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THE EFFECT OF GROUP COMPOSITION AND WEB DESTRUCTION ON
PERSONALITY

O efeito da composição do grupo e da destruição de teia sobre a personalidade

por

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RESUMO

Personalidade e plasticidade comportamental podem estar correlacionadas, o que pode restringir como um indivíduo responde ao seu ambiente. O contexto social pode ser de notável importância para algumas espécies, já que este pode modular o comportamento do indivíduo por diferentes mecanismos, incluindo conformidade. Nosso objetivo foi investigar o efeito da composição do grupo e destruição de teia sobre a personalidade. Medimos a ousadia da aranha social *Anelosimus domingo* e criamos grupos experimentais compostos de um indivíduo focal e quatro outros indivíduos, sendo que aranhas focais ousadas foram colocadas com indivíduos mais tímidos e vice-versa. A fim de explorar os efeitos da obliteração de teia, dividimos os grupos experimentais em uma condição não-perturbada, onde as colônias não sofreram nenhuma intervenção adicional ao longo da duração do experimento, ou uma condição perturbada, onde as colônias foram submetidas à destruição de teia dois dias após a formação dos grupos. Observamos que aranhas tímidas da condição perturbada se tornaram significativamente mais ousadas após o experimento, mostrando uma maior variação no índice de ousadia do que aranhas tímidas da condição não-perturbada. Além disso, notamos que aranhas ousadas não responderam a composição do grupo em nenhuma das condições. Portanto, aranhas tímidas e ousadas exibem níveis diferentes de plasticidade, o que pode afetar a maneira pela qual os indivíduos respondem ao contexto social. A resposta expressiva das aranhas tímidas pode estar relacionada a capacidade desses indivíduos de formar conexões mais fortes com co-específicos, tornando-os mais susceptíveis às influências do contexto social. Adicionalmente, o impacto da obliteração de teia na resposta do indivíduo ao contexto social sugere que a obliteração de teia aumenta as oportunidades para os indivíduos focais interagirem com os outros membros do grupo, promovendo um efeito mais acentuado do contexto social sobre o comportamento.

ABSTRACT

Personality and behavioural plasticity can be correlated, which may constrain how an individual respond to its environment. Social context can be of notable importance for some species, as it can modulate individual behaviour through different mechanisms, including conformity. Our aim was to investigate the effect of group composition and web destruction on personality. We assessed boldness in the social spider *Anelosimus domingo* and created experimental groups comprised of one focal individual and four groupmates, in which bold focal spiders were placed with shier groupmates and vice-versa. To explore the effects of web obliteration, we assigned experimental groups to either an undisturbed condition, in which colonies suffered no additional intervention for the duration of the experiment, or a disturbed condition, in which colonies were subjected to web obliteration two days after group formation. We found that shy spiders from the disturbed condition became significantly bolder after the experiment, showing a greater variation in their boldness indexes than their undisturbed counterparts. In addition, we noted that bold spiders failed to respond to group composition in both conditions. Therefore, shy and bold spiders show different levels of plasticity, which may affect how individuals respond to social context. The expressive response of shy spiders could be related to their capacity to form stronger connections to conspecifics, making them more susceptible to the influences of social context. Additionally, the impact of web obliteration on the response showed by individuals to social context suggests that web obliteration increases the opportunities for focal individuals to interact with groupmates, promoting an accentuated effect of social context on behaviour.

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1. INTRODUÇÃO GERAL

Personalidade, para a Psicologia, pode ser definida como “características dos indivíduos que descrevem e explicam padrões consistentes de sentimento, pensamento e comportamento” (PERVIN; JOHN, 1977 *apud* GOSLING, 2001). Essa definição, embora potencialmente satisfatória para seres humanos, pode apresentar diversas complicações quando aplicada a animais não-humanos (RÉALE *et al.*, 2007; RÉALE *et al.*, 2010). Isso se deve ao uso de estados internos que dificilmente podem ser mensurados em animais não-humanos, o que pode propiciar o antropomorfismo na tentativa de ajustar o conceito aos modelos animais, assim como levar a uma falta de interesse da parte de ecólogos em estudar personalidade (RÉALE *et al.*, 2007).

Tendo em vista os notáveis problemas que percolam a definição de personalidade comumente adotada para estudos em humanos, Réale *et al.* (2007) propôs que personalidade (ou temperamento) fosse definida como diferenças individuais de comportamento, sendo estas consistentes através do tempo e/ou diferentes contextos. Nesse sentido, consistência não implica na ausência de variação intra-individual de um contexto para outro, mas sim na permanência da variação entre indivíduos (RÉALE *et al.*, 2007; DINGEMANSE; WOLF, 2010; DINGEMANSE *et al.*, 2010; STAMPS; GROOTHIUS, 2010; WOLF; WEISSING, 2010). Em certos casos, dois ou mais eixos de personalidade podem estar correlacionado, formando uma síndrome comportamental (SIH; BELL; JOHNSON, 2004; STAMPS; GROOTHIUS, 2010).

A personalidade em animais não-humanos é um traço amplamente presente nos mais diversos táxons, de insetos e moluscos cefalópodes a mamíferos (GOSLING; JOHN, 1999; GOSLING, 2001). Tendo em vista o quanto a personalidade se mostra presente em variados grupos animais, ela passou a assumir um papel relevante no cenário da etologia e biologia evolutiva (RÉALE *et al.*, 2010).

Dentro da ecologia comportamental, acreditava-se que indivíduos agissem com base na optimalidade, ou seja, ajustando o seu comportamento de modo a exibir um fenótipo que promovesse aptidão máxima sob determinadas condições (DALL; HOUSTON, MCNAMARA, 2004; SIH; BELL; JOHNSON, 2004; DINGEMANSE; RÉALE, 2005). Logo, assumia-se que os indivíduos possuíam plasticidade comportamental - gama de fenótipos que um mesmo genótipo pode exibir sob diferentes condições ambientais - teoricamente ilimitada afim de comportar-se de maneira ótima sob diferentes situações (DALL; HOUSTON, MCNAMARA, 2004; SIH; BELL; JOHNSON, 2004; DINGEMANSE; RÉALE, 2005). Entretanto, na prática, indivíduos dificilmente exibem comportamentos ótimos, sugerindo que podem existir custos e limites associados à plasticidade comportamental (DEWITT; SIH;

WILSON, 1998; DALL; HOUSTON, MCNAMARA, 2004; SIH; BELL; JOHNSON, 2004). Tais restrições, por sua vez, poderiam levar fenótipos mais plásticos a desfrutarem de menor aptidão do que fenótipos mais rígidos em condições menos variáveis (DEWITT; SIH; WILSON, 1998; DALL; HOUSTON, MCNAMARA, 2004; SIH; BELL; JOHNSON, 2004).

