Body size shapes average behaviour, social impact, and social responsiveness in agonistic interactions

Tom Ratz[1,2]*, Melissa Bahtije Maliqi[1], Corné de Groot[1], Emily Herter[1], Rori Wijnhorst[1] & Niels J. Dingemanse[1]

[1]Behavioural Ecology, Faculty of Biology, LMU Munich, Planegg-Martinsried, Germany

[2]Department of Evolutionary Biology and Environmental Science, University of Zurich, Zurich, Switzerland

*Correspondence: T. Ratz, e-mail address: tom.ratz@uzh.ch

Abstract

Social interactions shape behavioural phenotypes and fitness, and therefore represent major drivers of evolution. Increasingly, it is recognised that plasticity in response to social partners ("social plasticity") operates through two causal pathways: an individual's *impact on* and *responsiveness to* partner phenotypes. Functional links among an individual's average behaviour, social impact, and social responsiveness may have unanticipated evolutionary consequences. Body size is likely to be a key driver of such links, as size often determines the outcome of social interactions. This is particularly true in competitive contexts, where larger contestants generally have an advantage and individuals are expected to decide whether to escalate a contest or retreat based on the difference between their own body size and that of their rivals. We quantified the extent to which the three components, average behaviour, social impact and responsiveness, vary as a function of body size in competitive interactions, using southern field crickets (*Gryllus bimaculatus*) as a study system. We found that smaller animals were on average less aggressive, elicited more aggression in their opponents, and were more responsive by reducing their aggression more strongly when interacting against large opponents. Thus, all three social behavioural components—average aggression, social impact and social responsiveness—were size-dependent. If heritable, such associations in traits mediating aggression may either constrain or facilitate evolutionary responses to selection in ways not previously recognised. Our findings provide the first empirical evidence for hidden relationships among the key components of social traits, highlighting the need for a multivariate perspective to better predict the evolution of social behaviour.

Keywords: Aggression, animal contests, animal personality, resource competition, *Gryllus bimaculatus*, individual-by-environment interaction, indirect genetic effects, reaction norm, social evolution, social plasticity.

Introduction

Social interactions affect the behavioural decisions, and fitness, of individuals and their social partners (Westneat & Fox, 2010). Social interactions are ubiquitous because all animals interact with conspecifics to forage, compete, and reproduce (Trivers, 1985; Frank, 2007). Two fields of evolutionary biology have extensively studied social interactions. First, behavioural ecology has focussed on predicting the behaviour that individuals should express to maximize fitness in situations where their phenotype is affecting, and affected by, the phenotype of conspecifics. To achieve this aim, behavioural ecologists have used game theory, for example, to predict behaviour expressed during cooperative or competitive interactions (Parker, 1974; Maynard Smith, 1982; McNamara & Leimar, 2020). Second, quantitative genetics has developed theoretical models to predict how selection on traits expressed during social interactions translates into micro-evolutionary change (Moore et al., 1997; McGlothlin et al., 2010; Bijma, 2014). Both fields emphasize the key role that social interactions play as drivers of variation, selection, and evolution.

Individual phenotypes expressed during social interactions (called "interacting phenotypes") arise from three key components: (1) the individual's average phenotype, (2) its partner's social impact, and (3) its social responsiveness (Figure 1) (Araya-Ajoy et al., 2020; de Groot et al., 2023; Wijnhorst et al., 2025). An individual's average phenotype is determined by environmental and genetic factors that permanently influence its phenotype, known as direct environmental (DEEs) and direct genetic effects (DGEs), respectively (Falconer & Mackay, 1996; Lynch & Walsh, 1998). Variation among individuals in these factors contributes to repeatable differences in average phenotype, which can give rise to broader suits of correlated traits, including behavioural syndromes and animal personalities (Dall et al. 2004; Sih et al. 2004; Réale et al. 2007, 2010). Social impact describes how interacting individuals elicit phenotypic change in their social partners (Araya-Ajoy et al., 2020; de Groot et al., 2023). When this influence has a genetic basis, it is called an indirect genetic effect (IGE; Moore et al., 1997; Wolf et al., 1998; McAdam et al., 2014). Social responsiveness, in contrast, is a form of phenotypic plasticity defined as the slope of the reaction norm, and captures how an individual's phenotype changes as a function of the phenotype of social partners (Dingemanse & Araya-Ajoy, 2015). Although conceptually related, social impact and social responsiveness arise from distinct causal pathways (Araya-Ajoy et al., 2020; de Groot et al., 2023; Wijnhorst et al., 2025). Previous research has primarily focused on covariance parameters that encapsulate effects of both social impact and social responsiveness, such as those called "responsiveness" (André & Day, 2007; André, 2015), "response coefficient" (Akçay et al., 2009; Akçay & Van Cleve, 2012; Van Cleve & Akçay, 2014), or the "interaction coefficient ψ" (Moore et al., 1997; Bleakley et al., 2010; McGlothlin et al., 2010). Consequently variation in both social responsiveness and social impact has so far mostly been disregarded.

Quantitative genetics theory predicts that the evolutionary response to selection on interacting phenotypes depends on the additive genetic variance in, and covariance between, direct and indirect genetic effects. Direct genetic effects (DGEs) influence an individual's average phenotype, while indirect genetic effects (IGEs) capture the impact of an individual's genotype on the phenotype of its social partners. Positive genetic correlations between DGEs and IGEs are expected to amplify the response to selection, whereas negative correlations should constrain it (Moore et al., 1997; McGlothlin et al., 2010; Bijma, 2014). In addition, genetic correlations between the average phenotype and the level of social responsiveness–the extent to which individuals adjust their phenotype in response to others–should also shape evolutionary trajectories (Bailey et al. 2021). Such correlations imply that the amount of variance explained by DGEs may change depending on the phenotype of social partners, potentially enhancing or dampening evolutionary responses depending on the correlation sign. If interacting phenotypes are indeed shaped by three components–average phenotype, social impact, and social responsiveness–then accurate predictions of micro-evolutionary change require estimates of genetic variance in, and covariance among, *all* three. This raises two key questions: (1) do populations harbour heritable variation in each component of interacting phenotypes, and (2) are these components genetically correlated?

