Cannibalism as an interacting phenotype: precannibalistic aggression is influenced by social partners in the endangered Socorro Isopod (*Thermosphaeroma thermophilum*)

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Abstract

Models for the evolution of cannibalism highlight the importance of asymmetries between individuals in initiating cannibalistic attacks. Studies may include measures of body size but typically group individuals into size/age classes or compare populations. Such broad comparisons may obscure the details of interactions that ultimately determine how socially contingent characteristics evolve. We propose that understanding cannibalism is facilitated by using an interacting phenotypes perspective that includes the influences of the phenotype of a social partner on the behaviour of a focal individual and focuses on variation in individual pairwise interactions. We investigated how relative body size, a composite trait between a focal individual and its social partner, and the sex of the partners influenced precannibalistic aggression in the endangered Socorro isopod, *Thermosphaeroma thermophilum*. We also investigated whether differences in mating interest among males and females influenced cannibalism in mixed sex pairs. We studied these questions in three populations that differ markedly in range of body size and opportunities for interactions among individuals. We found that relative body size influences the probability of and latency to attack. We observed differences in the likelihood of and latency to attack based on both an individual's sex and the sex of its partner but found no evidence of sexual conflict. The instigation of precannibalistic aggression in these isopods is therefore a property of both an individual and its social partner. Our results suggest that interacting phenotype models would be improved by incorporating a new conditional ψ, which describes the strength of a social partner's influence on focal behaviour.

Introduction

The causes and consequences of cannibalism, defined as the killing and ingestion of a conspecific (Polis, 1981; Elgar & Crespi, 1992), have long been the foci of evolutionary and applied studies of behaviour. Cannibalism attracts attention because it often evolves rapidly, may differ markedly between populations, and may evolve in apparent opposition to the direction of selection (Shuster *et al.*, 2005; Wade *et al.*, 2010). Levels of cannibalism can vary dramatically among populations or closely related species (Michaud, 2003; Alabi *et al.*, 2008; Fedina & Lewis, 2008). Cannibalism impacts many economically important species (Muir & Craig, 1998; Baras & Jobling, 2002; Cloutier *et al.*, 2002; Wade *et al.*, 2010) and yet can be difficult to eliminate in managed populations despite considerable effort

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(Rodenburg *et al.*, 2008; Bolhuis *et al.*, 2009; Ellen *et al.*, 2010; Wade *et al.*, 2010; Turner, 2011). Community composition and organization may be influenced by the presence of cannibalism (Cohen & Newman, 1985; Woodward *et al.*, 2005; Rudolf, 2006, 2007a,b). Reciprocally, population structure influences the occurrence of cannibalism, in part because which social partners an individual encounters (whether in the role of prey or predator) will be affected by population structure (Jormalainen & Shuster, 1997; Rudolf, 2008).

Much attention has been focussed on cannibalism as a function of variation in size classes within cohorts, as well as the ontogeny of cannibalism as variation within and among size classes increases (Crowley & Hopper, 1994; Folkvord, 1997; Van den Bosch & Gabriel, 1997; Claessen *et al.*, 2004; Rudolf, 2007a; Wissinger *et al.*, 2010; Reglero *et al.*, 2011). For example, cannibalism in many species of hatchery-reared fish begins when differences in individual growth rates generate variation in size (Cushing, 1992; Fagan & Odell, 1996; Persson *et al.*, 2000; Baras & Jobling, 2002). Similarly, populations are compared by looking for correlations between the coincidence of cannibalism and variance in body size (Huss *et al.*, 2010). These perspectives focus on variation within and among groups, rather than on individual interactions.

In contrast to population models of cannibalism, quantitative genetic models of cannibalism can use trait-based approaches (Bijma & Wade, 2008; McGlothlin & Brodie, 2009) to describe genetic and environmental influences on an individual's aggressive and/or cannibalistic behaviour (e.g. Stevens, 1989, 1994; Via, 1999). Traits that are expressed in social contexts and change based on the specific trait values of social partners are termed 'interacting phenotypes' (Moore *et al.*, 1997; Bleakley *et al.*, 2010; Kazancıoğlu *et al.*, 2012). The magnitude of a social partner's influence will depend both on the partner's traits and the specific response of a focal individual to those traits and is measured by the coefficient of the interaction, ψ (Wolf *et al.*, 1999; Bleakley & Brodie, 2009; Bleakley *et al.*, 2010). Cannibalism is a quintessential interacting phenotype, as it both requires a social interaction to be expressed and the level of expression is expected to depend on traits in a specific social partner, such as size or aggression. Interacting phenotype theory therefore predicts that variation among social partners and social interactions will shape the evolution of cannibalism. Yet, outside of livestock (Rodenburg *et al.*, 2008; Bolhuis *et al.*, 2009; Ellen *et al.*, 2010; Wade *et al.*, 2010; Turner, 2011), relatively few studies have applied a trait-based approach to understand the role that specific social partners play in shaping the instigation of cannibalistic interactions.