Os custos e limites da plasticidade, apesar de oferecerem um motivo pelo qual indivíduos possam não ser infinitamente plásticos, não explica como diferenças individuais possam surgir. Uma das hipóteses acerca da origem das personalidades diz respeito a diferenças de estado, isto é, algum aspecto mensurável do organismo, como nível das reservas energéticas (DALL; HOUSTON, MCNAMARA, 2004; DINGEMANSE; WOLF, 2010; WOLF; WEISSING, 2010). Considerando que o estado de um indivíduo afeta a relação custo-benefício das suas ações e sendo essas diferenças de estado estáveis ao longo do tempo, elas podem resultar em diferenças individuais de comportamento (DALL; HOUSTON, MCNAMARA, 2004; DINGEMANSE; WOLF, 2010; WOLF; WEISSING, 2010). Adicionalmente, estados menos estáveis também podem gerar personalidades caso haja uma retroalimentação positiva entre o estado e as experiências vivenciadas pelo indivíduo, de modo a aumentar a probabilidade do indivíduo de manter uma certa estratégia comportamental (DALL; HOUSTON, MCNAMARA, 2004; DINGEMANSE; WOLF, 2010; WOLF; WEISSING, 2010).

Enquanto diferenças de estado podem atuar na origem de personalidades, a coexistência de múltiplas estratégias comportamentais consistentes em uma população tem sido associada a seleção negativamente dependente de frequência (DALL; HOUSTON, MCNAMARA, 2004; SIH; BELL; JOHNSON, 2004; DINGEMANSE; WOLF, 2010; WOLF; WEISSING, 2010). Segundo essa visão, a aptidão desfrutada por um fenótipo é inversamente proporcional a sua frequência na população, ou seja, quanto menos indivíduos adotarem uma estratégia comportamental, maior aptidão dessa estratégia (DALL; HOUSTON, MCNAMARA, 2004; SIH; BELL; JOHNSON, 2004; DINGEMANSE; WOLF, 2010; WOLF; WEISSING, 2010). Logo, estratégias alternativas tendem a oscilar em termos de aptidão e assim, se mantêm coexistindo dentro de uma população (DALL; HOUSTON, MCNAMARA, 2004; SIH; BELL; JOHNSON, 2004; DINGEMANSE; WOLF, 2010; WOLF; WEISSING, 2010). Alguns estudos demonstraram que populações compostas por uma mistura de tipos comportamentais tendem a desfrutar de maior aptidão do que grupos homogêneos, reforçando como a seleção dependente de frequência pode atuar na manutenção das diferenças individuais de comportamento (DYER *et al.*, 2008; PRUITT; RIECHERT, 2011; PRUITT; RIECHERT, 2012; SIH *et al.*, 2012; WOLF; WEISSING, 2012). Na aranha social *Anelosimus studiosus*, a coexistência de diferentes tipos comportamentais pode estar

relacionada a uma complementariedade de tarefas, visto que indivíduos mais agressivos exercem um papel relevante na captura de presas e defesa contra predadores, enquanto que indivíduos mais tímidos contribuem para reduzir interações agonísticas e assim, tornar a colônia menos susceptível a parasitas e predadores (PRUITT; RIECHERT, 2011; PRUITT; RIECHERT, 2012; SIH *et al.*, 2012; WOLF; WEISSING, 2012).

A natureza generalizada da personalidade através de diversos táxons, e com isso, a coexistência de diferentes tipos comportamentais dentro de uma população implica em uma série de consequências para aspectos como dinâmica populacional, relações intra- e inter-específicas, potencial de dispersão, resposta a mudanças ambientais, entre outros (SIH *et al.*, 2012; WOLF; WEISSING, 2012). Os diferentes tipos comportamentais em uma população podem diferir quanto a estratégia de forrageio e uso do hábitat, de modo a afetar a capacidade de suporte do ambiente, o que, por sua vez, pode influenciar sobre a densidade populacional (SIH *et al.*, 2012; WOLF; WEISSING, 2012). Além disso, a personalidade pode favorecer ou limitar o potencial de resposta a mudanças ambientais, sendo que indivíduos mais ousados tendem a obter vantagem em zonas urbanas, embora, ao mesmo tempo, tais indivíduos podem estar sujeitos a maior mortalidade (SIH *et al.*, 2012). Sendo assim, fica evidente a necessidade de considerar a personalidade em estudos que envolvem processos ecológicos.

Uma ideia central comum às principais teorias acerca da origem e manutenção da personalidade se refere a limitação da plasticidade comportamental (DALL; HOUSTON, MCNAMARA, 2004; SIH; BELL; JOHNSON, 2004). Nesse contexto, Dingemanse *et al.* (2010) propuseram o uso das normas de reação comportamentais a fim conciliar personalidade e plasticidade em um único modelo, uma vez que a existência de um não implica na ausência do outro. Segundo as normas de reação, indivíduos podem diferir não apenas quanto ao nível de uma resposta comportamental, ou seja, personalidade, assim como na variação que essa resposta comportamental pode assumir ao longo do tempo ou através de diferentes contextos – plasticidade (DINGEMANSE *et al.*, 2010).

