected traits (e.g. weapons and ornaments) are used to acquire and secure mates (Berglund et al. 1996). However, how weapons and/or ornaments are used to achieve that goal differs substantially. Individuals use their weapons to threaten and subjugate same-sex opponents either through aggressive displays and/or use of strength, while ornaments are used to attract individuals of the opposite sex by signaling the quality of the bearer (Berglund et al. 1996). Additionally, there are instances in which traits can be dual-function - being both weapon and ornament simultaneously, such as *Uca* (fiddler crabs) claws that are used to grasp opponents and to draw the attention of the female (Dennenmoser and Christy 2013. Although weapons and ornaments can be distinguished based on the sex of their audience, weapons themselves can be differentiated from one another based on their uses. For instance, some weapons are used primarily for physical contact (e.g. beetles' horns, McCullogh et al. 2014), other weapons used mainly for visual displays of the bearer's fighting prowess (e.g. stalk-eyed fly' eye span, Panhuis and Wilkinson 1999), and others that are used for both purposes (e.g. ungulates' antlers, Jennings and Gammel 2013). Therefore, weapon function can be characterized within a weapon-signal continuum (*sensu* McCullough et al. 2016) – from purely mechanistic uses (i.e. fights) to purely display purposes – that should directly influence the trait's morphology and shape to maximize the bearer's fitness.

Weapons used during fights are expected to dominate conspecifics through trials of strength. Hence, selective pressures should favor robust and efficient structures capable of exerting great loads while also being resistant to the opponent's loads (McCullough et al. 2016). This increased selection on mechanical performance may biomechanically constrain the weapon's shape – a weapon can only be modified to a certain extent before it loses its' function, while a signal would not have such constraints (Berglund et al. 1996; McCullough et al. 2014). As traits move towards the signal side of the continuum, selection should favor conspicuousness rather than biomechanical performance as they need to draw attention to be effective (Husak & Swallow 2011). Consequently, we expect signaling weapons to be big, flashy, complex traits that are not constrained to particular shapes as weapons are. These distinctions can be difficult to assess due to the inherent variability of a sexually selected trait (Bonduriansky 2007). But if closely-related species use the same morphological trait as a weapon/signal and vary in how they are using it, we could assess these variations and understand the biomechanical modifications needed for a powerful weapon or a conspicuous signal. This is what makes crustaceans' claws an interesting trait for mechanical studies.

Claws function as a simple lever system: Muscles are attached to a cuticle (the apodeme; fig. 1) that when contracted close the mobile finger of the claw (i.e. dactyl; fig. 1). To be strong the claw needs large closing muscles, but to be efficient loads produced by the closing muscles need to be translated into actual pinching force. Since the claw is a lever, pinching force is correlated to the size of the lever – as levers increase in length, the loads produced at the tip becomes farther from the muscle, decreasing the claw's efficiency or mechanical advantage (MA, Levinton et al. 1995). Consequently, these biomechanical constraints should limit the amount of shapes a weapon-like claw can assume – weapons would require a large proximal area (i.e. manus) to house large muscles and a small dactyl (or spines/tubercles) to have a high MA (fig. 2). On the other hand, claws used for feeding or signaling are free of those biomechanical constraints and could assume various shapes to increase conspicuousness/complexity (e.g. size, color, spots) or effectiveness in prey capture (e.g. fast-closing claws, Anderson et al. 2014) with no regard to mechanical efficiency. Therefore, by combining biomechanics with shape analysis, we can have a better glimpse of what sort of selective pressures sexually selected traits are under.

Crabs can invest more in one claw than the other (i.e. heterochely) specializing the larger claw for one function (e.g. fighting, displaying, Mariappan et al. 2000), or invest equally in both claws (i.e. homochely), a pattern that may also be sexually dimorphic (Mariappan et al. 2000). Hence, the comparison of specialized larger claws of heterochelous species/sexes with homochelous species/sexes can demonstrate the adaptations for weapons while controlling for inherent biomechanical and shape differences of a claw. Males and females of the freshwater anomuran genus *Aegla* show this difference in claw investment which may correlate with male fighting dynamics (Ayres-Peres et al. 2015). *Aegla denticulata denticulata* is a homochelic species (i.e. a pair of non-specialized claws, or feeding claws) seldom using their claws to grasp (i.e. one of the most aggressive acts in a contest, Palaoro et al. 2014), thus being a low aggressiveness species (hereafter 'feeding appendage'). *Aegla abtao* is a heterochelous species that uses their claws both to grasp and to display to their opponents during fights, thus being an intermediate in the weapon-ornament continuum (hereafter 'intermediate weapon'). Lastly, *Aegla longirostri* is also a heterochelous species but do not use claw displays during fights only using their claw to grasp their opponents, meaning they have a purely weapon claw (hereafter 'pure weapon', Ayres-Peres et al 2015). Using *A. denticulata* as a control for a naturally selected claw, we expect to see adaptations of a sexually dimorphic pure weapon in *A. longirostri* and adaptations for a sexually dimorphic intermediate weapon in *A. abtao* due to their fighting displays (fig. 2).

Our goal is to test the biomechanical and shape adaptations needed to make a powerful weapon or a conspicuous signal using the freshwater decapod *Aegla* as a model system. Since weapons and signals differ in how they are used in a fight, and that these entails in differences in biomechanics and shape, we hypothesize that weapons will be strong and efficient whereas signals will be conspicuous and have a labile shape. Specifically, we predict that sexually selected claws (i.e. *A. longirostri* and *A. abtao*) will present sexual dimorphism, whereas *A. denticulata* will not. Additionally, the intermediate weapon will be larger in size than the other claws while the pure weapon will have: a larger muscle, higher mechanical advantage and less shape variability than the other claw types (fig. 2).

Material and Methods

Animal sampling and photographing

We used a hand net to collect 39 males and 43 females of *A. abtao*; 46 males and 40 females of *A. denticulata*; and traps to collect 48 males and 45 females of *A. longirostri*. *Aegla abtao* and *A. denticulata* were collected in South-Central Chile (40º02′29″ S; 72º54′34.4″ W), while *A. longirostri* was collected in Southern Brazil (29°40′13″ S; 53°45′44″ W). We photographed the dorsal side of the left claws of intact males (i.e. had all appendages and none were regenerating) in the laboratory positioned on a flat surface 20 cm below a Sony Handycam HDR-CX560®. We accommodated all claws on top of modelling clay with a linear scale, and we made sure that all claws remained parallel to the table and perpendicular to the camera, thus minimizing bias from orientation and possible camera distortions. We used these photographs for biomechanics measurements and geometric morphometrics analysis (see below). We chose only the left claw because they are the enlarged claws of *A. longirostri* and *A. abtao* and are thus the traits we are interested in. Lastly, we measured the cephalothorax length (CL) of all individuals from the eye orbit to the posterior end of the carapace using a digital calliper (precision: 0.01 mm) and used this measure as a proxy of body size.

Claw biomechanical measurements

The muscle that closes the claw is anchored to a flat cuticle, the apodeme (fig. 1), which is attached to the dactyl and longitudinally bisects the manus. The force this muscle can exert on the apodeme is thus related to the area of apodeme, which is highly correlated to the cross-sectional area of the muscle (Warner and Jones 1976). By measuring the area of the apodeme, we have a good proxy of the claw maximum strength (Levinton et al. 1995). Hence, we dissected the same claws used for biomechanical measurements and geometric morphometric analyses, removed all the muscle contained within it and photographed the apodeme (fig. 1) in the same way as the claws (i.e. on top of modelling clay and linear scale).