Heritable variation in average trait values is already well established for interacting phenotypes, as demonstrated by studies reporting non-zero variance attributable to direct genetic effects (DGEs; Stirling et al., 2002; Dochtermann et al., 2015, 2019; Santostefano et al., 2025). Indeed, heritable variation in aggression has been documented across a wide diversity of taxa, including mammals (Kessler et al., 1977; Benus et al., 1991), birds (Verbeek et al., 1996; Duckworth & Kruuk, 2009), and insects (Edwards et al., 2006; Santostefano et al., 2017b). Likewise, heritable variation in social impact is evidenced by studies reporting non-zero variance attributable to indirect genetic effects (IGEs; Bailey & Desjonquères, 2022; Santostefano et al., 2025). Meanwhile, evidence for heritable variation in social responsiveness comes from studies reporting genetic differences in plastic responses to social partners (*e.g.*, Kent et al., 2008; Bleakley & Brodie, 2009; Chenoweth et al., 2010; Bailey & Zuk, 2012). Correlations between DGE and IGE have also been reported (*e.g.*, McAdam & Boutin, 2004; Wilson et al., 2009, 2011), indicating genetic covariance between average phenotype and social impact. Genetic correlations between average phenotype and social responsiveness may also exist, as suggested by among-individual correlations between these components observed across a range of species (*e.g.*, Benus et al., 1990; Natarajan et al., 2009; Strickland et al., 2021). Nevertheless, to our knowledge, no study has yet attempted to infer variation or covariation across all three components of interacting phenotypes.

This study aims to address this gap by testing whether average behaviour, social responsiveness, and social impact (co)vary across individuals due to variation in body size. We designed an experiment to quantify, first, the three components of interacting phenotypes (average trait expression, social impact, and social responsiveness) and, second, test whether body size mediates their expression. We used agonistic interactions in male southern field crickets (*Gryllus bimaculatus*) as model system. Our analysis indirectly addresses patterns of (co)variance that—in line with Cheverud (1988)'s conjecture—are predictive of genetic (co)variance in this species (Santostefano et al., 2017a,b; Han et al., 2018). This is because aggression and aggression elicited in conspecifics are both repeatable and heritable, and are negatively correlated at the individual and additive genetic level (Santostefano et al., 2017b). We hypothesised that functional links between average aggression, social impact, and social responsiveness would arise due to variation in a non-behavioural trait: body size. In many animals, including field crickets, body size is a critical determinant of fighting success and influences aggression during contests (Gammell & Hardy 2003; Briffa, 2015). Larger individuals are more likely to win fights (Simmons, 1986; Shackleton et al., 2005; Reaney et al., 2011) and tend to be more aggressive (Dixon & Cade, 1986; Simmons, 1986). We thus predicted that (1) larger males to be more aggressive and that (2) males should in general reduce their aggression when faced with large opponents. We also expected that larger, more aggressive males are less responsive to opponent size, thereby linking average aggression and responsiveness (Figure 1A). Lastly, larger males should reduce their opponent's aggression, thereby linking body size and social impact, and average aggression and impact (Figure 1B).

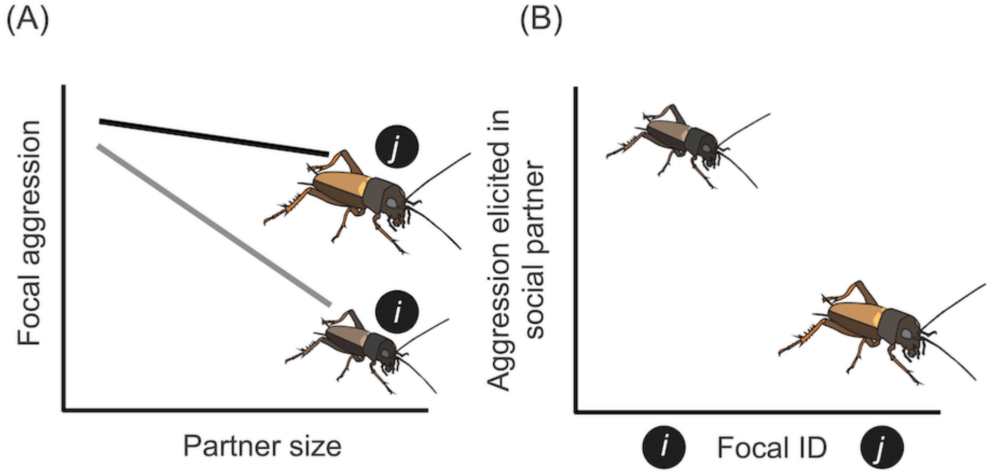

Figure 1. Illustration of size-mediated differences in social responsiveness (A) and social impact (B). In this example, individual *i* is smaller, more responsive to social partners' phenotype, and elicits more aggression in social partners than individual *j*.

Materials and methods

Origin and maintenance of the crickets

All crickets were derived from our stock population that originated from Sevilla (Spain) and was maintained under controlled conditions at LMU Munich for four generations (Ratz et al. 2024). The stock was kept under a 12L:12D photoperiod at 28°C and 60% humidity, and provided with commercial dry cat food, fish flakes, and water. We separated a total of 340 males as juveniles in their last nymphal stage and housed them in individual containers (10 × 10 × 9 cm) furnished with a plastic tube section for shelter, and supplied with ad libitum water and dry cat food.