Os indivíduos podem variar quanto ao seu grau de plasticidade comportamental e tal variação pode estar correlacionada com a personalidade (MATHOT; DINGEMANSE, 2014). Tal associação já havia sido mencionada na literatura dos *coping styles*, os quais se referem a respostas comportamentais e fisiológicas ao estresse que são consistentes ao longo do tempo (KOOLHAAS *et al.*, 1999; KOOLHAAS *et al.*, 2007). Indivíduos podem adotar uma estratégia proativa ou reativa de resposta ao estresse. Indivíduos proativos são caracterizados por agressividade, formação de rotinas e menor flexibilidade, enquanto que indivíduos reativos são caracterizados por docilidade, imobilidade e maior

flexibilidade (KOOLHAAS *et al.*, 1999; KOOLHAAS *et al.*, 2007; DINGEMANSE *et al.*, 2010; MATHOT; DINGEMANSE, 2014). Na aranha social *Anelosimus studiosus*, indivíduos mais dóceis conseguem desempenhar uma maior gama de tarefas do que indivíduos mais agressivos (HOLBROOK; WRIGHT; PRUITT, 2014). Resultados similares foram encontrados para o chapim-azul (*Cyanistes caeruleus*), onde indivíduos menos exploradores se mostraram mais capazes de ajustar o uso de comedouros de acordo com a temperatura ambiental do que indivíduos mais exploradores, reforçando o papel que a personalidade pode exercer sobre o grau de plasticidade comportamental do indivíduo (HERBORN *et al.*, 2014).

Uma das hipóteses acerca das diferenças de plasticidade relacionadas a personalidade propõe que diferenças no comportamento de amostragem podem levar alguns fenótipos a serem mais plásticos do que outros (MATHOT; DINGEMANSE, 2014). Segundo essa hipótese, indivíduos que investem mais tempo e energia em adquirir informações do ambiente são capazes de perceber modificações no ambiente mais rapidamente e assim ajustar seu comportamento de maneira mais efetiva (MATHOT; DINGEMANSE, 2014). No chapim-real (*Parus major*), indivíduos mais neofóbicos se ajustaram mais rapidamente a uma mudança na localização do alimento do que indivíduos mais neofílicos, sugerindo como, em certas condições, explorar o ambiente mais lentamente pode permitir uma aquisição de mais informação e assim promover uma resposta mais rápida a mudanças no ambiente (VERBEEK; DRENT; WIEPKEMA, 1994).

Tendo em vista como a personalidade se relaciona a plasticidade comportamental, torna-se evidente como indivíduos podem exibir diferentes respostas a diferentes estímulos ambientais, como o contexto social. Desse modo, é intuitivo pensar que a presença de co-específicos pode influenciar o comportamento do indivíduo (WEBSTER; WARD, 2011). Em seu nível mais básico, indivíduos podem obter informações a partir de outros indivíduos e assim ajustar seu comportamento (WEBSTER; WARD, 2011). Para o peixe *Gasterosteus aculeatus*, indivíduos que se mostraram mais tímidos em isolamento, se tornaram relativamente ousados quando forrageavam na presença do grupo social, embora tendessem a retardar a entrada em uma zona de alimentação na presença de co-específicos (ÓLAFSDÓTTIR; MAGELLAN, 2016). Similarmente, na truta arco-íris (*Oncorhynchus mykiss*) indivíduos ousados retardam sua latência de aproximação de um objeto novo ao observarem indivíduos tímidos, enquanto que indivíduos tímidos exibem uma tendência oposta, reduzindo a latência nas mesmas condições, sugerindo que indivíduos de tipos comportamentais distintos podem diferir quanto ao uso de informações sociais (FROST *et al.*, 2007). No entanto, no peixe *Gasterosteus aculeatus*, a personalidade não afetou

o uso de informação social, embora os indivíduos como um todo tendem a passar mais tempo em uma zona de alimentação após observar outros indivíduos se alimentando no mesmo local (HARCOURT *et al.*, 2010). Desse modo, nota-se que indivíduos com personalidades diferentes podem empregar estratégias distintas quanto ao uso de informação social, embora essa relação entre personalidade e informação social possa depender da espécie e dos paradigmas experimentais adotados.

Uma das maneiras através da qual o contexto social pode afetar o comportamento é por meio da conformidade, isto é, tendência dos indivíduos a se comportarem de forma mais similar ao grupo em que estão inseridos (WEBSTER; WARD, 2011). Em grupos do sagui-de-tufo-branco (*Callithrix jacchus*), a personalidade de indivíduos dentro de um mesmo grupo tende a assumir valores similares, de modo que personalidade em isolamento não está necessariamente correlacionada a personalidade quando no grupo social (KOSKI; BURKART, 2015). Fenômeno semelhante foi observado no diamante-de-Gould (*Erythrura gouldiae*), onde indivíduos menos exploradores tendem a se tornar mais exploradores quando pareados com um indivíduo mais explorador e vice-versa, reforçando o papel da conformidade sobre o comportamento exibido pelo indivíduo (KING; WILLIAMS; METKE-HOFMANN, 2015).

A conformidade pode atuar de modo a favorecer uma convergência simétrica, onde todos os indivíduos do grupo tendem a um valor médio para um certo comportamento, ou uma convergência assimétrica, onde os indivíduos do grupo tendem a assumir o comportamento de algum segmento do grupo (WEBSTER; WARD, 2011). Alguns estudos indicam que, em muitos casos, a conformidade tende a ser assimétrica. No peixe-zebra (*Danio rerio*), indivíduos menos exploradores tendem a se tornar mais exploradores quando colocados com co-específicos de maior atividade, porém o oposto não ocorre, ou seja, indivíduos mais exploradores não sofrem uma redução na tendência exploratória quando pareados com indivíduos menos exploradores (GUAYASAMIN; COUZIN; MILLER, 2017).

Tendo em vista o caráter assimétrico que a conformidade parece exercer em algumas espécies, tem-se que alguns indivíduos de uma população podem atuar como indivíduos-chave, exercendo um efeito desproporcionalmente mais acentuado sobre a dinâmica populacional (WEBSTER; WARD, 2011; SIH *et al.*, 2012; MONTIGLIO; FERRARI; RÉALE, 2013). Na aranha social *Stegodyphus dumicola*, indivíduos extremamente ousados afetam o comportamento de forrageio da colônia, promovendo um aumento na ousadia dos outros membros da colônia e tais alterações se mantêm mesmo após a remoção do indivíduo ousado (PRUITT; GRINSTED; SETTEPANI, 2013; PRUITT; KEISER, 2014; PRUITT; PINTER-WOLLMAN, 2015). Similarmente, peixes da espécie *Gasterosteus aculeatus* não apenas

exibem uma preferência para cardumes de indivíduos ousados, como a introdução de um indivíduo ousado, mas não de um indivíduo tímido, resulta em um aumento do nível da atividade do cardume (HARCOURT *et al.*, 2009). Esses resultados evidenciam como indivíduos-chave podem afetar a aptidão do grupo em que se encontram, influenciando o comportamento dos outros membros do grupo.