To measure the efficiency of the claw, we measured the MA. The MA is the ratio of the in-lever (i.e. dactyl height shown as (a) in fig. 1) to the out-lever (i.e. shown as (b) or (c) in fig. 1). We measured the height of the dactyl (fig. 1) equally in the three species, but we were unable to measure the out-lever equally because *A. denticulata* and females of *A. abtao* do not have any tubercle in the dactyl. Consequently, we had to the measure the out-lever as the distance from the fulcrum (i.e. where the dactyl rotates, landmark 4, fig. 1) to the tip of the dactyl. For males of *A. abtao* and *A. longirostri* we measured the out-lever from the fulcrum to the first tubercle (fig. 1). We did not use the same measure for all species and sexes because they reflect the different uses of the claw: males of *A. abtao* and *A. longirostri* only grab their opponents in fights if they are within the tubercle range, otherwise they do not grab their opponents (Palaoro et al. 2014; Ayres-Peres et al. 2015). Thus, if we used the same measures, we would be discarding an element of weapon functionality and leaving all differences to sheer muscle size, which could bias our results and conclusions. We used ImageJ (Schneider et al. 2012) to measure the levers and the area of the apodeme.

Measuring shape via geometric morphometrics

Geometric morphometric methods are ideal for studying the shape of morphological structures. First, they provide detailed information about shape variation while retaining the visual representation of the morphology (Mitterœcker and Gunz 2009). Second, they separate size from shape, which can then be used in statistical tests as independent measures. It allows researchers to test for the allometric effects of size on shape, for instance (Klingenberg 2016). We used five landmarks to capture major changes in claw shape and 12 semi-landmarks to capture functionally relevant shapes (e.g. tubercle at the pollex). These landmark coordinates were digitized using TpsDig 2 (Rohlf 2015).

Landmark (and semi-landmarks) configurations of every claw were superimposed using a generalized Procrustes analysis. During superimposition, landmarks are translated to origin, scaled to unit-centroid size and rotated until they are aligned (Rohlf and Slice 1990). The resulting Procrustes coordinates represent the shape of each specimen and trait size is extracted as centroid size (i.e. square-root of the sum of squared distances of a set of landmarks from their centroid). During superimposition, semi-landmarks were slid along their directions by minimizing the Procrustes distance between two semi-landmarks (Rohlf 2015). We used Procrustes coordinates as our quantitative measure of claw shape (hereafter "shape") and centroid size as our measure of claw size in all subsequent analysis.

Data analyses

To test if species and sexes invest differently in claw size we used generalized linear model (GLM) with a Gamma distribution and a log-link. Log-transformed centroid size was our dependent variable and log-transformed cephalothorax length was our continuous co-variable while sex and species were our factors. Next, we tested for differences in claw strength using a generalized least squares regression (GLS). We used the square-rooted apodeme area as the dependent variable, log-transformed centroid size as our continuous co-variable and sex and species as factors. The variance function we used to describe the changes in standard deviation consisted of an exponential of the log-transformed centroid size and the factor species (Pekár and Brabec 2016). Additionally, we regressed the square-rooted apodeme area on Procrustes distance (co-variable) and sex and species (factors). Procrustes distance is a measure of shape distance in “shape space” in which each individual has a unique value, thus being useful when used as a co-variate. To test if claws differ in their mechanical efficiency, we used a beta regression (i.e. a regression model with a beta distribution, Cribari-Neto and Zeileis 2010) with MA as the dependent variable, log-transformed centroid size as our continuous co-variable and species and sex as factors. In this model, we also controlled for residual dispersion using species and sex as our precision parameters. We also performed this analysis using Procrustes distance as our covariate instead of centroid size. Lastly, we scaled our continuous co-variables by centering their means to zero and making their variances uniform by dividing the co-variable by one-time their standard deviation. Centering and scaling variables help in parameter estimation and make parameters easily interpretable and comparable when significant interactions are present (Schielzeth 2010).

To summarize shape variability, we performed a principal ordination analysis on the Procrustes coordinates. Although geometric morphometric methods separate shape from size, both variables can still be correlated (i.e. allometry between size and shape, (Klingenberg 2016). Thus, to account for a common allometric slope, we regressed shape on centroid size using a Procrustes ANOVA. Then, we extracted the residuals of this analysis and performed a principal components analysis (PCA) with the residuals (i.e. size-corrected coordinates, Klingenberg 2016). This is a useful tool because it allows visualizing how shapes are changing along the axes of ordination using thin-plate spines. Next, to test for differences in the investment in shape (i.e. significant differences in slopes), we used a Procrustes ANOVA – similar to a non-parametric MANOVA, in which the sum-of-squared Procrustes distances is used instead of the sum of squares found in parametric MANOVAs (see Goodall 1991). For this test, we built a simpler model containing the interaction between species and sexes (i.e. each group has its own intercept) but only controlled for the continuous co-variable log-transformed centroid size (i.e. ~ log(centroid size) + species * sex). We then compared this simpler model to a model incorporating the interaction between the co-variable and the factors, which would thus generate slope values for all factor (i.e. ~ log(centroid size) * species * sex). In case these models differed, it would mean that species are investing differently in shape, rather than overall shape *per se*. Next, we made pairwise comparisons to test which groups differ from one another in investment. In both models Procrustes coordinates were used as dependent variables.

To test how much shape is varying we performed a morphological disparity analysis. In this analysis, Procrustes variance is estimated as the residuals of a linear model fit, and then a pairwise comparison of groups is performed. To do this, we used the Procrustes coordinates as our response variables and for our linear model fit we used log-transformed centroid size to control for allometric effects of size on shape. Afterwards, we tested the differences in the residuals of variance between species and sex - larger Procrustes variance values indicate a more variable shape (Zelditch et al. 2012). Lastly, to test how shapes are changing according to species and sex, we used a phenotypic trajectory analysis using Procrustes coordinates as the dependent variables and species and sex as factors. Since this analysis cannot control for the allometry between size and shape, we also performed this test using the size-corrected coordinates as dependent variables. All tests were performed in the R environment (R Core Team 2015). The beta regression model was built using 'betareg' package (Cribari-Neto and Zeileis 2010), GLS models were built using 'nlme' package (Pinheiro et al. 2016) and all geometric morphometric analysis were performed using the 'geomorph' package (Adams and Otarola-Castillo 2013).

Results

Sexes differed in their investment in claw size (table S1) – all species showed clear dimorphism with males having larger claws than females (fig. S1 A) but only *A. longirostri* males invested more in claw size (i.e. had higher slopes) than females (figs. 3 A and S1 B). Species also differed in their investment in claw size (table S1), with *A. abtao* and *A. longirostri* having larger claws than *A. denticulata* (figs. 3 A and S1 A), but we found no difference in slopes (fig. S1 B). Regarding the apodeme (table S2), *A. abtao* and *A. longirostri* showed dimorphism – in *A. abtao* males had larger apodemes than females and a higher investment as well (figs. 3 B and S2 A,B). However, *A. longirostri* males had a smaller apodeme but a much higher investment than females (figs 3 B and S2 A,B). Males did not show differences in apodeme size among themselves, but *A. longirostri* had the largest investment in apodeme with a small overlap with *A. abtao* (fig. S2 B) while *A. denticulata* had the lowest investment in apodeme. When Procrustes distance was used as the co-variable, all species showed dimorphism (table S3). Males of *A. longirostri* and *A. abtao* had larger apodemes and invested more in apodeme for a given shape than females while males of *A. denticulata* had smaller apodemes for a given shape and invested equally in the apodeme (fig. 3 C and fig. S3 A,B). For MA, the only species that showed dimorphism was *A. abtao* – males had higher MA than females. *Aegla longirostri* and *A. abtao* also had larger MAs than *A. denticulata* (figs. 3 D and S4 A,B). The same pattern was found when using Procrustes' distance as the co-variable (figs. 3 E and S5 A,B).