Experimental design

Our aim was to evaluate the relationships among body size, average aggression, social impact, and social responsiveness to partner body size. We thus designed an experiment where each individual was first categorized as "small" or "large" (Figure 2); we then created dyads of all combinations based on these size groups (focal-opponent: small-small, small-large, large-small, large-large). While doing so, we ensured that each individual interacted (repeatedly) with "small" and with "large" opponents. To this end, we allocated males that had reached sexual maturity (*i.e.*, ≥10 days after adult moulting) to one of two size groups based on the population-average body size. As a proxy for body size, we used the length of the rear femur measured using digital callipers (Mousseau & Roff, 1989; Nosil, 2002). To purge measurement error in our analysis, we used the mean of three measurements of femur length taken from each individual (Arnqvist & Martensson, 1998; Fruciano, 2016). We assigned males below the population mean to the "small" group, and males above the population mean to the "large" group measured on approximately 80 experimental males.

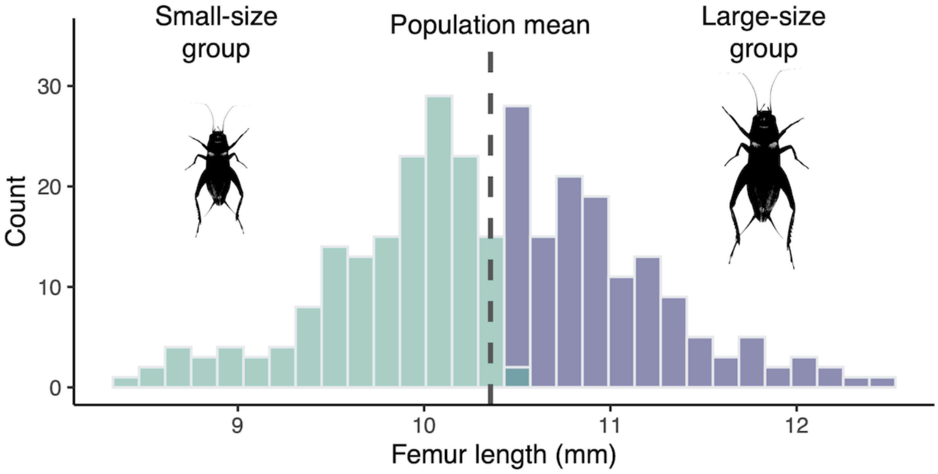

Figure 2. Distribution of the rear femur size among the 340 experimental males. As part of our experiment, males below the population mean were assigned to the "small" group, while males above the population mean were assigned to the "large" group.

Aggression assays

Aggression was assayed repeatedly using a well-established protocol (Santostefano et al., 2016, 2017a,b; Han et al., 2018; Jäger et al., 2019). Briefly, males were first marked with non-toxic acrylic paint one day prior to their first aggression assay. To begin an assay, we placed a focal male and an opponent male (arbitrarily assigned) in the centre of an arena (14.5 × 15.5 × 9 cm^3). We allowed approximately 1 min for acclimation, and recorded the interaction for five minutes using a high-resolution digital video camera (Basler GenICam, Germany) at a distance of 43 cm above the arena, and set at 25 frames/s and 1600 × 1200 pixels resolution. Males generally rapidly engage in agonistic displays that often escalate into fights (Adamo & Hoy, 1995; Hofmann & Stevenson, 2000). After each test, males were returned to their original individual containers.

Over the course of the experiment, each male was assayed 8 times with a "small" opponent and 8 times with a "large" opponent. While our goal was to test each male in a total of 16 times (realized mean = 12.5 times), individuals that died or lost two or more legs were removed from the experiment before completing all contests. All videos were scored using the EthoVision software (Noldus EthoVision XT 10, Noldus Information Technology). To prevent carry-over effects across assays caused by winner or loser effects, we allowed a minimum of one day before conducting repeat aggression assays on the same individuals (Han & Dingemanse, 2017; Santostefano et al., 2017b; Han et al., 2018). This interval is conservative as such effects generally disappear within 6 h after fighting (Khazraïe & Campan, 1999; Rillich & Stevenson, 2011). As a measure of aggressiveness, we used the total movement toward the opponent, which is computed in EthoVision as the total distance focal males moved relative to their opponents calculated across all video frames (Santostefano et al., 2016, 2017b). We recorded a total of 1822 dyadic interactions involving 289 males.

Statistical analysis

All analyses were performed using R (v.4.1.2; R Development Core Team, 2021). The following packages were used for general analysis and plotting: *car* (v.3.0; Fox et al., 2019), *MASS* (v.7.3; Venables & Ripley, 2002), *rstan* (v. 2.21.5; Stan Development Team, 2022), *shinystan* (v.2.6.0; Gabry & Veen, 2022), *bayesplot* (v.1.9.0; Gabry & Mahr, 2024), *ggplot2* (v.3.4.0; Wickham, 2016), and *cowplot* (v.1.1.1; Wilke, 2020).

Our aim was to estimate the main effects of focal body size (*i.e.*, size-related average behaviour), opponent body size (*i.e.*, size-related social impact) and the interaction between focal and opponent body size (*i.e.*, size-related social plasticity). Aggression was standardized, and log-transformed to approach normality. The model was fitted in *rstan* using common regularizing priors for all model parameters, assuming normal distributions of mean 0 and standard deviation of 1. Priors for standard deviations and variances followed a half–normal probability function. All correlations were assigned a Lewandowski-Kurowicka-Joe (LKJ) prior with shape parameter 1, which specifies a uniform probability density function bounded between −1 and 1 (Lewandowski et al., 2009). The model was fitted with 4 chains, a warmup of 2000 iterations, 4000 sampling iterations, and a thinning interval set to one. Visual inspection of plots of posterior distributions versus fitted values using the *shinystan* interface revealed satisfactory fit.