Aggression leading to cannibalism is predicted in circumstances where animals exhibit asymmetries in risk (Fox, 1975; Smith, 1979; Polis, 1981), with larger individuals expected to attack smaller individuals more often. For example, size-related risk has been well studied for sexual cannibalism where females eat comparatively smaller males (Elgar, 1991; Elgar & Jones, 2008; Wilder & Rypstra, 2008). However, asymmetry in other traits such as age, body condition or aggression may also influence attacks (Polis, 1981; Claessen *et al.*, 2004; Kralj-Fišer *et al.*, 2012). Even in size-asymmetrical systems, the absolute body size of a social partner is unlikely to be the only salient cue for instigating a cannibalistic attack. Few data outside of those for sexual cannibalism are available to evaluate potential specific interactions between characteristics of the focal individual and its social partner in generating aggression and cannibalism and little remains known about how sometimes subtle differences between partners can yield different behavioural outcomes.

In this study, we adopt an experimental approach informed by the interacting phenotype perspective to investigate how specific individual pairwise interactions, rather than averages or population measures, influence cannibalism in the endangered freshwater Socorro Isopod (*Thermosphaeroma thermophilum*). This allows us to relate our work to formal evolutionary theory for how socially contingent traits, traits whose expression depend on the specific trait values of social partners, may evolve, as has been so successfully done in applied livestock breeding programs (Rodenburg *et al.*, 2008; Bolhuis *et al.*, 2009; Ellen *et al.*, 2010; Wade *et al.*, 2010; Turner, 2011). We measured the effects of relative body size, which provides a composite of focal and partner traits, and sex on the instigation of precannibalistic attacks. We then compare the results across three populations that differ substantially in ranges of body size and population structure. On the basis of previous observations (Jormalainen & Shuster, 1997), we predicted that isopods from two man-made pools, which have larger mean body size as well as a much greater variance in body size producing the largest asymmetries, would be more likely to attack in all conspecific interactions. Following previous theoretical work (Jormalainen & Shuster, 1999; Moore & Pizzari, 2005), we predicted that males, which are substantially larger than females, would be more likely to attack than females. We also investigated whether potential conflict in interest between males and females over mate guarding influenced the likelihood of attack in those pairs, predicting that conflict would lead to increased aggression associated with cannibalism.

Materials and methods

Study species

Thermosphaeroma thermophilum (Fig. 1; Crustacea: Isopoda: Sphaeromatidae; Cole & Bane, 1978) inhabit a single thermal spring in Socorro, NM, USA (Shuster,

Fig. 1 Shows a *Thermosphaeroma thermophilum* male from the North-3 population. Scale is in mm.

Table 1 Differences in variance in body size for males and females from three populations of Socorro isopods and among relative body size for the three populations at $\alpha = 0.05$. Upper and lower decision lines (DL) are indicated for rejecting equality of means. Mean standard error for females was 0.622 and mean standard error for males was 2.113.

Sex	Population	Lower DL	Variance	Upper DL	Exceeds limit
Female	N3	0.465	0.879	0.794	Upper
	S1	0.490	0.584	0.761	NS
	Sedillo	0.477	0.440	0.778	Lower
Male	N3	1.438	2.790	2.868	NS
	S1	1.559	2.830	2.699	Upper
	Sedillo	1.493	0.677	2.789	Lower
Relative body size	N3	2.258	2.783	2.786	NS
	S1	2.306	2.993	2.736	Upper
	Sedillo	2.281	1.489	2.762	Lower

1981a). The isopods are listed as an IUCN endangered species (Inland Water Crustacean Specialist Group, 1996) and are managed within their native spring as well as in a set of eight manmade pools as part of the Socorro Isopod Propagation Facility (SIPF) outside of Socorro, NM. The manmade pools are segregated into North (N) and South (S) series that allow some level of gene flow within each series but little or no gene flow between the two series and no natural gene flow with the native spring. In addition, the pools have been populated for various lengths of time, as the pools have occasionally gone extinct and have been repopulated from the native spring (Inland Water Crustacean Specialist Group, 1996; Shuster *et al.*, 2005).