The first PC (PC1) explained 51.11% of the shape variation and PC2 18.4%, together explaining 69.5% of the total variance in claw shape. Groups separated relatively well with *A. abtao* males being the most distinct group (fig. 4 A). Individuals with negative PC1 values (mainly males of *A. longirostri* and *A. abtao*) had larger manus and shorter fingers than individuals with positive PC1 values (fig. 4 A), indicating that these species have more space in the claw to build muscle and may have higher MAs. In PC2, individuals with positive values (*A. longirostri*) had more angular claws, while negative PC2 values were more globose. However, when we corrected for claw size, differences were not as clear. PC1 explained 34% of the variation while PC2 24.15%, together explaining 58.15% of the total variance in claw shape. Males of *A. abtao* were again the most distinct group (fig. 4 B) with their globose claws, while *A. denticulata* and *A. longirostri* were now almost indistinguishable, which suggest a significant role of allometry in weapon shape.

Procrustes ANOVA showed that species and sexes invest differently in shape (table S4), with *A. longirostri* differing from everyone except their female counterparts, and *A. abtao* also differing from everyone except females of *A. longirostri* and *A. denticulata* (table S5). Regarding shape variability, males of *A. abtao* had the most variable shape, followed by *A. denticulata*, and *A. longirostri* had the least variable shape in all groups (table S6). Lastly, the phenotypic trajectory analysis showed that, when size is not accounted for, all three species differ in how much their shapes changes and the directions they do (figs. 4 A and S7,8). However, when we correct for claw size, *A. abtao* differs from the other two species in length and direction of shape changes, while *A. denticulata* and *A. longirostri* do not differ from each other (fig. 4 B and table S9,10).

Discussion

As we predicted, species that possess weapons were indeed more sexually dimorphic than the other species (*A. denticulata*) - this difference was evident even within *A. longirostri*, a species in which females also possess a claw adapted for fighting, according to our results. Furthermore, our hypothesis was partly corroborated – the pure weapon was indeed stronger and had a less variable shape than the feeding claw, but was more similar to the intermediate weapon than hypothesized. Pure weapons were slightly stronger than intermediate weapons, but not significantly more efficient which suggests that intermediate weapons retain some attributes (i.e. strength and efficiency) to function as a weapon. Notwithstanding, not only did we find that the pure weapon had a less variable shape than the intermediate weapon, but we also found that these groups differed in how shape is modified - changes in the pure weapon shape seem correlated to trait size, suggesting that it grows in an expected pattern. On the other hand, the intermediate weapon modifies the overall shape of the trait regardless of trait size, suggesting that size, biomechanics, and shape may be under different selective pressures and that these differential pressures may provide a possible mechanism for weapon diversification.

According to sexual selection theory, weapons are selected mainly through male-male competition (McCullough et al. 2016). Selection should thus favor traits with high mechanical performance. Our results agree with this prediction – both weapon types (pure and intermediate) presented the same levels of biomechanical dimorphism, being stronger and more efficient than the non-weapon type. However, the intermediate weapon type has a slightly smaller muscle than the pure weapon and a mean negative slope for MA (fig. 3). It is expected that as weapons increase their use as a signal, strength and efficiency will become less important to settle contests, decreasing the need for high mechanical performance (Berglund et al. 1996; McCullough et al. 2016). This pattern was also found in *Uca* crabs. As the enlarged claws of *Uca* became stronger (i.e. more weapon-like), it's function as a signal decreased, with some of the strongest species not being known for displaying their claws to females (Swanson et al. 2013). In our case, the intermediate weapon of *A. abtao* is displayed during male contests but fighting dynamics have not been altered – claws are more often used to grab opponents than for punching, pushing or displaying (Ayres-Peres et al. 2015). Additionally, we do not know whether it is also employed in a mating context. It is thus safe to assume that, although the trait has a signaling purpose, it is not being extensively used as a signal which corroborates with the small differences between the intermediate and the pure weapon. Our results thus add evidence that weapons and signals may face opposing selection pressures – and moreover that even a weapon that is not extensively used as a signal shows a slight decrease in mechanical performance (fig. 3 B,D).

We predicted that the pure weapon would have a less variable shape than the feeding claw and the intermediate weapon, and our results support this prediction. Additionally, it provided support for the long-standing claim that weapons should have more constraints than signals (Berglund et al. 1996; Bonduriansky 2007; McCullough et al. 2016). This has two major implications. First, trait size, biomechanics and shape can be under different selective pressures. Second, the importance of novelty in weapon diversification may be context-dependent. It is widely accepted that sexually selected traits are usually under directional selection that can be strong to a point of causing trait exaggeration in some taxa (Lavine et al. 2015; Voje 2016). This directional selection, however, is almost always used to explain trait size or dimorphism, not shape variability. As far as we are aware, there are no studies on the selection forces acting on the shape variability of sexually selected traits.

The pure weapon of *A. longirostri* is sexually dimorphic regarding trait size (males have bigger claws and invest more on its size; figs. 3 A and S1) and function (males invest more on claw size (figs. 3 A and S1) and strength (figs. 3 B and S2)). On the other hand, they are not dimorphic when it comes to shape (males do not invest differently than females (fig. 4 B and table S5)) and the mean shape is similar (fig. 4 A). Males and females of *A. longirostri* only differ in the amount of shape variability – females have more variable claws than males (table S6). The pure weapon of males could then be seen as a larger, stronger and less variable version of the female's claw that changes in a predictable path (fig. 4 B). Moreover, both sexes have a weaponized claw: females of *A. longirostri* have larger, more efficient claws, and larger muscles than females of *A. abtao* and *A. denticulata* (figs. 3, S2, S3 and S4).

Consequently, if male's shape is a larger version of female's shape, we could argue that as the trait increases in size its' variability decreases. This complex scenario suggests that trait size and biomechanics could be under directional selection, while shape is not. If shape was under directional selection some level of dimorphism would be found, as found in the intermediate weapon type: *A. abtao* presents dimorphism in size, biomechanics and shape – *A. abtao* even invests differently in shape than males of *A. longirostri* (table S5). This decrease in trait shape variation could be occurring via a stabilizing selection acting due to biomechanical constraints on weapon shape.

Similar results were found for other groups, although did not test directly for it. For instance, functional mechanisms (i.e. MA and force amplification) of the striking appendages of mantis shrimp are not evolving independently of each other (Anderson et al. 2014). This correlation between functional mechanisms result in a wide array of possible shapes that are not found within Stomatopoda. Similarly, the functional mechanisms of stag beetles' jaws do not evolve independently of each other – which makes several possible shapes non-existent in nature despite the already high diversity of jaw shapes (Goyens et al. 2016). Another example can be seen in the sexually dimorphic hind legs of *Narnia femorata* (Hemiptera). Males presented heightened condition-dependence but low evolvability - even though the trait is highly variable among species (Miller et al. 2016). Stabilizing selection is also thought to occur on exaggerated traits used for feeding, prey capture and locomotion, but these are mainly naturally- and not sexually-selected (Lavine et al. 2015). As far as we are aware, we are the first to provide evidence that different aspects of a sexually selected trait may be under different selective pressures, adding to the current literature that weapons may not be as variable within species as thought. Therefore, we need more studies associating weapons' shape and function to understand what sort of selective pressures weapons are under -

comparative studies are paramount for this, especially in groups with high variability such as beetles or *Uca* crabs.