As aranhas sociais se tornaram importantes organismos modelo em estudos de personalidade (PRUITT; RIECHERT, 2012). Essas espécies representam uma pequena proporção das espécies de aranhas, oriundas de múltiplos eventos de evolução independentes (AVILÉS, 1997; LUBIN; BILDE, 2007). As aranhas sociais, de maneira geral, são caracterizadas pela cooperação na captura de presa, manutenção da teia e cuidado com a prole, além de possuírem uma razão fêmea-macho consideravelmente acentuada (AVILÉS, 1997; LUBIN; BILDE, 2007). Alguns estudos apontam que a personalidade afeta diversos aspectos da ecologia das aranhas sociais (PRUITT; RIECHERT, 2012). A personalidade influencia na divisão de tarefas, uma vez que indivíduos com personalidades diferentes tendem a ser alocados para tarefas diferentes (GRINSTED *et al.*, 2013; HOLBROOK; WRIGHT; PRUITT, 2014; WRIGHT; KEISER; PRUITT, 2016). Além disso, a personalidade dos indivíduos de uma colônia exerce um efeito maior sobre o comportamento de forrageio do que o número de indivíduos (KEISER; PRUITT, 2014), sendo que a distribuição de diferentes tipos comportamentais influencia o ganho de massa e chances de sobrevivência da colônia, evidenciando a relevância da personalidade em aranhas sociais, tanto para o indivíduo como para a colônia (PRUITT; RIECHERT, 2011).

Apesar de sabermos o quanto alguns indivíduos-chave podem afetar a personalidade dos outros membros do grupo, pouco se sabe sobre o efeito que o grupo exerce sobre o indivíduo e como isso se relaciona com as interações entre indivíduos. Sendo assim, nosso objetivo foi elucidar os efeitos da composição do grupo e da destruição de teia sobre a personalidade na aranha social *Anelosimus domingo* (Araneomorphae: Theridiidae).

2. CAPÍTULO 1

Título: The effect of group composition and web destruction on personality in the social spider *Anelosimus domingo*

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Abstract

English version: Social context can modulate individual behaviour through different mechanisms, including conformity, potentially affecting personality. Our aim was to investigate the effect of group composition and web destruction on personality in the social spider *Anelosimus domingo*. We created experimental groups comprised of one focal individual and four groupmates, in which bold focal spiders were placed with shier groupmates and vice-versa. Experimental groups were assigned to either an undisturbed condition or a disturbed condition, in which colonies were subjected to web obliteration. We found that shy spiders from the disturbed condition became significantly bolder than their undisturbed counterparts, whereas bold spiders failed to respond to group composition in both conditions.

Portuguese version: Contexto social pode modular o comportamento do indivíduo por diferentes mecanismos, incluindo conformidade, potencialmente afetando a personalidade. Nosso objetivo foi investigar os efeitos da composição do grupo e destruição da teia sobre a personalidade na aranha social *Anelosimus domingo*. Criamos grupos experimentais compostos por um indivíduo focal e quatro outros indivíduos, nos quais indivíduos focais ousados foram colocados com indivíduos mais tímidos e vice-versa. Grupos experimentais foram designados para uma condição não-perturbada ou uma condição perturbada, na qual colônias foram submetidas à destruição de teia. Observamos que aranhas tímidas da condição perturbada se tornaram significativamente mais ousadas do que as aranhas tímidas da condição não-perturbada, enquanto que aranhas ousadas não responderam à composição do grupo em nenhuma das condições.

Keywords

English version: Social context; boldness; disturbance

Portuguese version: Contexto social; ousadia; distúrbio

Introduction

Personality and behavioural plasticity may not only coexist within a population, but both traits can also show a correlation (Mathot and Dingemanse, 2014). Such association has been proposed within the proactive-reactive literature, which assumes that animals can be classified based on their coping style, i.e. a suite of consistent behavioural and physiological responses to stress (Koolhaas et al., 1999; Koolhaas et al., 2007). Proactive animals are characterized by higher levels of aggressiveness and boldness, while reactive animals are characterized by lower levels of aggressiveness and boldness (Koolhaas et al., 1999; Koolhaas et al., 2007).

Rodent studies have showed that proactive individuals tend to be less flexible and more prone to adopt routines than reactive individuals, which tend to adjust their behaviour more readily depending on the environmental conditions (Koolhaas et al., 1999). Such correlation, however, is not restricted to rodent species. Holbrook et al. (2014) have shown that for the social spider *Anelosimus studiosus*, docile individuals are more capable of adjusting their participation in different tasks than aggressive individuals. Similar results were found for blue tits (*Cyanistes caeruleus*), where “slow” individuals, which were more neophobic, less exploratory and less aggressive, showed greater adjustment of feeder use according to environmental temperature (Herborn et al., 2014). Hence, the personality of an individual may predict its degree of behavioural plasticity (Mathot and Dingemanse, 2014).

Considering how personality is the result of an interaction between both genetic and environmental factors (Dingemanse et al., 2010), it seems plausible to assume that environmental conditions, both biotic and abiotic may affect behaviour. For instance, it has been suggested that social context could have a relevant influence on behaviour, especially in social species (Webster and Ward, 2011). Frost et al. (2007) observed that, for the rainbow trout (*Oncorhynchus mykiss*), shy fish decreased their latency to approach a novel object when they watched a shy observer, whereas bold fish increased their latency when subjected to same condition, indicating that different behavioural types might respond differently to social information, further reinforcing the role of personality on behavioural plasticity.

One of the potential mechanisms through which the social context might modulate behaviour is conformity, i.e. a trend for individuals to behave more similarly when alongside conspecifics than when those same individuals are considered in isolation (Webster and Ward, 2011). In pairs of Gouldian finches (*Erythrura gouldiae*), the focal individual’s exploration tendency was modulated by its partner’s

tendency (King et al., 2014). In other words, when a more exploratory finch was partnered with a less exploratory finch, its exploratory behaviour tended to decrease and vice-versa. Similar results were found for common marmosets (*Callithrix jacchus*), in which groupmates tended to show similar personality scores (Koski and Burkart, 2015). Therefore, individuals might adjust their behaviour in the presence of conspecifics through conformity.