Socorro isopods engage in cannibalistic interactions that appear to be structured by size (Jormalainen & Shuster, 1997). Males and females display sexual size dimorphism, with males achieving larger size in all populations. However, variation in body size is much greater in the manmade pools, with females slightly enlarged compared to the females in the native spring and males exhibiting extreme variance in body size resulting from some males attaining extremely large body size (Table 1; Jormalainen & Shuster, 1997; Shuster *et al.*, 2005). In addition, mean body size increased rapidly in the manmade pools, consistent with strong social selection favouring large body size through cannibalistic interactions (Shuster *et al.*, 2005). As these isopods breed throughout the year and the populations are both age and size structured, substantial variation for body size can be found in each pool (Shuster, 1981a). We made use of this natural variation in body size to document aggressive interactions among individuals and applied an interacting phenotypes perspective to understand precannibalistic aggressive interactions in this endangered freshwater isopod.

Isopods were collected haphazardly using a dipnet from several locations within each of three pools: the native Sedillo spring and two of the manmade pools,

S1 and N3. All three populations are separately monitored by New Mexico Fish and Game (NMFG) and were selected for this experiment through discussion with NMFG to obtain sufficient sample sizes while also protecting all existing populations from substantial disturbance. A total of 402 animals were used: 148 from Sedillo, 108 from N3, and 146 from S1. Isopods were immediately separated into individual containers filled with water from the pool from which they were collected. Each animal was then placed briefly on ice, sexed and photographed on both dorsal and ventral sides with a size standard using a Nikon Coolpix 4500 (Nikon, Melville, NY, USA) mounted on a field dissecting scope (Fig. 1). Body size was measured at a later time using Image J (Rasband, 1997–2008) by taking length and width measurements on both dorsal and ventral sides. Each isopod was held overnight after photographing and sexing without being fed. While this ensured that the animals were hungry, all animals had food visible in their guts for the duration of the experiment and were therefore not starved.

Behavioural trials

We created pairs by assigning each individual within each population a random number and sorting the closest values into pairs. We therefore created male–male, female–female and male–female pairs, with normally distributed differences in body size (see Results). We introduced each pair into a 51 mm plastic petri-dish with 1 cm of water and filmed the isopods for up to twelve and a half minutes using a Sony DVD403 digital video recorder at 2.048 effective megapixels (Sony Electronics, Inc., San Diego, CA, USA) under natural light. We defined aggressive attacks as a movement by one individual directed at the pleopods of the social partner. Pleopods are delicate respiratory structures located on the ventral posterior aspect of sphaeromatid isopods;

attacks on these structures rapidly immobilize the victim, allowing cannibalism to proceed, and are distinct from mate-guarding attempts and nonaggressive encounters by isopods (SMS & BHB, *pers. obs.*; Brian Lang, *pers. comm.*, New Mexico Fish and Game, May 2009). Immediately upon the initiation of an attack, we separated the isopods with a gentle puff of water and moved them back into individual containers. We then gave each isopod a second randomly assigned partner from their population and allowed them to interact a second time later that day in exactly the same manner as before. We subsequently scored latency to attack, the identity of the attacker, and any occurrence of mate-guarding behaviour, defined as a male grasping a female and holding or attempting to hold her while curling around her (Shuster, 1981b) from the video. We held the animals for no more than 36 h before returning them to their pool of origin. All animals survived in good health and were released.

Statistical analysis

We performed all statistical analyses using JMP 9.0.2 (SAS Institute, 2010). We first reduced body size to a single measure using principle components analysis on correlations to combine the four measures of size taken for each individual (dorsal and ventral width and length). The first component explained 96.1% of the variance, with an eigenvalue of 3.84, and correlations between measures ranged from 0.936 to 0.980. The second principle component explained only 2.0% of the variance and had an eigenvalue less than 0.1. We therefore used the first principle component as a composite measure of body size. Relative body size for each individual was calculated as the individual's body size score minus the body size score of the social partner. Therefore, positive relative body size indicates that the focal individual was larger than its social partner, while negative relative body size indicates the focal individual was smaller than its social partner. Relative body size was normally distributed and did not require transformation.

We compared both the body size and relative body size between populations for males and females separately using an ANOVA. We then compared variances for the body sizes across the three populations separately for males and females using a Levine's test for equal variances followed by an Analysis of Means for Variances (ANOM; Nelson & Dudewicz, 2002) to visualize differences between the variances. We did not differentiate by sex for variance in relative body size because relative body size included partners of all three possible combinations.