The model was fitted with focal ($A_{D,i}$), opponent ($A_{S,j}$) and dyad ($Dyad_{i,j}$) identity as random effects (Equation 1), and random slopes for focal identity (ψ_i) as a function of opponent size group Z_j (small or large). For measurement *k* of focal individual *i* interacting with individual j, focal aggression Y was modelled as:

$$Y_{ijk} = \mu + A_{D,i} + \beta_1 Z_i + (\bar{\psi} + \psi_i) Z_j + \beta_2 Z_i Z_j + A_{S,j} + Dyad_{i,j} + e_{ijk} \tag{1}$$

Where μ represents the population average aggression, β_1 the fixed effect of focal size group Z_i (coded as small or large), $\bar{\psi}$ the population-level social responsiveness to social partner size , β_2 the fixed interaction effect between focal and partner size, and e_{ijk} the residual error. Prior model checks revealed that the residual variance varied as a function of opponent size (see Table S2), and we thus modelled heteroskedasticity by allowing the residual variance to depend on opponent size: $e_{ijk} \sim \mathcal{N}(0, \sqrt{e^{\mu_e + \beta_e Z_j}})$, where μ_e is the residual variance in the average social environment, and β_e the difference in between-social-environment variance across the two size groups.

Results

Size-driven average behaviour, social responsiveness, and social impact

We detected strong evidence for size effects on average level of aggression, social responsiveness, and social impact (Table 1; Fig. 3). Small and large animals differed in both their average aggression and level of social responsiveness: large individuals were on average more aggressive (positive effect of "focal size"; Table 1, Fig. 3) and reduced their aggression less strongly with opponent size (positive effect of focal × opponent size; Table 1, Fig. 3). Thus, body size mediated the magnitude of social responsiveness. Meanwhile there was a negative main effect of opponent size on focal aggression (Table 1; Fig. 3), indicating that larger opponents overall supressed aggression in focal individuals. Thus, body size also mediated the magnitude of social impact.

Table 1: Median estimates (± 95% CI) of the main effects on focal aggression.

	Estimate (log)	Estimate (back-transformed)
Fixed effects (β)[1]		
Intercept (μ)	0.008 (–0.043, 0.062)	0.141 (0.130, 0.143)
Focal size (β_1)	0.117 (0.046, 0.189)	0.004 (0.001, 0.006)
Opponent size ($\bar{\psi}$)	–0.253 (–0.322, –0.185)	–0.008 (–0.010, –0.006)
Focal × opponent size (β_2)	0.130 (0.004, 0.255)	—

[1] Focal size measures size-related average behaviour, opponent size measures size-related impact, focal × opponent size measures size-related social responsiveness.

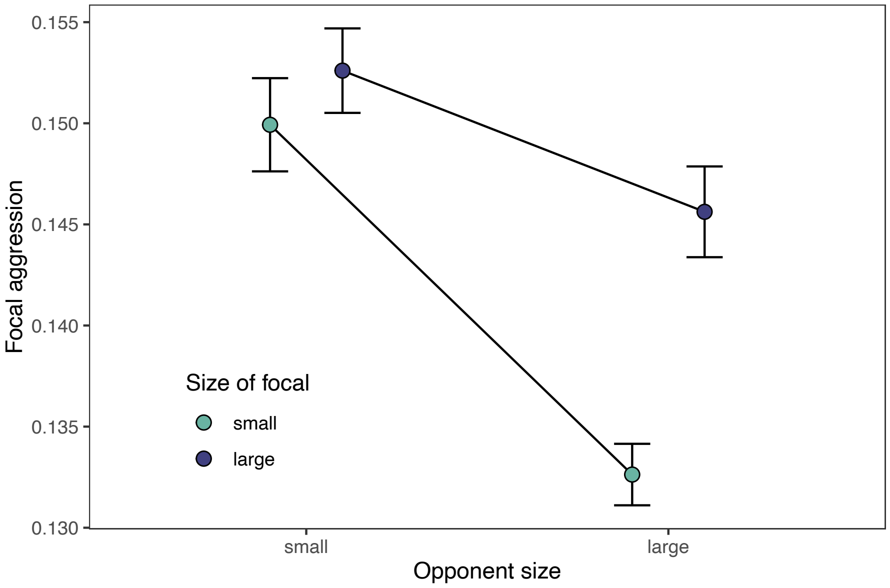

Figure 3. Large males were on average more aggressive, more socially impactful, and less responsive to opponent body size. Circles and error bars indicate means ± standard errors. Data are based on 1822 dyadic interactions involving 289 males.

Discussion

We have shown that body size affects all three major components of contest behaviour: average aggression, social impact, and social responsiveness. Specifically, small individuals were less aggressive, less impactful, but more responsive to size differences in opponents compared to large individuals. Overall, our findings indicate that body size can constrain the expression, and plausibly evolution, of flexible social behaviours.

Our findings that focal body size mediates all three components (*i.e.* average aggression, social impact, and social responsiveness) highlight the plurality of roles that size can play in social interactions. The level of aggression and the magnitude of the impact on conspecifics were greater in large males, whereas responsiveness was greater in small males. The association between size and average aggression is expected given that larger males, which are typically stronger competitors (Shackleton et al., 2005; Reaney et al., 2011), should benefit from maintaining high levels of aggression to assert dominance (Dixon & Cade, 1986; Simmons, 1986). Likewise, the association between size and impact is expected given that large males should supress aggression in their competitors, as these competitors should retreat and avoid escalating a contest when the likely to win is relatively low (Rillich et al. 2007). Importantly, this association between size and impact implies that variance attributable to differences among social partners, and potentially to indirect genetic effects (IGEs), can be shaped by its body size. Yet body size in insects is subject to developmental plasticity, being largely determined by resource acquisition during juvenile development (Edgar, 2006; Mirth et al., 2007; Chown & Gaston, 2010). Thus, genes influencing resource acquisition and allocation during juvenile development might play a predominant role in driving indirect genetic effects during social interactions. To our knowledge, this perspective is yet to be considered, and we encourage future work testing possible genetic links between juvenile growth and social impact in interacting adults.