The smaller shape variation in the pure weapon counters the hypothesis that novel forms of weapons may increase competitive advantage and weapon diversification (McCullough et al. 2016). If the shape of pure weapons is indeed under stabilizing selection, this hypothesis will not work because selection would work against novelty. It is possible, though, that as weapons becomes adapted to signaling the strong selection on mechanical performance relaxes. Our analysis of shape adds to that idea in showing that intermediate weapons can change their shape in opposite directions of the pure weapon without losing much of their functionality. The manus area of the pure weapon has a greater distal elongation, making the claw more angular and increasing the area for the muscle to develop (fig. 4 A,B). Meanwhile, the intermediate weapon shows a greater elongation of the proximal area of the manus, which makes the claw more globose while maintaining most of its mechanical performance. However, when traits are shifting utility (i.e. from weapon to signal), female choice will become the major selective force acting and will drive the evolution of these traits. Thus, although selection on mechanical performance is relaxed, variability may already be eroded (Miller et al. 2016) and female choice needs to act and reward trait novelty for it to occur and increase trait diversification. This complex scenario could gain further insights from game-theoretical models that test the invasiveness of ‘novel’ mutants in a population with ‘stable’ traits. The evolution of sexually selected traits is driven by multiple selection pressures acting concomitantly, and by extension these ideas could also be tested in a group in which the sexually selected trait varies in how much it is being selected by female choice and male-male-competition. A good group would be earwigs (Dermaptera). The forceps at the end of their abdomen assume different shapes, sizes and patterns of sexual dimorphism – discussions of how forceps is perceived by females and is used in fights in most species are still underway (Kamimura 2014). If signaling can indeed relax selection on weapons, we expect that shapes will become more diversified as clades start to use their weapons as signals rather than mechanical performers. It could then be correlated with the importance of female choice in male fitness in each clade to test the relationship between traits of shifting utility and female choice (e.g. higher evolutionary rates of intermediate weapons and higher female preference for more elaborate traits).

In summary, we found that weapons can vary in their degree of mechanical performance depending on whether it is solely used as a weapon or if it is also used as a signal – even a weapon that is not extensively used as a signal shows a slight decrease in mechanical performance. Our results also suggest that weapon size, mechanics and shape can be under different selective pressures. Although the pure weapon is dimorphic regarding size and mechanics, it is not dimorphic in shape while also showing the least amount of shape variation in all groups analyzed. Thus, it is possible that size and mechanics are under directional selection while shape is under stabilizing selection. Furthermore, the low shape variation in the pure weapon suggests that novelty does not play a large role in the diversification of pure weapons. However, as weapons get adapted toward signaling, biomechanical selection on shape may relax and female choice will play a larger role in trait evolution, which may trigger weapon diversification. As far as we know, we are the first to study weapon size, shape and function separately, and we were able to provide several insights into how weapons evolve and function. Notwithstanding, as stated by McCullough et al. (2016), studies on weapon shape, function and evolution are clearly lacking in the literature and more studies can help us understand the selective pressures acting on each aspect.

Data accessibility. All data and relevant codes can be found on GitHub: https://github.com/alexandrepalaoro/ForgingWeapons

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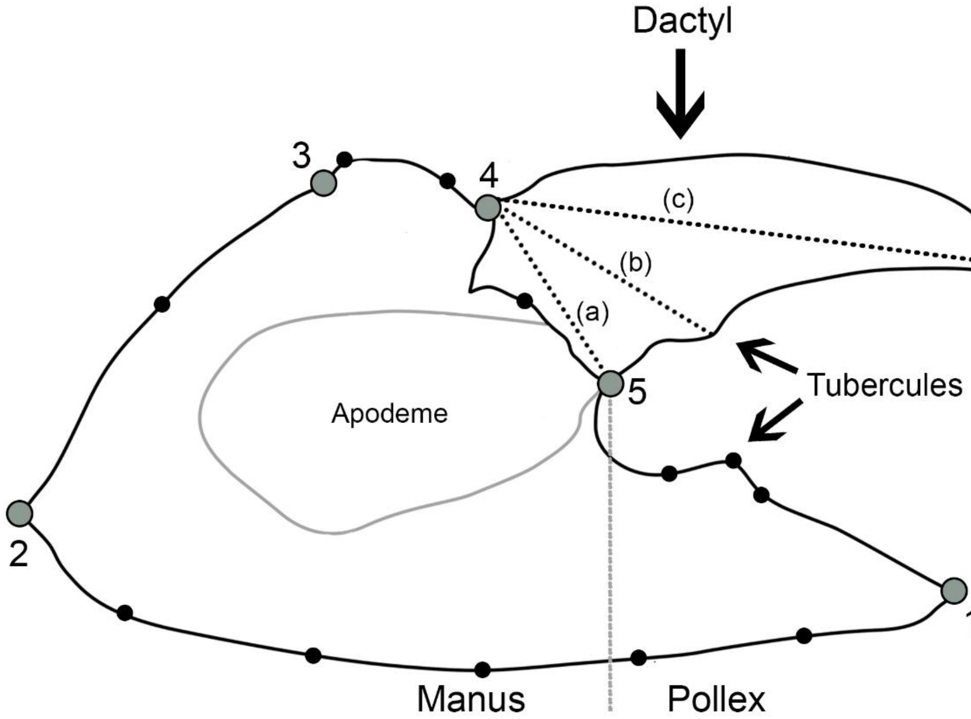

Figure 1: Depiction of an aeglid's claw. Grey dots are the five landmarks and black dots are the twelve semi-landmarks used for the morphometrics geometrics analyses (see Material and Methods). Since the manus and the pollex are not clearly divided, we used the landmark five to mark the division and traced the grey dashed line straight downwards. Inside the grey line we show a depiction of the apodeme: a cuticle in which the muscles attach to close the claw. Finally, (a) denotes the in-lever used to calculate the mechanical advantage, (b) denotes the out-lever for *Aegla longirostri* and *Aegla abtao*, and (c) the out-lever for *Aegla denticulata*. We could not measure the out-lever for *A. denticulata* and females of *A. abtao* in (b) because they do not have the tubercle in the dactyl.

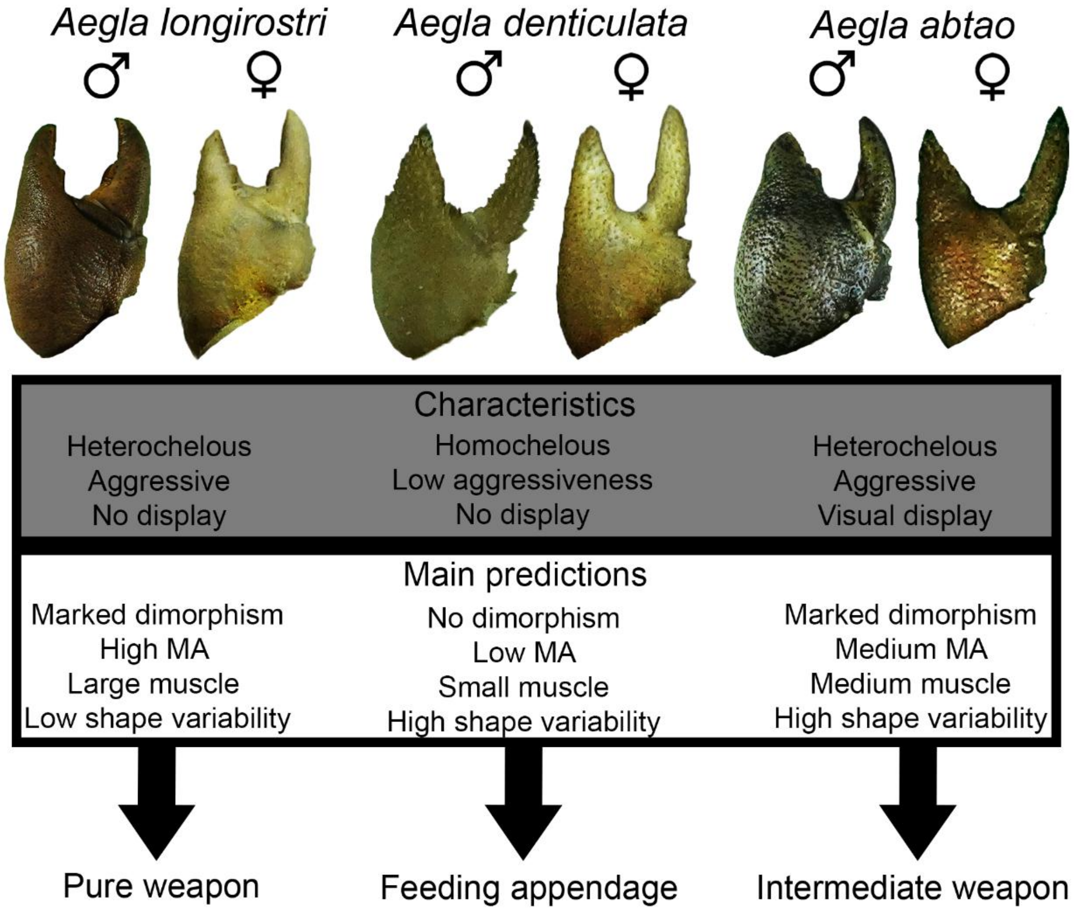

Figure 2: Schematic depiction of our predictions. MA = mechanical advantage. Arrows denote claw type.