We used a generalized linear model with a binomial distribution and a logit function to evaluate the effects of trial (first or second), population, sex, partner sex, sex*partner sex interaction and relative body size on

the likelihood of attack ($n = 802$). No effect of trial order was found and was therefore removed from the analysis ($\chi^2 = 0.480$, 1 d.f., $P = 0.4885$). We then used a contingency analysis with the subset of individuals ($n = 372$) that interacted in mixed sex pairs to determine if attempted guarding behaviour on the part of the male influenced either his propensity to attack the female or the female's propensity to attack him.

We used a linear regression to explore the influence of trial, population, sex, sex of partner, sex*partner sex interactions and relative body size on the latency to attack (Table 2, Model I). Using relative body size statistically controls for differences in mean and variance between populations for body size. To obtain estimates of the coefficient of the interaction, ψ, we also evaluated the model by breaking relative body size into its constitutive parts: the body size of an individual, the body size of its social partner, and the interactions between the two (Table 2, Model II). This second model is necessary because there is as yet no definition of ψ that allows the interacting trait to be conditional. As in the generalized linear model above, trial did not affect the latency to attack and all data were pooled for both analyses ($F_{1,624} = 0.352$, $P = 0.554$). We excluded all individuals from the analysis that were attacked and were removed from the interaction prior to initiating an attack themselves or finishing a full 12:30 minute

Table 2 Estimates of the coefficient of the interaction, ψ, which provides an estimate of the strength of the influence of the relative body size of the social partner on latency to attack. ψ is measured for females paired with female social partners, females paired with males, males paired with females and males paired with other males.

Effect	DF	F	P	$\psi \pm$ SE	$P(\psi)$
Model	6	29.766	< 0.0001		
Error	618				
Population	2	2.037	0.1313		
Sex	1	29.561	< 0.0001		
Partner sex	1	59.306	< 0.0001		
Sex * partner sex	1	96.416	< 0.0001		
Relative body size	1	5.588	0.0184	**−0.048 ± 0.020**	0.0184
Model	8	32.296	< 0.0001		
Error	616				
Population	2	5.634	0.0038		
Sex	1	7.813	0.0054		
Partner sex	1	14.466	0.0002		
Sex * partner sex	1	44.561	< 0.0001		
Focal size	1	14.836	0.0001	**−0.105 ± 0.027**	0.0001
Partner size	1	2.132	0.1448	−0.040 ± 0.028	0.1448
Partner size * focal size	1	32.533	< 0.0001	**−0.060 ± 0.011**	< 0.0001

Estimates of ψ that are statistically significant are bolded.

trial without attacking, leaving 625 observations for which we had accurate latency data.

Finally, we investigated plasticity in latency to attack for those individuals that attacked their social partners. We used linear regression to relate difference in latencies (trial 1 latency – trial 2 latency) to the difference in body size between the two social partners (body size of social partner 1 – body size of social partner 2). The initial multiple regression found a significant effect of sex ($F_{1,151} = 7.124$, $P = 0.0085$) but no effect of population ($F_{2,151} = 0.0927$, $P = 0.9274$). As a result data were pooled and the least squares linear regression of difference in latency on difference in partner body sizes was completed for all males and all females separately.

Results

Mean body size differed significantly among females in all three populations, with Sedillo females being the smallest, S1 females the largest, and N3 females intermediate but closer to S1 females than Sedillo females (see Fig. S1 in the Supporting Information; $F_{2,252} = 99.077$, $P < 0.001$, Tukey–Kramer *post hoc* test $P < 0.001$ to $P = 0.009$). Males were significantly larger in the N3 and S1 populations compared to males from the native Sedillo Spring ($F_{2,156} = 82.717$, $P < 0.001$, Tukey–Kramer *post hoc* test $P < 0.001$). However, relative body size did not vary across the populations (see Fig. S2; $F_{2,624} = 0.562$, $P = 0.572$). Variance in body size differed significantly among all three populations for both sexes (Levene test for unequal variances $F_{2,250} = 9.555$, $P < 0.001$ and $F_{2,154} = 14.925$, $P < 0.001$ for females and males respectively; Table 1). Variance structure differed between the sexes, with females from N3 greatly exceeding mean variance, S1 females matching mean variance and Sedillo females exhibiting much lower variance. Both S1 and N3 males exceeded mean variance, while males from Sedillo had markedly lower variance (ANOM, Table 1).