Large focal individuals showed a weaker response to variation in their opponents' size, and were thus less socially responsive than small individuals. This finding demonstrates that body size not only influences aggression in agonistic interactions but also shapes how interacting individuals adjust their own behaviour to others. It further raises the question as to why body size influences the level of responsiveness in social interactions. One reason to expect responsiveness to decrease with body size is because males larger that the population mean are statistically more likely to encounter smaller rivals and win fights (Simmons, 1986; Shackleton et al., 2005; Reaney et al., 2011). Given their higher probability of success, large males may benefit from maintaining high aggression toward any rivals, as predicted by game theory (*e.g.*, Phillips et al., 2018; Fouilloux et al., 2022). In contrast, small males, who are more likely to lose contests, may gain by finely tuning their behaviour to the phenotype of their opponents, avoiding the costs of escalated fights with stronger competitors while still exploiting opportunities to win against weaker ones. More generally, the coexistence of socially responsive and unresponsive strategies within a population is predicted by game theory (Wolf et al., 2008, 2011) and reflects commonly observed patterns in natural populations (*e.g.*, Araya-Ajoy & Dingemanse, 2017; Montiglio et al., 2017; Perez et al., 2019). While responsiveness might be maintained as a mechanism to adaptively adjust behaviour in aggressive disputes (Tello-Ramos et al., 2019; Wolf et al., 2008), behavioural consistency can be an alternative successful strategy. This can be the case, for example, when individuals gain information about conspecifics by monitoring their interactions with others and where behavioural consistency could therefore reduce the occurrence of extended fights (Dall et al., 2004; Schuett et al., 2010).

To our knowledge, only a handful of studies have examined such links between an average social behaviour and its associated *impact on* and *responsiveness to* others. In mice, highly aggressive males are less responsive, reducing less their aggression toward females compared with less aggressive males (Benus et al., 1990; Caramaschi et al., 2008; Natarajan et al., 2009). Meanwhile, in agamid lizards, individuals that are more responsive to changes in population density are more likely to form social associations (Strickland et al., 2021). From an evolutionary perspective, our findings suggest that variation in key traits mediating social interactions, such as body size, could help maintain multiple aggression–impact–responsiveness strategies in populations, provided that alternative strategies yield comparable selective advantages. Such size dependence of social impact and social responsiveness also implies that indirect genetic effects (IGEs) could exert stronger or weaker evolutionary effects, either accelerating or constraining responses to selection (Wolf et al., 1998; McAdam et al., 2014), depending on the phenotypic composition of the group. For example, IGEs may have a stronger influence on the expression and evolution of aggression in populations composed of predominantly smaller individuals. As with other environmentally dependent traits (Postma & van Noordwijk, 2005; Nussey et al., 2007), these findings suggest that group composition could alter heritability, the ratio of genetic to phenotypic variance (Falconer & Mackay, 1996), thereby increasing or reducing the evolutionary potential of interacting phenotypes (Bijma & Wade, 2008). There is now a pressing need for empirical research to test these evolutionary implications. Quantitative genetic studies adopting a multivariate perspective on interacting phenotypes are particularly promising to tackle this gap as they allow quantifying the genetic (co)variances underlying social traits. Such work will be crucial to identify genetic associations that may constrain or promote social evolution (Figure S1).

It is becoming clear that two distinct mechanisms, social impact and social responsiveness, cause plastic responses during social interactions, and that underlying correlations have the potential to shape the evolutionary trajectory of interacting phenotypes (Araya-Ajoy et al., 2020; de Groot et al., 2023). Using a reaction norm framework, we show that these components covary with body size, a key morphological trait mediating social interactions. These findings imply that social effects, and IGEs, can themselves be plastic and shaped by the social environment. This is an important and unsuspected property of social interactions and their evolutionary consequences which merits further investigation. If the association between body size and the social behaviour has a genetic basis, selection on one will also drive evolutionary change in the other, as expected for any pair of genetically correlated traits (Lande, 1979; Lande & Arnold, 1983; Walsh & Blows, 2009). Social interactions are central to many processes that drive the evolution of both social and non-social traits. Our study highlights the importance of considering the multivariate nature of traits mediating social interactions. We suggest that the reaction norm approach provides a useful framework to explore phenotypic plasticity in the social context, opening up novel and exciting directions in the study of social evolution.

Acknowledgements

We thank Magdalena Matzke for the collection of crickets from the wild, Yvonne Cämmerer and Cristina Tuni for assistance with maintaining the populations. We also thank Yimen Araya-Ajoy, Barbara Class, Francesca Santostefano, and Jonathan Wright for fruitful discussions and suggestions. TR was funded by an Alexander von Humboldt Fellowship (3.3-FRA-1217005-HFST-P), NJD, CdG, RW by the German Science Foundation (DI 1694/1-2, DI 1694/5-1).

Data and code availability

https://osf.io/jgrez

Conflict of interest

We declare no conflicts of interest.

References

Adamo, S.A., & Hoy, R. R. (1995). Agonistic behaviour in male and female field crickets, *Gryllus bimaculatus*, and how behavioural context influences its expression. *Animal Behaviour*, 49, 1491–1501.

Akçay, E., Van Cleve, J., Feldman, M. W. & Roughgarden, J. (2009). A theory for the evolution of other-regard integrating proximate and ultimate perspectives. *Proceedings of the National Academy of Sciences*, 106, 19061–19066.

Akçay, E., & Van Cleve, J. (2012). Behavioral responses in structured populations pave the way to group optimality. *American Naturalist*, 179, 257–269.

André, J.B. (2015). Contingency in the evolutionary emergence of reciprocal cooperation. *American Naturalist*, 185, 303–316.

André, J.B., & Day, T. (2007). Perfect reciprocity is the only evolutionarily stable strategy in the continuous iterated prisoner's dilemma. *Journal of Theoretical Biology*, 247, 11–22.

Araya-Ajoy, Y. G., & Dingemanse, N. J. (2017). Repeatability, heritability, and age-dependence of seasonal plasticity in aggressiveness in a wild passerine bird. *Journal of Animal Ecology*, 86, 227–238.