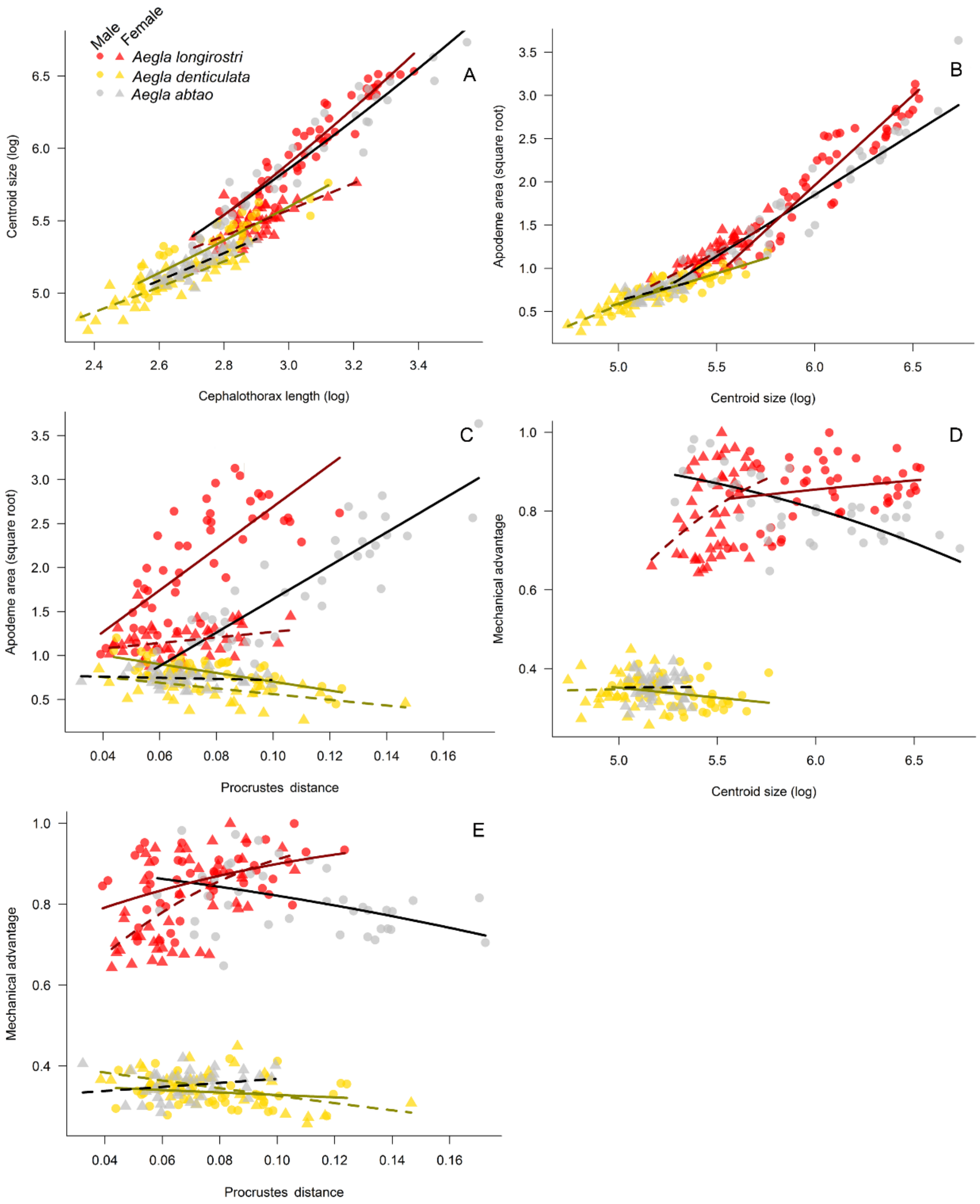

Figure 3: A, Log-transformed centroid size (i.e. a proxy for claw size) shows a positive allometric relationship with cephalothorax length that differs between size and sexes; B, The square rooted apodeme area also shows a positive relationship with log-transformed centroid size that differs between species and sexes; C, only *Aegla abtao* and *Aegla longirostri* show a positive relationship between the square root of the apodeme area and Procrustes distance (i.e. a large Procrustes distance value denotes a larger change in shape); D, *A. longirostri* and males of *A. abtao* show higher mechanical advantage than females of *A. abtao*

and both sexes of *A. denticulata* when concerning log-transformed centroid size; and E, Procrustes distance. Solid lines indicate relations for males and dashed lines for females. Intercepts and slopes with confidence intervals can be found in the Supplementary File (figs. S1-5).

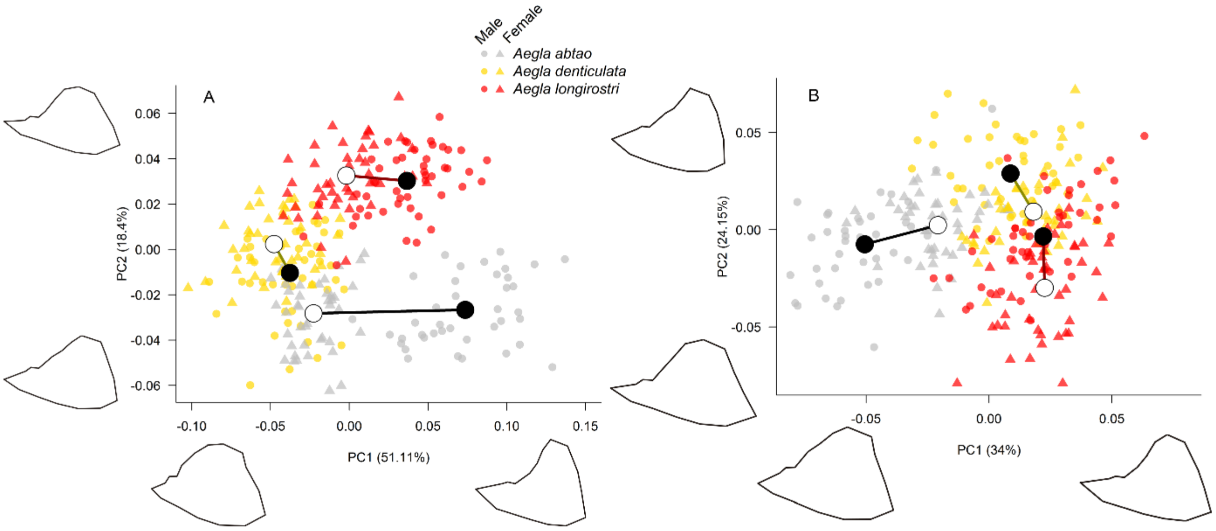

Figure 4: Phenotypic trajectory analyses showing how much shape is changing (i.e. length of the line) and in which direction (i.e. the angle of the line). Black dots denote males' centroid while white dots denote females' centroid. Claws depicted are the shapes predicted at the minimum or maximum of that principal component axis. A, does not account for the allometric effect of claw size on shape, while B, corrects for it.

SUPPLEMENTARY FILES

Table S1. Results of a generalized linear model (GLM) with a gamma distribution and a log link. We used the log-transformed centroid size (a correlate of claw size) as the dependent variable. CL = log-transformed cephalothorax length; DF = degrees of freedom. Deviance were drawn from a chi-squared distribution.