The population from which the isopods originated was a significant factor influencing the probability of attack. Individuals from the native spring attacked more often than individuals from the N3 or S1 pools ($\chi^2 = 11.257$, 2 d.f., $P = 0.004$). Neither the sex of focal individuals nor the sex of their social partner alone influenced whether an attack was initiated ($\chi^2 = 2.983$, 1 d.f., $P = 0.084$ and $\chi^2 = 1.550$, 1 d.f., $P = 0.213$ respectively). However, the interaction between a focal individual's sex and the sex of its partner significantly influenced attacks ($\chi^2 = 21.564$, 1 d.f., $P < 0.001$), with males attacking males and females attacking females more frequently than either attacked the opposite sex (Fig. 2). Males were not more likely to attack females they had attempted to guard than those they did not attempt to guard (Pearson's $\chi^2 = 2.045$, 1 d.f., $P = 0.153$; Fig. 3), nor were females more likely to attack males that had attempted to guard them (Pearson's $\chi^2 = 0.694$, 1 d.f., $P = 0.405$; Fig. 3).
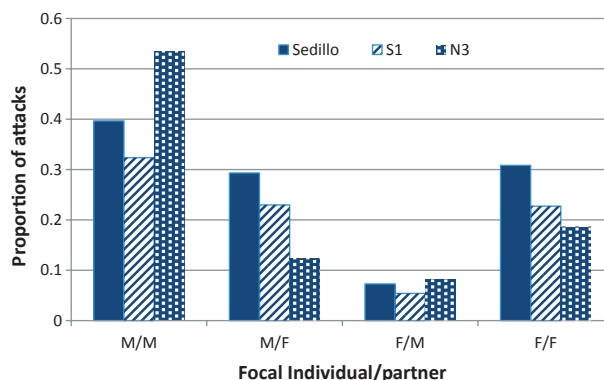

Fig. 2 Shows the proportion of individuals that initiated attacks on their social partners, broken down by population of origin and the sex of the interactants.
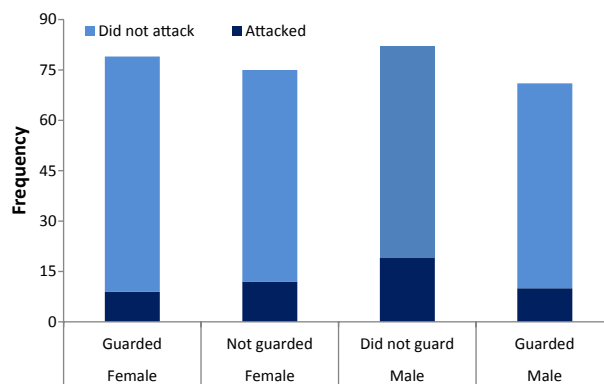

Fig. 3 Shows that guarding attempts by a male do not influence the likelihood that he will attack or be attacked by the female experiencing the guarding.

The relative body size of an individual significantly influenced the likelihood to initiate an attack ($\chi^2 = 4.326$, 1 d.f., $P = 0.038$). A *post hoc* set of *t*-tests showed no difference in the relative body size of females that attacked other females and those that did not attack ($F_{1,305} = 0.457$, $P = 0.500$); however, females that attacked males have a slightly larger relative body size than those who did not attack males ($F_{1,189} = 4.323$, $P = 0.039$). Males that attacked other males had substantially larger relative body sizes than males that did not attack ($F_{1,119} = 11.917$, $P = 0.008$), while males that attacked females had a slightly smaller relative body size than males that interacted with but did not attack females ($F_{1,187} = 4.317$, $P = 0.039$).

Latency to attack was not affected by the population from which the isopods originated, when differences in mean body size are controlled for with relative body size ($F_{2,624} = 2.037$, $P = 0.131$; Table 2, Model I). Population differences in latency to attack were identified in
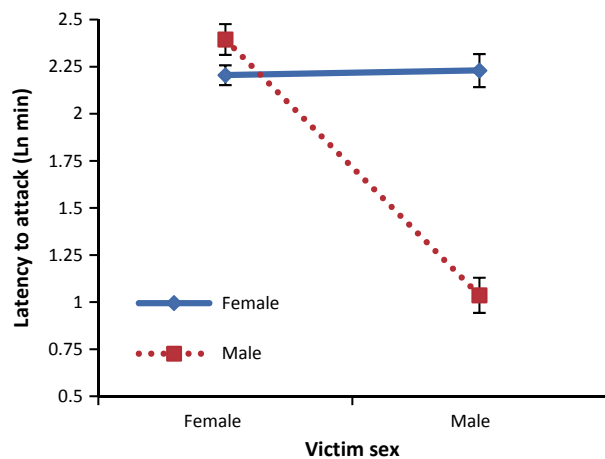
Fig. 4 Demonstrates that males respond to the sex of their social partner by altering the latency of attack when they instigate precannibalistic aggression, while females do not change latency in response to the sex of their social partner.
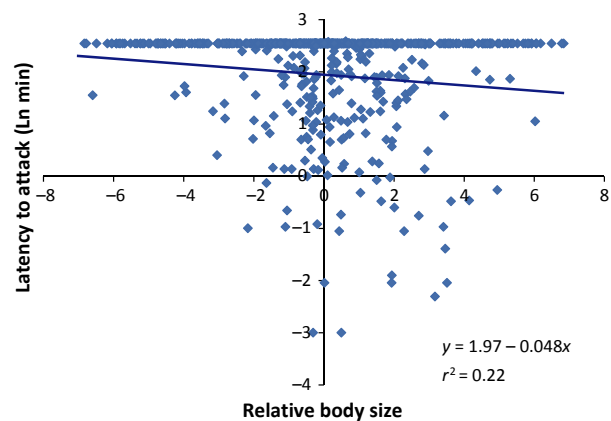