The effect of conformity can result from either a symmetric convergence in the behaviour of individuals, in which all individuals tend to shift towards a ‘mean’ value, or an asymmetric convergence, in which individuals tend to adopt the behaviour of the most or least responsive individuals in the group (Webster and Ward, 2011). Current evidence mostly supports the latter, as personality-related differences in plasticity may limit the capacity of animals to adjust its behaviour (Mathot and Dingemanse, 2014). In guppies (*Poecilia reticulata*), when fishes with different exploration scores were paired, the difference in their behaviour tended to decrease due to an increased in exploration by less exploratory fish, further indicating the higher adjustment potential of less exploratory individuals (Dyer et al., 2008).

Some groups might bear keystone individuals, which exert a disproportionately large effect on group dynamics as shown by Sih and Watters (2005), in which the presence of hyper-aggressive males in groups of water striders (*Aquarius remigis*) significantly decreased the overall mating success of the group by driving out females. The importance of keystone individuals has been highlighted for social spiders, which are characterized by high levels of inbreeding, female biased sex-ratio and communal prey capture, brood care and web maintenance (Áviles, 1997; Lubin and Bilde, 2007). It has been shown that personality may determine division of labour for some social spiders, as individuals with different behavioural types tend to engage in different tasks (Grinsted et al., 2013; Holbrook et al., 2014). In addition, personality serve as a more reliable indicator of collective foraging parameters than group size (Keiser and Pruitt, 2014). The presence of extremely bold individuals appears to be better predictors of collective foraging than the average boldness of colony members, indicating the role of keystone individuals in determining how a colony responds to prey (Pruitt et al., 2013). When an extremely bold spider is placed alongside shier colony-mates, the colony exhibited a decrease in latency to attack prey and increase in number of attackers, mass gain and survival (Pruitt et al., 2014). The effects of keystone individuals seem to be mediated by an increase in the boldness of shier colony-mates, which, in turn, might stimulate greater participation in prey capture events (Pruitt et al., 2015). Curiously, the participation of the keystone tends to decrease over time (Pruitt et al., 2015), raising the suggestion that

they might habituate to the simulated prey stimuli in the test and thus, stop responding to it (Pruitt et al., 2015). Alternatively, keystone individuals might increase the boldness of their colony-mates at the expense of a decrease in their own boldness. However, the impact of the group on keystone individuals remain to be addressed.

The presence and maintenance of the social group can affect behaviour at individual and colony level. When social spiders suffered a shift to a novel environment alongside conspecifics, there was no effect on boldness, whereas if the same shift occurred in isolation, spiders became bolder and this effect persisted for as long as five weeks following the shift (Keiser et al., 2014). However, if a shift to a novel habitat was associated with a change in habitat structure, there was a loss of colony-level repeatability of prey capture behaviour (Modlmeier et al., 2014a). Thus, the social group might buffer the effect of reallocation to a novel environment, but not of more drastic physical changes in the environment. In addition, the length of time individuals remain within a social group can also affect personality. In groups that remained together for a longer period of time, there was a significant increase in boldness repeatability, marked by an increase in inter-individual variation and a decrease in intra-individual variation (Modlmeier et al., 2014b). Therefore, repeated social interactions might accentuate personalities and this effect is likely dependent on the time spent with the social group. However, so far, little is known about how modest disturbances, including web destruction, might affect the response of individual spiders to the social context.

The aim of this study was to elucidate the effects of group composition and web obliteration on personality in the social spider *Anelosimus domingo*. We sought to address three main issues: 1) if different personality types, i.e. bold vs. shy, had different degrees of behavioural plasticity, 2) if individuals adjusted their behaviour according to group composition via conformity and 3) if a modest disturbance (i.e. web obliteration) affected personality and/or how individuals responded to group composition. We expected shy spiders to be more plastic and thus to show greater variation in behaviour in response to group composition than bold spiders. If focal individuals responded to the shift in group composition through conformity, we expected individual boldness scores to become more similar to group average boldness score. Additionally, we expected web obliteration to enhance the effects of social context, causing a larger variation in behaviour and thus, simulating the effects of a longer timespan with the social group.

Material and Methods

Study species

We used the social spider *Anelosimus domingo* Levi (1963) (Araneomorphae: Theridiidae), which is commonly found in the understory of rainforests in South America (Avilés, 1997). Colonies can range up to 1000 individuals, and are highly female-biased (Avilés, 1997). They build basket-shaped webs and their retreats are located within the nest, which is made up of vegetation and threads (Avilés, 1997). We collected four colonies at the Reserva Ecológica Michelin, located in Igrapiúna, Bahia, Brazil [S 13°46'53,59" W 38°49'44,26"]. Colonies were then transported to the Núcleo de Etologia e Evolução (NuEVo), located at Universidade Federal da Bahia, Salvador, Brazil. Adult females were kept in isolation on a previously identified 14mL Falcon tube until the beginning of behavioural assays on the following day.

Boldness assay

The boldness assay consisted in a simulated aerial predation event, which has been used in previous research to assess boldness in spiders (Riechert and Hedrick, 1990; Pruitt *et al.* 2013). Individual spiders were placed in a Petri dish (13 x 4cm) and given 60s as acclimation period before we applied two successive jets of air using an infant nose cleaner bulb, which elicited a freezing response in *A. domingo*. We then measured the latency to resume activity following the freezing response. The maximum test duration was 10min, after which the test was terminated even if the spider failed to resume activity. To assess repeatability, boldness assays took place once a day for three consecutive days. In order to make our results more intuitive, latency to resume activity was converted into a boldness index (BI) by subtracting the maximum test duration (600s) by individual latency.

Formation of artificial colonies

After the boldness assay, we randomly selected our bold (N = 8) and shy (N = 8) focal individuals from the 20 boldest and 20 shiest individuals out of 118 assessed spiders. Remaining individuals and those not chosen in our focal individual selection were separated in the 46 boldest and 46 shiest, from which we randomly selected 64 individuals (32 bold and 32 shy) to form our bold and shy groups. The 10 most intermediate individuals were excluded from our sample.