	DF	Deviance	Residual DF	Residual Deviance	*P*
CL	1	1.36143	260	0.15930	< 0.0001
Species	2	0.00399	258	0.15531	< 0.001
Sex	1	0.06398	257	0.09133	< 0.0001
CL:Species	2	0.01873	255	0.07260	< 0.0001
CL:Sex	1	0.01137	254	0.06122	< 0.0001
Species:Sex	2	0.00183	252	0.05940	0.019
CL:Species:Sex	2	0.00201	250	0.05739	0.013

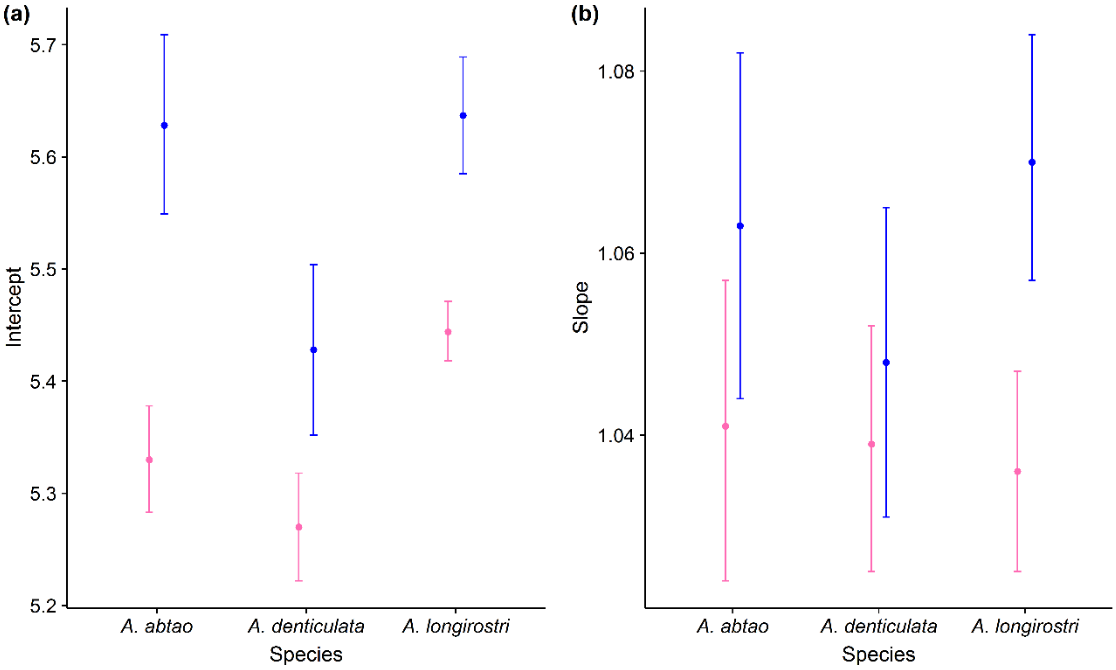

Fig S1. Intercept (a) and slope (b) estimated in the model in table S1 with confidence intervals. When confidence intervals do not overlap, we can assume that groups are significantly different. Males are denoted in blue while females in pink.

Table S2. Results of a generalized least squares regression (GLS). We used the square-root of the apodeme area as the dependent variable. LnCS = log-transformed centroid size; DF = degrees of freedom.

	DF	F-value	*P*
LnCS	1	3432.895	< 0.0001
Species	2	11.074	< 0.0001
Sex	1	2.952	0.087
LnCS:Species	2	59.726	< 0.0001
LnCS:Sex	1	3.959	0.048
Species:Sex	2	13.020	< 0.0001
LnCS:Species:Sex	2	25.256	< 0.0001

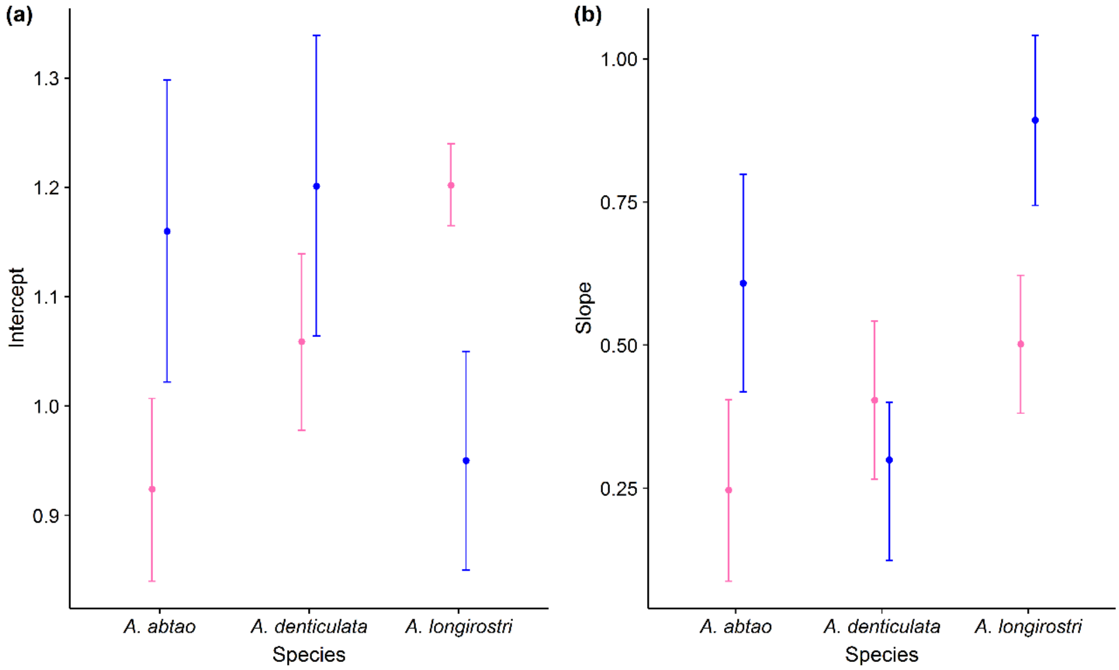

Fig S2. Intercept (a) and slope (b) estimated in the model in table S2 with confidence intervals. When confidence intervals do not overlap, we can assume that groups are significantly different. Males are denoted as blue while females as pink.

Table S3. Results of a generalized least squares regression (GLS). We used the square-root of the apodeme area as the dependent variable. ProcDist = Procrustes distance; DF = degrees of freedom.

	DF	F-value	P
ProcDist	1	19.401	< 0.0001
Species	2	234.650	< 0.0001
Sex	1	330.466	< 0.0001
ProcDist:Species	2	87.206	< 0.0001
ProcDist:Sex	1	77.397	< 0.0001
Species:Sex	2	72.823	< 0.0001
ProcDist:Species:Sex	2	54.090	< 0.0001