Fig. 5 Shows the relationship between relative body size and latency to attack (ln-minutes). Individuals with larger relative body size instigate precannibalistic attacks faster than those with smaller relative body sizes.

Model II ($F_{2,624} = 5.634$, $P < 0.001$; Table 2). Latency to attack was significantly affected by the sex of the individual. Males attacked significantly more quickly than females ($F_{1,624} = 29.561$, $P < 0.001$ and $F_{1,624} = 7.813$, $P = 0.005$ respectively; Fig. 4). The sex of the social partner also influenced the latency to attack. Male victims were attacked more quickly than female victims ($F_{1,624} = 59.306$ and $F_{1,624} = 14.466$, $P < 0.001$; Fig. 4). A significant interaction effect between the sex of the attacker and the victim was also identified, with males attacking females much more slowly than other males, while females did not differ in the latency to attack based on the sex of their partner ($F_{1,624} = 96.416$ and $F_{1,624} = 44.561$, $P < 0.001$; Fig. 4). Comparing latencies across partners, males responded to the size of their specific partners and attacked the smaller of their two partners faster than the larger of their partners ($F_{1,66} = 5.892$, $P = 0.018$; Fig. 6), while females did not alter their latency to attack based on specific partners of different sizes ($F_{1,66} = 0.405$, $P = 0.526$; Fig. 6).

Latency to attack was significantly influenced by the relative body size of the attacker with individuals of larger relative body size, irrespective of sex, attacking more quickly than individuals of smaller relative body size ($F_{1,624} = 5.588$, $P = 0.018$; Fig. 5). Although a partner's body size alone did not influence latency to attack in Model II ($F_{1,624} = 2.132$, $P = 0.145$; Table 2), the interaction between an individual's size and the size of its partner, which is directly analogous to relative body size, did influence latency to attack ($F_{1,624} = 32.533$, $P < 0.001$; Fig. 5). The estimate of the coefficient of the interaction, ψ, was not significant for the body size of a social partner alone ($\psi = -0.040 \pm 0.028$, $t = -1.460$, $P = 0.145$; Table 2, Model II). Both relative body size and the interaction between an individual's body size and that of its social partner had statistically significant negative effects on latency to attack ($\psi = -0.048 \pm 0.020$, $t = -2.360$, $P = 0.0184$ and $\psi = -0.060 \pm 0.011$, $t = -5.700$, $P < 0.001$; Table 2).

Discussion

Following an interacting phenotypes model of behaviour, we focussed on how individual interactions influenced the instigation of precannibalistic attacks in pairs of the Socorro isopod. Specifically, we investigated the influences of relative body size, differences in the size of multiple partners and sex. The relative body size of an individual influenced its likelihood of attacking. Relatively larger individuals attack more frequently, which is generally consistent with a large body of literature showing size-asymmetries driving cannibalism in a variety of species (reviewed in De Roos *et al.*, 2003; Crumrine, 2010; Huss *et al.*, 2010; Reglero *et al.*, 2011). However, large body size alone is not sufficient to explain whether and how quickly an individual attacks because an individual's body size interacts with the body size of its social partners. Given previous field observations of aggression and larger mean body size for the N3 and S1 populations, we predicted that individuals from the N3 and S1 population should attack more quickly than the smaller individuals found in the Sedillo population. Scaling individual body size by the social partner, via relative body size, ameliorates population differences.