Araya-Ajoy, Y. G., Westneat, D. F., & Wright, J. (2020). Pathways to social evolution and their evolutionary feedbacks. *Evolution*, 74, 1894–1907.

Arnqvist, G., & Martensson, T. (1998). Measurement error in geometric morphometrics: empirical strategies to assess and reduce its impact on measures of shape. *Acta Zoologica Academiae Scientiarum Hungaricae*, 44, 73–96.

Bailey, N. W., Desjonquères, C., Drago, A., Rayner, J. G., Sturiale, S. L., & Zhang, X. (2021). A neglected conceptual problem regarding phenotypic plasticity's role in adaptive evolution: The importance of genetic covariance and social drive. *Evolution Letters*, 5, 444–457.

Bailey, N. W., & Desjonquères, C. (2022). The indirect genetic effect interaction coefficient ψ: theoretically essential and empirically neglected. *Journal of Heredity*, 113, 79–90.

Bailey, N. W., & Zuk, M. (2012). Socially flexible female choice differs among populations of the Pacific field cricket: geographical variation in the interaction coefficient psi (ψ). *Proceedings of the Royal Society B: Biological Sciences*, 279, 3589–3596.

Benus, R. F., Bohus, B., Koolhaas, J. M., & Van Oortmerssen, G. A. (1991). Heritable variation for aggression as a reflection of individual coping strategies. *Experientia*, 47, 1008–1019.

Benus, R.F., Den Daas, S., Koolhaas, J.M., & Van Oortmerssen, G.A. (1990). Routine formation and flexibility in social and non-social behaviour of aggressive and non-aggressive male mice. *Behaviour*, 112, 176–193.

Bijma, P. (2014). The quantitative genetics of indirect genetic effects: a selective review of modelling issues. *Heredity*, 112, 61–69.

Bijma, P., & Wade, M.J. (2008). The joint effects of kin, multilevel selection and indirect genetic effects on response to genetic selection. *Journal of Evolutionary Biology*, 21, 1175–1188.

Bleakley, B. H., & Brodie III, E. D. (2009). Indirect genetic effects influence antipredator behavior in guppies: estimates of the coefficient of interaction psi and the inheritance of reciprocity. *Evolution*, 63, 1796–1806.

Bleakley, B. H., Wolf, J. B., & Moore, A. J. (2010). The quantitative genetics of social behaviour. In T. Székely, A. J. Moore, & J. Komdeur (Eds.), *Social Behaviour: Genes, Ecology and Evolution* (pp. 29–54). Cambridge University Press, Cambridge.

Briffa, M. (2015). Agonistic signals: integrating analysis of functions and mechanisms. In D. J. Irschick, M. Briffa, & J. Podos (Eds.), *Animal signaling and function, an integrative approach* (pp. 141–173). Wiley, Hoboken.

Caramaschi, D., de Boer, S.F., de Vries, H., & Koolhaas, J.M. (2008). Development of violence in mice through repeated victory along with changes in prefrontal cortex neurochemistry. *Behavioural Brain Research*, 189, 263–272.

Chenoweth, S. F., Rundle, H. D., & Blows, M. W. (2010). Experimental evidence for the evolution of indirect genetic effects: changes in the interaction effect coefficient, psi (ψ), due to sexual selection. *Evolution*, 64, 1849–1856.

Cheverud, J.M. (1988). A comparison of genetic and phenotypic correlations. *Evolution*, 42, 958–968.

Chown, S. L., & Gaston, K.J. (2010). Body size variation in insects: a macroecological perspective. *Biological Reviews*, 85, 139–169.

Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology letters*, 7, 734–739.

Dingemanse, N. J., & Araya-Ajoy, Y.G. (2015). Interacting personalities: behavioural ecology meets quantitative genetics. *Trends in Ecology & Evolution*, 30, 88–97.

Dixon, K. A., & Cade, W. H. (1986). Some factors influencing male-male aggression in the field cricket *Gryllus integer* (time of day, age, weight and sexual maturity). *Animal Behaviour*, 34, 340–346.

Dochtermann, N.A., Schwab, T., Anderson Berdal, M., Dalos, J., & Royauté, R. (2019). The heritability of behavior: a meta-analysis. *Journal of Heredity*, 110, 403–410.

Dochtermann, N.A., Schwab, T., & Sih, A. (2015). The contribution of additive genetic variation to personality variation: heritability of personality. *Proceedings of the Royal Society B: Biological Sciences*, 282, p.20142201.

Duckworth, R. A., & Kruuk, L. E. (2009). Evolution of genetic integration between dispersal and colonization ability in a bird. *Evolution*, 63, 968–977.

Edgar, B.A. (2006). How flies get their size: genetics meets physiology. *Nature Reviews Genetics*, 7, 907–916.

Edwards, A. C., Rollmann, S. M., Morgan, T. J., & Mackay, T. F. C. (2006). Quantitative genomics of aggressive behavior in *Drosophila melanogaster*. *PLoS Genetics*, 2, p.e154.

Falconer, D. S., & Mackay, T. F. C. (1996). *Introduction to Quantitative Genetics*, 4th ed. Pearson Education Limited, Essex.

Fouilloux, C.A., Fromhage, L., Valkonen, J.K., & Rojas, B. (2022). Size-dependent aggression towards kin in a cannibalistic species. *Behavioral Ecology*, 33, 582–591.

Fox, J., & Weisberg, S. (2019). *An {R} companion to applied regression.* 3rd edition. Thousand Oaks, Sage.

Frank, S. A. (2007). All of life is social. *Current Biology*, 17, R648–R650.

Fruciano, C. (2016). Measurement error in geometric morphometrics. *Development Genes and Evolution*, 226, 139–158.