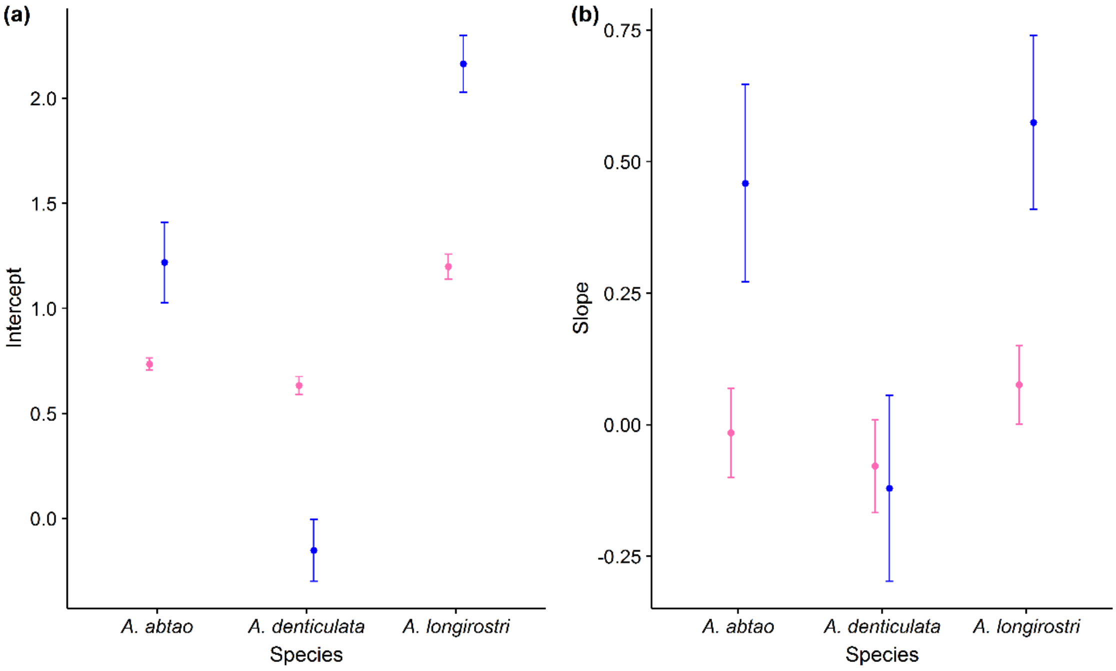

Fig S3. Intercept (a) and slope (b) estimated in the model in table S3 with confidence intervals. When confidence intervals do not overlap, we can assume that groups are significantly different. Males are denoted as blue while females as pink.

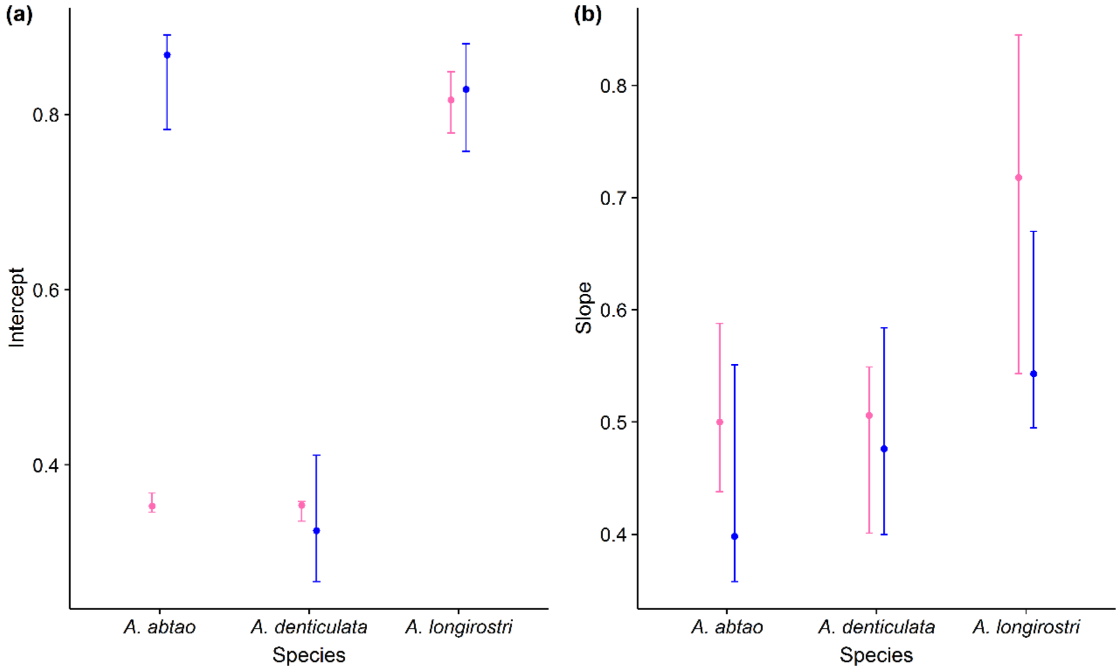

Fig S4. Intercept (a) and slope (b) estimated using a beta regression model. We used the mechanical advantage of the claw as the dependent variable, log-transformed centroid size as our continuous co-variable, and species and sex as factors. Additionally, we used the interaction between species and sex to model the precision parameter. When confidence intervals do not overlap, we can assume that groups are significantly different. Males are denoted as blue while females as pink.

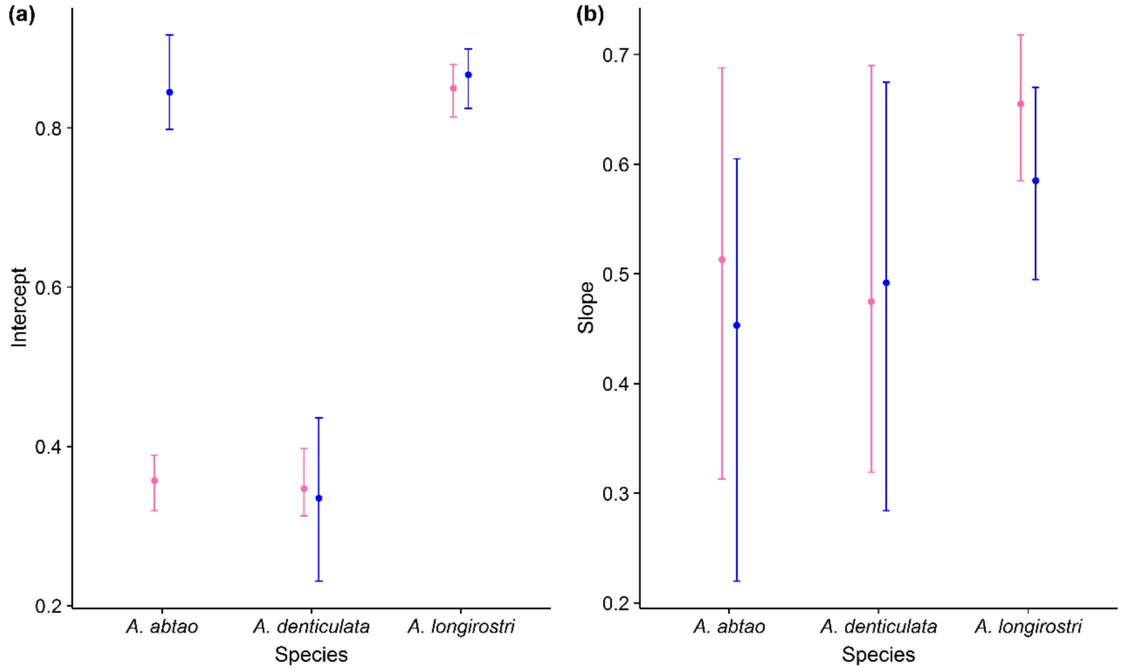

Fig S5. Intercept (a) and slope (b) estimated using a beta regression model. We used the mechanical advantage of the claw as the dependent variable, Procrustes distance as our continuous co-variable, and species and sex as factors. Additionally, we used the interaction between species and sex to model the precision parameter. When confidence intervals do not overlap, we can assume that groups are significantly different. Males are denoted as blue while females as pink.

Table S4. Results of a Procrustes ANOVA. We used Procrustes coordinates as dependent variables. LnCS = log-transformed centroid size; DF = degrees of freedom; SS = Sum of squares; MS = Mean sum of squares; Z = effect sizes.

	DF	SS	MS	R^2	F-value	Z	*P*
LnCS	1	0.389	0.389	0.331	223.513	28.427	< 0.001
Species	2	0.242	0.121	0.206	69.575	23.935	< 0.001
Sex	1	0.037	0.370	0.032	21.361	13.849	< 0.001
LnCS:Species	2	0.030	0.151	0.026	8.714	7.063	< 0.001
LnCS:Sex	1	0.007	0.007	0.006	4.019	3.174	0.005
Species:Sex	2	0.033	0.163	0.028	9.325	8.038	< 0.001
LnCS:Species:Sex	2	0.004	0.002	0.004	1.246	1.198	0.188
Residuals	249	0.433	0.001	-	-	-	-

Table S5. Pairwise comparisons of slope angles using a Procrustes ANOVA. We used Procrustes coordinates as dependent variables. Upper diagonal shows the effect sizes (Z-statistic), lower diagonal denotes the p-values. Bolded values denote significant p-values, which mean that species differ in their investment in claw shape.