Each group was comprised of one focal individual, either bold or shy, and four groupmates that were either shier or bolder than the focal individual, i.e. bold focal spiders were placed with shier

groupmates and shy focal spiders were placed with bolder groupmates. Due to our low availability of spiders, we were unable to form colonies composed exclusively of individuals from the same source colonies. Considering how several social spider species appear to lack mechanisms to discriminate kin from non-kin (Lubin and Bilde, 2007), we mixed individuals from multiple source colonies during the formation of our experimental groups. Artificial colonies were housed in 430 mL clear plastic containers under the average temperature of 24° C.

Since we were interested in assessing the effect of web destruction on personality, our artificial colonies were assigned to either an undisturbed or a disturbed condition. In our undisturbed condition, artificial colonies were kept in their containers for five days so interactions between individuals could emerge (Pruitt et al., 2014) and fed a single *Tenebrio* sp. larva, two days following group formation. In our disturbed condition, on the second day after group formation, we removed spiders from their containers and destroyed their webs before reintroducing them into the containers and allowing individuals to interact for five days. Colonies were fed a single *Tenebrio* sp. larva, two days following web obliteration. Thus, focal individuals of undisturbed colonies were reassessed following five days of group formation and focal individuals of disturbed colonies were reassessed five days following web obliteration (seven days after group formation).

Statistical analyses

Parameters assessed were: i) mean boldness index (BI) and its standard deviation (SD), and ii) plasticity, defined here as the variation in mean BI between both assessment points (before vs. after experimental manipulation), in module.

We used the intraclass correlation coefficient (ICC) to assess the repeatability of BI (Bell et al., 2009; Wolak et al., 2012). The ICC calculates total variance in a sample, comprised of between-individual variance and within-individual variance to estimate the repeatability of a trait (Wolak et al., 2012). In order to evaluate the significance of repeatability scores, we employed a non-parametric Friedman's test, which assessed between-individual and within-individual differences in boldness index within each time of assessment separately.

We employed a mixed ANOVA with one within-subject factor (time of assessment) and two between-subject factors (condition and personality). In addition to that, we conducted a two-way ANOVA to assess the effects of both factors – condition and personality – on plasticity. Post-hoc pairwise

t-tests with Bonferroni correction were used to investigate simple main effects. All statistical analyses were conducted in the software R v. 3.4.1 (<https://cran.r-project.org>) and we assumed an alpha of 0.05.

Results

Table 1. Initial and final boldness index (BI), plasticity and group average BI for shy and bold focal spiders in both undisturbed and disturbed condition

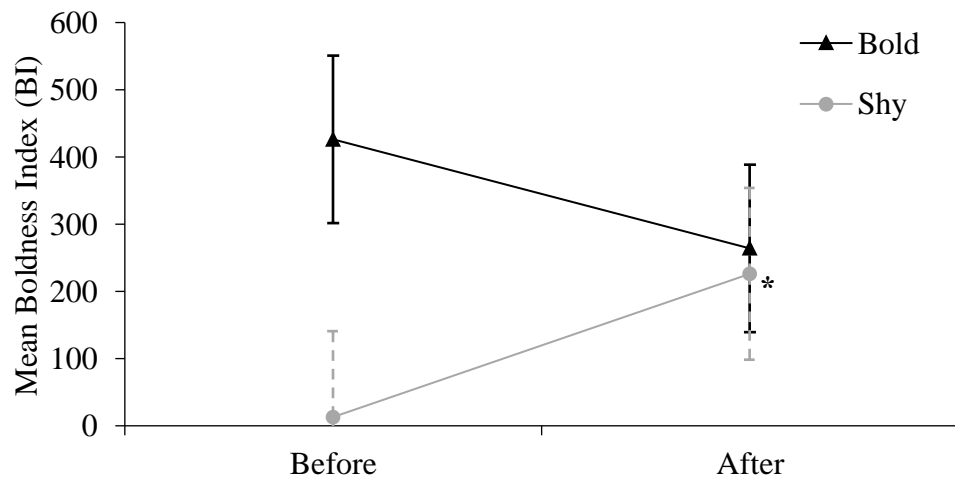
Condition	Focal spider	Initial BI	Final BI	Plasticity	Group BI
Undisturbed	Shy	0 (\pm 0)	12.833 (\pm 20.491)	12.833 (\pm 20.491)	372.521 (\pm 32.546)
	Bold	459.667 (\pm 23.358)	224.667 (\pm 94.979)	235 (\pm 209.29)	141.694 (\pm 126.754)
Disturbed	Shy	26.083 (\pm 18.385)	439.417 (\pm 97.183)	413.333 (\pm 97.765)	317.845 (\pm 29.470)
	Bold	401.083 (\pm 32.507)	293.333 (\pm 242.013)	225.25 (\pm 135.732)	79.813 (\pm 75.344)

Our results are summarized in Table 1. Overall, boldness index (BI) had good repeatability on both times of assessment ($ICC_{\text{before}} = 0.939$; $ICC_{\text{after}} = 0.952$). Pre-intervention, between-individual differences were significant ($X^2(2) = 29.086$; $P = 0.01017$; $N = 15$), but no difference was found within-individual measures ($X^2(14) = 1.1915$; $P = 0.5512$; $N = 15$). Similar results were found on our post-intervention assay for between-individual values ($X^2(2) = 34.232$; $P = 0.001908$; $N = 15$) and within-individual values ($X^2(14) = 0.11321$; $P = 0.945$; $N = 15$). Thus, corroborating the existence of personalities in *A. domingo*.

There was a significant effect of both condition and boldness on mean BI, as well as significant interactions between the factors condition: boldness, condition: time of assessment and boldness: time of assessment (Table 2).