We also predicted that isopods from the N3 and S1 pools would be more likely to attack (Jormalainen & Shuster, 1997; Shuster *et al.*, 2005). Although population did influence the likelihood of attack, in contrast to our predictions, individuals from the native spring were actually more likely to attack than isopods from

either N3 or S1. The difference in likelihood of attack between populations appears driven in large part by female–female interactions, which were more frequent in the Sedillo population. It is likely that females most often interact with females of similar size and the likelihood of attack may be related to competition among females in this population (Claessen *et al.*, 2004). Although Sedillo isopods have the smallest mean body size for both males and females, mean relative body size for this experiment does not differ among the populations, potentially mitigating differences in the likelihood of attack between the other two populations. This suggests that both large body size and large variance in body size for a population, which are often used to describe managed populations (Baras & Jobling, 2002; Reglero *et al.*, 2011), may be insufficient proxies for aggressive or cannibalistic tendencies.

Behavioural differences among the populations may reflect more than just differences in the traits of the isopods, such as body size or aggressiveness, leading to differential expression of interacting phenotypes. The populations vary in the physical structure and microhabitat segregation of their pools (Jormalainen & Shuster, 1997). The native spring offers the most physical structure, which has been demonstrated to create size structured populations in which isopods are most likely to interact with similarly sized social partners (Jormalainen & Shuster, 1997; Shuster *et al.*, 2005). In addition, because two of the populations are man-made and have been continuously maintained for differing lengths of time; were established at different times from different samples of the native population; and have undergone different bottlenecks, the populations likely differ in the genetic architecture of many traits (Shuster *et al.*, 2005; Lang *et al.*, 2006).

The strongest effects on the likelihood of attack were the sexes of the interactants. Consistent with previous studies, males were most likely to attack other males while females were least likely to attack males (Jormalainen & Shuster, 1997). Males attacked females and females attacked other females at intermediate frequencies. Males and females varied differently in body size across the three populations, contributed unequally to negative and positive relative body sizes, and responded differently to the same social cues (see Fig. 6). As a result, natural selection for cannibalism may operate differently on males and females in this species because they experience different conspecific predation risks even when paired with the same partner. Jormalainen & Shuster (1999) found evidence of conflicts of interest between male and female *T. thermophilum* resulting from mate guarding, which begins with males grappling females. Small males are less successful at grasping and guarding females (Jormalainen *et al.*, 1999). We found that males that attacked females have smaller relative body sizes than those that did not attack females; we

therefore investigated whether sexual conflict might influence aggressive interactions by determining whether males attacked females more often after attempting, but failing, to guard them and/or whether females attacked males more often after a failed guarding attempt. However, we found no evidence to suggest that attacks in male–female interactions were associated with failed guarding attempts. These data are therefore most consistent with population models in which cannibalism functions to reduce competition between individuals, where it is also beneficial to not consume potential mates (Van den Bosch & Gabriel, 1997; Claessen *et al.*, 2000; Kralj-Fišer *et al.*, 2012).

One factor that shapes the evolutionary trajectory of interacting phenotypes is the action of indirect genetic effects. Indirect genetic effects (IGEs) are the influences of an individual's genes on the phenotype of its social partner (Moore *et al.*, 1997; Wolf & Moore, 2010). Body size in *T. thermophilum* is heritable (Shuster *et al.*, 2005). As such, an individual's own body size will be determined in part by direct genetic effects (DGEs). The same is true for the body size of a social partner; however, the DGEs on the partner's body size influence the expression of precannibalistic aggression by the focal as indirect genetic effects (Table 2, Model 2). These IGEs of partner body size interact with the focal individual's own size; individuals respond differently to a particular body size in a partner depending on their own body size (Table 2). Our results are consistent with the prediction that the strength of IGEs should vary among individuals (Wolf, 2000; Meffert *et al.*, 2002; Kazancıoğlu *et al.*, 2012).