	Abtao:female	Abtao: male	Denticulata: female	Denticulata: male	Longirostri: female	Longirostri: male
Abtao:female		2.831	1.065	2.262	1.385	2.717
Abtao:male	**0.006**		2.205	2.824	1.076	1.803
Denticulata:female	0.293	**0.034**		1.403	0.501	2.015
Denticulata:male	**0.019**	**0.007**	0.132		1.350	2.593
Longirostri:female	0.148	0.243	0.783	0.157		0.745
Longirostri:male	**0.007**	**0.042**	**0.046**	**0.012**	0.462	

Table S6. Morphological disparity analysis testing how much shape space each species and sex uses (i.e. how variable they are). Diagonal values show Procrustes variance values while lower diagonal values denote p-values (significant values are bolded).

	Abtao:female	Abtao: male	Denticulata: female	Denticulata: male	Longirostri:female	Longirostri: male
Abtao:female	2.438 * 10^{-3}					
Abtao:male	**0.001**	4.557 * 10^{-3}				
Denticulata:female	0.503	**0.001**	2.212 * 10^{-3}			
Denticulata:male	**0.026**	**0.001**	**0.004**	3.225 * 10^{-3}		
Longirostri:female	0.138	**0.001**	**0.032**	0.433	2.943 * 10^{-3}	
Longirostri:male	0.239	**0.001**	0.601	**0.002**	**0.004**	2.037 * 10^{-3}

Table S7. Phenotypic trajectory analysis testing how much the shape changed among species while accounting for sexual dimorphism (i.e. the length of the line in figure 4a). Diagonal values show observed path distances, upper diagonal denotes effect sizes and lower diagonal denotes p-values (significant values are bolded).

	Aegla abtao	*Aegla denticulata*	*Aegla longirostri*
Aegla abtao	9.951 * 10^{-2}	8.689	6.803
Aegla denticulata	**0.001**	2.765 * 10^{-2}	2.299
Aegla longirostri	**0.001**	**0.019**	4.522 * 10^{-2}

Table S8. Phenotypic trajectory analysis testing in which direction the shape changed among species while accounting for sexual dimorphism (i.e. the direction of the line in figure 4a). Upper diagonal denotes effect sizes and lower diagonal denotes p-values (significant values are bolded).

	Aegla abtao	*Aegla denticulata*	*Aegla longirostri*
Aegla abtao		4.370	1.952
Aegla denticulata	**0.001**		3.841

Aegla longirostri	**0.003**	**0.001**

Table S9. Phenotypic trajectory analysis testing how much the shape changed among species while accounting for sexual dimorphism and size (i.e. the length of the line in figure 4b). Diagonal values show observed path distances, upper diagonal denotes effect sizes and lower diagonal denotes p-values (significant values are bolded).

	Aegla abtao	*Aegla denticulata*	*Aegla longirostri*
Aegla abtao	$4.477 * 10^{-2}$	4.122	3.703
Aegla denticulata	**0.001**	$2.693 * 10^{-2}$	0.230
Aegla longirostri	**0.001**	0.826	$2.279 * 10^{-2}$

Table S10. Phenotypic trajectory analysis testing in which direction the shape changed among species while accounting for sexual dimorphism and size (i.e. the direction of the line in figure 4b). Upper diagonal denotes effect sizes and lower diagonal denotes p-values (significant values are bolded).

	Aegla abtao	*Aegla denticulata*	*Aegla longirostri*
Aegla abtao		2.269	3.249
Aegla denticulata	**0.001**		1.437
Aegla longirostri	**0.003**	0.069	

Conclusão Geral

Os resultados desta tese trazem algumas respostas interessantes para a compreensão da agressividade e evolução de armamentos. Por exemplo, o capítulo 1 demonstra que a variabilidade cíclica e intrínseca do ambiente afeta a motivação dos animais para brigar. Esse resultado ressalta a influência dos componentes temporais e espaciais do comportamento agressivo, transformando a paisagem em um verdadeiro mosaico. Quando pensamos em uma escala geográfica mais ampla, isso poderia afetar os padrões de distribuições de espécies, uma ideia que aos poucos está sendo testada e ganhando tração (PEIXOTO ET AL., 2014; FERREITA ET AL., 2016).

O segundo capítulo traz resultados que se somam a literatura corrente, ou seja, há problemas nos modelos teóricos sobre avaliação de oponentes (VIEIRA & PEIXOTO, 2013; FAWCETT & MOWLES, 2013). Os modelos teóricos correntes não são suficientes para explicar parcimoniosamente os dados obtidos nessa tese e em outros artigos. Portanto, dado que o problema foi detectado, necessitam-se de mais estudos para tentar prever melhor que tipo de informação os animais estão utilizando para desistir do confronto. Algumas tentativas para melhorar os modelos já foram elaboradas (e.g., MESTERTON-GIBBONS & HEAP, 2014; PALAORO & BRIFFA, 2017), mas necessitam de testes rigorosos. O terceiro capítulo, por sua vez, mostra as adaptações de uma estrutura morfológica utilizada apenas para alimentação em um armamento eficiente em confrontos. Além disso, também indica que armamentos possuem restrições biomecânicas para a elaboração da sua forma, o que pode influenciar na diversificação desses armamentos e possivelmente em padrões de especiação.

De maneira geral, os resultados desta tese preenchem as lacunas propostas nos objetivos e, mais importantemente, abrem novas perspectivas de estudos: Qual a importância da variação ambiental cíclica no comportamento de acasalamento dos indivíduos e qual sua influência em padrões de especiação? Qual a importância da alometria nas decisões que só animais fazem durante o confronto? Se armamentos possuem restrições biomecânicas para o desenvolvimento de suas formas, porque há uma diversidade tão grande de armamentos? Essas são apenas algumas das perguntas que esta tese deixa em aberto para futuras pesquisas.

Indo-se adiante, qual a importância dos nossos resultados para o comportamento humano? Primeiramente, a variação ambiental cíclica sempre foi importante para as guerras. Até a Idade Média as guerras só eram travadas no final da primavera e verão, pois as condições climáticas do inverno e outono europeu tornava a guerra inviável pelas baixas temperaturas e risco de doença e morte de soldados. Portanto, a motivação para lutar no inverno era baixa devido aos altos custos da agressão, os quais diminuíam nas épocas mais quentes, ocasionando invasões e guerras. Segundo, os modelos teóricos de agressão já foram utilizados para tentar explicar as durações de guerra (FIELD & BRIFFA, 2013; BRIFFA, 2014) e demonstraram os mesmos problemas que em confrontos de animais. Quem sabe se melhorarmos o poder preditivo desses modelos não teremos um melhor entendimento das nossas próprias guerras. Terceiro e último, a diversificação de armamentos humanos pode seguir um padrão similar a diversificação dos armamentos em animais: por muitos anos as únicas modificações no armamento foram na maneira de se forjar uma espada (restrição biomecânica); porém, quando houve uma modificação tecnológica (i.e., armaduras de placas), as espadas não eram mais tão eficientes e vários novos armamentos surgiram em decorrência dessa inovação (novos tipos de armamentos feitos para perfurar armamduras, e.g., estrelas-da-manhã, alabardas, manguais). Portanto, esta tese não só preencheu lacunas do conhecimento empírico sobre a agressão, mas também colabora com paralelos sobre a agressão humana (contudo, esses paralelos devem ser utilizados com cuidado, pois não é um estudo rigoroso, apenas analogias baseadas na experiência do doutorando e, logo, podem conter algumas falácias decorrentes do viés de confirmação).

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