Table 2. Summary of results from mixed ANOVA (N = 15)

Factor	DFn	DFd	F	P
<i>Condition</i>	1	11	10.213	0.0085
<i>Boldness</i>	1	11	31.062	0.0002
<i>Time of assessment</i>	1	11	0.726	0.4122
<i>Condition: Boldness</i>	1	11	8.058	0.0166
<i>Condition: Time</i>	1	11	9.424	0.0107
<i>Boldness: Time</i>	1	11	19.527	0.0010
<i>Condition: Boldness: Time</i>	1	11	2.323	0.1557

**Figure 1.** Variation in boldness index following intervention for bold and shy focal individuals.

* P = 0.03 (N = 8)

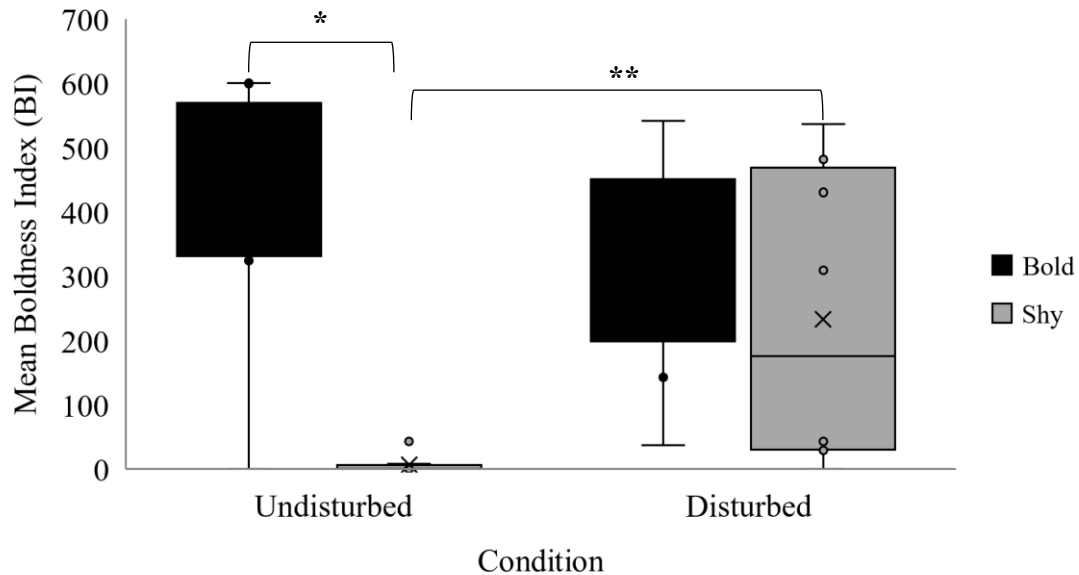


Figure 2. Mean boldness index (BI) for bold and shy focal individuals of the disturbed and undisturbed condition. * $P < 0.001$ ($N = 7$); ** $P = 0.015$ ($N = 8$).

Shy focal spiders became bolder after the intervention, which did not occur for bold focal spiders (Fig 1). Additionally, we noted that disturbed shy spiders were bolder than their undisturbed counterparts (Fig 2). For bold spiders, there were no significant differences between conditions (Fig 2). In the undisturbed condition there was a significant difference in BI between bold and shy spiders, which was not found in the disturbed condition (Fig 2). It is worth noting that only under the disturbed condition, did shy spiders suffer a significant increase in boldness (Fig. 3).

Mean plasticity was significantly affected by condition ($F(1,11) = 10.7867$, $P = 0.007278$, $N = 15$), but not by boldness ($F(1,11) = 0.004$, $P = 0.984726$, $N = 15$). In addition to that, we found a significant interaction between condition and boldness ($F(1,11) = 10.0591$, $P = 0.008893$, $N = 15$). Disturbed focal spiders had significantly higher plasticity than undisturbed focal spiders ($P = 0.023$, $N = 7$).

There was no effect of condition ($F(1,11) = 0.7105$, $P = 0.4172$, $N = 15$) nor boldness ($F(1,11) = 0.3338$, $P = 0.5751$, $N = 15$) on post-intervention mean SD.

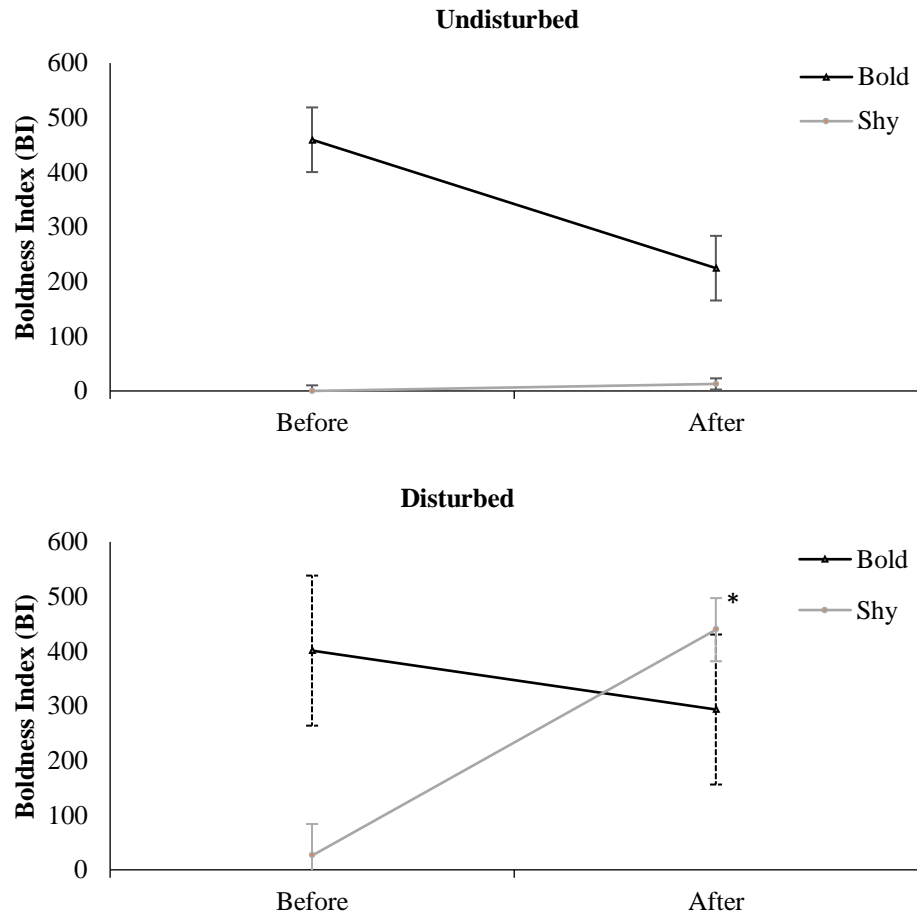


Figure 3. Variation in boldness index (BI) under undisturbed and disturbed conditions for bold and shy focal individuals. * $P = 0.003$ ($N = 4$).