The strength of IGEs is typically measured using the coefficient of the interaction, ψ (Moore *et al.*, 1997; Bleakley & Brodie, 2009; Bleakley *et al.*, 2010). We found that ψ was negative and influenced aggression approximately half as strongly as an individual's DGEs for body size. Indirect genetics effects models currently define ψ as the strength of the influence of a trait in social partners (e.g. body size) on a trait in focal individuals (e.g. aggression; Moore *et al.*, 1997; Wolf & Moore, 2010). This definition of ψ imposes an additive relationship between the two traits. Our measures of ψ were obtained using relative body size or the interaction term between focal body size and partner body size (Table 2). Both of these measures scale the effect of a partner's body size by a focal's own body size and therefore identify nonadditive effects of partner body size. As such, ψ may not adequately capture a conditional relationship between traits in social partners and focal individuals. When the relative difference in a trait between interacting individuals (e.g. when there is a significant interaction) is important, models of indirect genetic effects require a different coefficient than ψ – a 'conditional ψ'. Although a strong ψ is predicted to drive rapid and/or large evolutionary change, a strong conditional ψ might constrain evolution because the
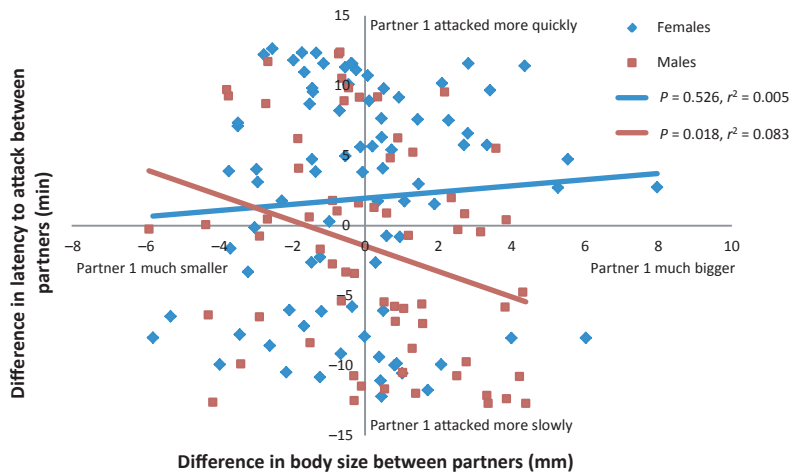
Fig. 6 Shows plasticity in latency (Latency 1 – Latency 2) to attack related to the body size of the social partners (Partner 1 – Partner 2) across two trials. Males were slower to attack the larger of the two partners with which they were paired while females did not differ in their latency to attack based on the body size of their social partners.

population mean for relative difference between social partners will always be zero (Wolf & Moore, 2010; Wilson *et al.*, 2011). Incorporating a conditional ψ into models could yield additional insight into why behaviour such as cannibalism evolves in some populations but not in others.

Strong indirect genetic effects have been measured in a number of taxa; however, those empirical studies have focussed on the behaviour of a single sex or same-sex diads (e.g. Bleakley & Brodie, 2009; Wilson *et al.*, 2009, 2011). Male isopods exhibited large responses to their social environment, changing their latency to attack a partner depending on the body size of the partner, while females did not respond to differences in partners' body sizes. Differences in the response of males and female isopods to the same social cues might constrain, rather than enhance, the evolution of cannibalism in this species.

Cannibalism can stabilize or destabilize populations, but the evolutionary trajectory taken by the population depends on the trade-offs between reproductive and growth benefits for cannibals and the survival and growth costs incurred by victims (Kohlmeier & Ebenhöh, 1995; Persson *et al.*, 2000; Wissinger *et al.*, 2010). The specific size asymmetries present within a population contribute to this trade-off because they influence the strength of selection acting on both cannibals and victims (Wissinger *et al.*, 2010). Such size asymmetries are usually modelled as the result of age structuring where adults overlap with and eat juveniles or where asynchrony in hatching generates different size classes of juveniles that may eat each other (Kohlmeier & Ebenhöh, 1995; Crumrine, 2010). However, even subtle differences in relative body size among adults influenced whether an attack was initiated and, if initiated, how quickly the attack was made.

Social cues structure population dynamics by influencing which individuals interact (Agrawal *et al.*, 2001; McGlothlin *et al.*, 2010). The influence of relative body size on probability of and latency to initiate a cannibalistic attack could interact with male and female preferences for particular microhabitats to generate social selection (Jormalainen & Shuster, 1997; Formica *et al.*, 2011). Isopods with larger relative body size were more aggressive. Aggression is known to structure how individuals join and interact in social groups (Sih & Watters, 2005; Saltz & Foley, 2011) and these interactions can additionally lead to gene-environment correlations between individuals and their social environments (Saltz, 2011). Understanding the expression of aggression and the evolution of cannibalism thus requires an explicit understanding of the influences of social environment on behaviour and estimates of the relative influences of an individual's genes and environment vs. the effects of the social environment (Moorad & Linksvayer, 2008; Bijma, 2010).

Acknowledgments

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Shows differences in body size according to sex and population as a boxplot.

Figure S2 Shows differences in relative body size according to population.

Data deposited at Dryad: doi:10.5061/dryad.5h51p