Gabry, J., & Mahr, T. (2024). bayesplot: Plotting for Bayesian Models. *R package version 1.11.1*, https://mc-stan.org/bayesplot/

Gabry, J., & Veen, D. (2022). shinystan: interactive visual and numerical diagnostics and posterior analysis for bayesian models. *R package version 2.6.0.* https://CRAN.R-project.org/package=shinystan

Gammell, M. P., & Hardy, I. C. (2003). Contest duration: sizing up the opposition?. *Trends in Ecology & Evolution*, 18, 491–493.

de Groot, C., Wijnhorst, R. E., Ratz, T., Murray, M., Araya-Ajoy, Y. G., Wright, J., & Dingemanse, N. J. (2023). The importance of distinguishing individual differences in ‘social impact’ versus ‘social responsiveness’ when quantifying indirect genetic effects on the evolution of social plasticity. *Neuroscience & Biobehavioral Reviews*, 144, p.104996.

Han, C.S., & Dingemanse, N.J. (2017). Sex-dependent expression of behavioural genetic architectures and the evolution of sexual dimorphism. *Proceedings of the Royal Society B: Biological Sciences*, 284, p.20171658.

Han, C. S., Tuni, C., Ulcik, J., & Dingemanse, N. J. (2018). Increased developmental density decreases the magnitude of indirect genetic effects expressed during agonistic interactions in an insect. *Evolution*, 72, 2435–2448.

Hofmann, H. A., & Stevenson, P. A. (2000). Flight restores fight in crickets. *Nature*, 403, 613–613.

Jäger, H.Y., Han, C.S. & Dingemanse, N.J. (2019). Social experiences shape behavioral individuality and within-individual stability. *Behavioral Ecology*, 30, 1012–1019.

Kent, C., Azanchi, R., Smith, B., Formosa, A., & Levine, J.D. (2008). Social context influences chemical communication in *D. melanogaster* males. *Current Biology*, 18, 1384–1389.

Kessler, S., Elliott, G. R., Orenberg, E.K., & Barchas, J. D. (1977). A genetic analysis of aggressive behavior in two strains of mice. *Behavior Genetics*, 7, 313–321.

Khazraïe, K. and Campan, M. (1999). The role of prior agonistic experience in dominance relationships in male crickets *Gryllus bimaculatus* (Orthoptera: Gryllidae). *Behavioural Processes*, 44, 341–348.

Lande, R. (1979). Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. *Evolution*. 33:42–416.

Lande, R., & Arnold, S.J. (1983). The measurement of selection on correlated characters. *Evolution*, 37, 1210–1226.

Lewandowski, D., Kurowicka, D., & Joe, H. (2009) Generating random correlation matrices based on vines and extended onion method. *Journal of Multivariate Analysis*, 100, 1989–2001.

Lynch, M., & Walsh, B. (1998). *Genetics and Analysis of Quantitative Traits*. Sunderland, MA : Sinauer Associates.

Maynard Smith, J. (1982). *Evolution and the theory of games*. Cambridge University Press, Cambridge.

McAdam, A.G., & Boutin, S. (2004). Maternal effects and the response to selection in red squirrels. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271, 75–79.

McAdam, A.G., Garant, D., & Wilson, A.J. (2014). The effects of others’ genes: maternal and other indirect genetic effects. In: A. Charmantier, D. Garant, & L. E. B. Kruuk (Eds.), *Quantitative genetics in the wild*. Oxford University Press.

McGlothlin, J.W., Moore, A.J., Wolf, J.B., & Brodie III, E.D. (2010). Interacting phenotypes and the evolutionary process. III. Social evolution. *Evolution*, 64, 2558–2574.

McNamara, J.M., & Leimar, O. (2020). *Game theory in biology: concepts and frontiers*. Oxford University Press, USA.

Mirth, C.K., & Riddiford, L.M. (2007). Size assessment and growth control: how adult size is determined in insects. *Bioessays*, 29, 344–355.

Montiglio, P.O., Wey, T.W., Chang, A.T., Fogarty, S., & Sih, A. (2017). Correlational selection on personality and social plasticity: morphology and social context determine behavioural effects on mating success. *Journal of Animal Ecology*, 86, 213–226.

Moore, A.J., Brodie III, E.D., & Wolf, J.N. (1997). Interacting phenotypes and the evolutionary process: I. Direct and indirect genetic effects of social interactions. *Evolution*, 51, 1352–1362.

Mousseau, T.A., & Roff, D.A. (1989). Adaptation to seasonality in a cricket: patterns of phenotypic and genotypic variation in body size and diapause expression along a cline in season length. *Evolution*, 43, 1483–1496.

Natarajan D, de Vries H, Saaltink, D.J., de Boer, S.F., & Koolhaas, J.M. (2009). Delineation of violence from functional aggression in mice: an ethological approach. *Behavior Genetics*, 39, 73–90

Nosil, P. (2002). Food fights in house crickets, *Acheta domesticus*, and the effects of body size and hunger level. *Canadian Journal of Zoology*, 80, 409–417.

Nussey, D.H., Wilson, A.J., & Brommer, J. (2007). The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of Evolutionary Biology*, 20, 831–844.

Parker, G.A. (1974). Assessment strategy and the evolution of fighting behaviour. *Journal of Theoretical Biology*, 47, 223–243.

Perez, A., Montiglio, P.O., Wey, T.W., & Sih, A. (2019). Male social plasticity influences transient dynamics in the emergence of alternative mating systems in water striders. *Behavioral Ecology*, 30, 1530–1538.

Phillips, J.A., Peacock, S.J., Bateman, A., Bartlett, M., Lewis, M.A., & Krkošek, M. (2018). An asymmetric producer-scrounger game: body size and the social foraging behavior of coho salmon. *Theoretical Ecology*, 11, 417–431.

Postma, E., & van Noordwijk, A. J. (2005). Genetic variation for clutch size in natural populations of birds from a reaction norm perspective. *Ecology*, 86, 2344–2357.

R Core Team. (2021). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. http://www.R-project.org

Ratz, T., Chechi, T. S., Dimopoulou, A. I., Sedlmair, S. D., & Tuni, C. (2024). Heatwaves inflict reproductive but not survival costs to male insects. *Journal of Experimental Biology*, 227, p.jeb246698.