Discussion

In our study, we observed that when undisturbed, focal individuals regardless of personality were unresponsive to group composition. On the other hand, when groups were subjected to web destruction, shy spiders became significantly bolder, suffering a greater variation in behavior than their undisturbed counterparts, whereas bold spiders remained unresponsive and had similar levels of variation in behavior for both conditions.

The proactive-reactive literature has demonstrated a correlation between aggressiveness and behavioural plasticity, in which aggressive individuals tend to be less capable of adjusting their behaviour and being more prone to follow routines, whereas docile individuals usually show greater ability to adjust

their behaviour according to environmental conditions (Koolhaas *et al.*, 1999; Dingemanse *et al.*, 2010; Holbrook *et al.*, 2014; Wright *et al.*, 2016). Given how, in some species, including social spiders, boldness and aggressiveness are positively correlated, forming a behavioural syndrome, it is intuitive to assume that bold spiders might be less responsive than shy spiders (Sih *et al.*, 2004; Grinsted *et al.*, 2013). Overall, we found that shy spiders indeed suffered a larger change boldness index than bold spiders, further supporting the correlation between personality and behavioural plasticity, in which, individuals that adopt a reactive strategy, i.e. shier, are likely more flexible than those that adopt a proactive strategy, i.e. bolder.

It is a reoccurring observation that a single bold individual, when placed with shy colony-mates, can have drastic effects on foraging success, colony-level personality and colony survival (Pruitt *et al.*, 2013; Pruitt and Keiser, 2014; Pruitt and Pinter-Wollmann, 2015). The presence of a single bold individual causes a significant increase in the boldness of shy colony mates, but those effects do not seem to result from a direct involvement of the bold individual in prey capture events, as its participation tends to decrease over time (Pruitt and Keiser, 2014; Pruitt and Pinter-Wollmann, 2015). Pruitt and Pinter-Wollmann (2015) suggest that bold keystone individuals may habituate to the prey stimuli and thus stop responding to it. We observed that only shy spiders adjusted their behaviour according to group composition, which indicates that on *A. domingo* the conformity effect is asymmetric, i.e. shy spiders become bolder when placed among bold groupmates, but bold spiders do not become shier when placed with shy groupmates. Therefore, the decrease in participation of bold keystone individuals seen in previous studies does not likely arise from a reduction in the keystone's boldness. Taken together, those studies indicate how individual differences in plasticity might limit the capacity of individuals to conform to their group's behaviour and thus favour a skewed conformity effect.

When focal individuals were subjected to web obliteration, the picture changed. Disturbed shy spiders showed an expressive response, becoming significantly bolder, whereas disturbed bold spiders failed to respond to group composition. On great tits (*Pars major*), Aplin *et al.* (2013) noted that less exploratory, shier individuals formed less albeit stronger connections with conspecifics than more exploratory, bolder individuals, suggesting that the ability of shy individuals to engage in stronger connections may make them more prone to the effects of the social group and thus, show greater behavioural change than bold individuals. Considering how web construction and maintenance are cooperative tasks in social spider colonies (Avilés, 1997; Lubin and Bilde, 2007), web obliteration could

have potentially created new opportunities for shy spiders to interact with their bold groupmates, permitting the formation of stronger social connections, which, in turn, led to a more pronounced effect of group composition on the behaviour of focal individuals. Since bold spiders have lower plasticity, even more opportunities for interaction may not permit greater adjustment in behaviour.

The contrasting response exhibited by shy spiders between the undisturbed and disturbed conditions led us to believe that insufficient interactions might prevent individuals to respond to social context, emphasizing how the presence of groupmates itself might not led to changes in behaviour. However, we did not detect an effect of disturbance on intra-individual variation, indicating that an acute disturbance might not necessarily provoke a loss or reduction in repeatability, unlike what has been observed for chronic perturbations (Keiser et al., 2014; Modlmeier et al., 2014a).

We consider it necessary to point out that due to our small sample, our power of analysis might have been limited. We did note non-significant trends for bold individuals regarding both variation in boldness index and plasticity, which could indicate that our small sample size and/or moderate size effect might have prevented us from assessing the phenomena. Yet, we firmly believe that the difference showed by bold and shy focal spiders indicates that our findings are in agreement with current literature, remaining valid and relevant for the field of animal personality despite its limitations. Nonetheless, our results should be interpreted with care and future studies should attempt to assess the phenomena within larger samples.

In conclusion, we found that shy individuals were more plastic than bold ones. Specifically, when shy spiders were placed alongside bold groupmates, they became bolder, supporting the presence conformity albeit skewed in *A. domingo*. However, this only occurred when individuals were subjected to web obliteration, emphasizing how this moderate disturbance might mimic the effects of longer times with the social group, resulting in a higher effect of social context on personality. Future research should investigate how group size and/or time spent in a social group might interact with group composition to affect the behaviour of focal individuals.

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3.CONCLUSÕES

Indivíduos tímidos se mostraram mais responsivos à composição do grupo do que indivíduos ousados, sofrendo uma maior variação no índice de ousadia. Tendo em vista como os indivíduos tímidos se tornaram significativamente mais ousados quando colocados em um grupo composto por indivíduos de maior ousadia, evidenciamos o papel da conformidade em *Anelosimus domingo* onde indivíduos tímidos ajustam seu comportamento em função dos indivíduos ousados, porém o oposto não ocorre. Entretanto, a variação observada nos indivíduos focais tímidos apenas se mostrou significativa mediante a destruição de teia, indicando que essa forma de distúrbio pode simular os efeitos de interações mais prolongadas, reforçando como a força das interações entre indivíduos é importante para determinar a resposta ao contexto social.

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ANEXOS

Table 1. Summary of intra-class correlation coefficient (ICC) parameters for multiple measurements taken before and after the intervention ($N = 15$)

	ICC	LowerCI	UpperCI	Varw	vara
Before	0.939	0.857	0.978	2836.188	44007.59
After	0.952	0.888	0.983	2323.653	46951.71

LowerCI: lower limit confidence interval; *UpperCI*: upper limit confidence interval; *varw*: intra-individual variance; *vara*: inter-individual variance.