Réale, D., Dingemanse, N. J., Kazem, A. J. N., & Wright, J. (2010). Evolutionary and ecological approaches to the study of personality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 3937–3946.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82, 291–318.

Reaney, L.T., Drayton, J.M., & Jennions, M.D., 2011. The role of body size and fighting experience in predicting contest behaviour in the black field cricket, *Teleogryllus commodus*. *Behavioral Ecology and Sociobiology*, 65, 217–225.

Rillich, J., Schildberger, K. and Stevenson, P.A. (2007). Assessment strategy of fighting crickets revealed by manipulating information exchange. *Animal Behaviour*, 74, 823–836.

Rillich, J., & Stevenson, P.A. (2011). Winning fights induces hyperaggression via the action of the biogenic amine octopamine in crickets. *PLoS One*, 6, p.e28891.

Santostefano, F., Moiron, M., Sánchez-Tójar, A., & Fisher, D.N. (2025). Indirect genetic effects increase the heritable variation available to selection and are largest for behaviors: a meta-analysis. *Evolution Letters*, 9, 89–104.

Santostefano, F., Wilson, A.J., Araya-Ajoy, Y.G., & Dingemanse, N.J. (2016). Interacting with the enemy: indirect effects of personality on conspecific aggression in crickets. *Behavioral Ecology*, 27, 1235–1246.

Santostefano, F., Wilson, A.J., Niemelä, P.T., & Dingemanse, N.J. (2017a). Behavioural mediators of genetic life-history trade-offs: a test of the pace-of-life syndrome hypothesis in field crickets. *Proceedings of the Royal Society B: Biological Sciences*, 284, p.20171567.

Santostefano, F., Wilson, A.J., Niemelä, P.T., & Dingemanse, N.J. (2017b). Indirect genetic effects: a key component of the genetic architecture of behaviour. *Scientific Reports*, 7, p1–9.

Schuett, W., Tregenza, T., & Dall, S.R.X. (2010). Sexual selection and animal personality. *Biological Reviews*, 85, 217–246.

Shackleton, M.A., Jennions, M.D., & Hunt, J. (2005). Fighting success and attractiveness as predictors of male mating success in the black field cricket, *Teleogryllus commodus*: the effectiveness of no-choice tests. *Behavioral Ecology & Sociobiology*, 58, 1–8.

Sih, A., Bell, A. M., & Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19, 372–378.

Simmons, L.W. (1986). Inter-male competition and mating success in the field cricket, *Gryllus bimaculatus* (De Geer). *Animal Behaviour*, 34, 567–579.

Stan Development Team. (2022). RStan: the R interface to Stan. *R package version 2.21.5*. https://mc-stan.org

Stirling, D.G., Réale, D., & Roff, D.A. (2002). Selection, structure and the heritability of behaviour. *Journal of Evolutionary Biology*, 15, 277–289.

Strickland, K., Mitchell, D.J., Delmé, C., & Frère, C.H. (2021). Repeatability and heritability of social reaction norms in a wild agamid lizard. *Evolution*, 75, 1953–1965.

Tello-Ramos, M.C., Branch, C.L., Kozlovsky, D.Y., Pitera, A.M., & Pravosudov, V.V. (2019). Spatial memory and cognitive flexibility trade-offs: to be or not to be flexible, that is the question. *Animal Behaviour*, 147, 129–136.

Trivers, R. (1985). *Social evolution*. Benjamin Cummings, Menlo Park.

Van Cleve, J., & Akçay, E. (2014). Pathways to social evolution: reciprocity, relatedness, and synergy. *Evolution*, 68, 2245–2258.

Venables, W.N., & Ripley, B.D. (2002). *Modern applied statistics with S*. 4th edition. Springer, New York.

Verbeek, M.E., Boon, A., & Drent, P.J. (1996). Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour*, 133, 945–963.

Walsh, B., & Blows, M.W. (2009). Abundant genetic variation + strong selection = multivariate genetic constraints: a geometric view of adaptation. *Annual Review of Ecology, Evolution, & Systematics*, 40, 41–59.

Westneat, D., & Fox, C.W. (2010). *Evolutionary behavioral ecology*. Oxford University Press.

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer, New York.

Wijnhorst, R.E., de Groot, C., Ajoy, Y.G.A., Wright, J., & Dingemanse, N.J. (2025). Decomposing social interactions: a statistical method for estimating social impact and social responsiveness. *EcoEvoRxiv*, https://doi.org/10.32942/X2F65M.

Wilke, C.O. (2020). cowplot: streamlined plot theme and plot annotations for ‘ggplot2’. *R package version 1.1.1*. https://CRAN.R-project.org/package=cowplot

Wilson, A.J., Gelin, U., Perron, M.C., & Réale, D. (2009). Indirect genetic effects and the evolution of aggression in a vertebrate system. *Proceedings of the Royal Society B: Biological Sciences*, 276, 533541.

Wilson, A.J., Morrissey, M.B., Adams, M.J., Walling, C.A., Guinness, F.E., Pemberton, J.M., Clutton-Brock, T.H., & Kruuk, L.E.B. (2011). Indirect genetics effects and evolutionary constraint: an analysis of social dominance in red deer, *Cervus elaphus*. *Journal of Evolutionary Biology*, 24, 772–783.

Wolf, J.B., Brodie III, E.D., Cheverud, J. M., A. J. Moore, & Wade, M. J. (1998). Evolutionary consequences of indirect genetic effects. *Trends in Ecology & Evolution*, 13, 64–69.

Wolf, M., Van Doorn, G.S., Weissing, F.J. (2008). Evolutionary emergence of responsive and unresponsive personalities. *Proceedings of the National Academy of Sciences*, 105, 15825–15830.

Wolf, M., Van Doorn, G.S., Weissing, F.J. (2011). On the coevolution of social responsiveness and behavioural consistency. *Proceedings of the Royal Society B: Biological Sciences*, 278, 440–448.