The hidden cost of group living for aggregating juveniles in a sexually dimorphic species

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The number of conspecifics present during the juvenile stages can have profound consequences on development rates and adult body size, traits often closely related to fitness. Conspecifics can have direct negative effects on each other due to resource competition, and also direct positive effects due to benefits like improved thermoregulation. We investigated morphological and developmental consequences of juvenile group size in the leaf-footed cactus bug *Narnia femorata* (Hemiptera: Coreidae). These insects are ideal to test the consequences of social environment during development because nymphs naturally aggregate in groups of varying size. Furthermore, the sexual dimorphism of this species allowed us to test for sex-specific effects of developmental density. Males possess enlarged hind legs used as weapons in male-male contests, yet females are physically larger. We found insects from smaller groups had 43% higher mortality than those from the larger groups. On average, adult body and hind leg sizes did not differ across densities for either sex. Interestingly, we found that those first to mature into adults within a sibling group became the largest adults. The largest, fastest males to adulthood also wielded the biggest weapons due to the positive allometry of this trait.

ADDITIONAL KEYWORDS: developmental time – gregariousness – heightened condition-dependence – nymphal density – sexually selected traits – sibling competition.

INTRODUCTION

The group size of juveniles during development can influence adult phenotypes in positive or negative ways, depending on the ecology of each species (Peters & Barbosa, 1977; Averill & Prokopy, 1987; Costa, 2006; Rödel *et al.*, 2008; Allen, 2010; Laws & Belovsky, 2010; Hudson *et al.*, 2011; Schrader *et al.*, 2015). In the case of gregarious insect species, large group size during the development stages can provide several advantages like higher survival rates and larger body sizes as adults due to, for example, increased thermal control, reduced individual predation risk and feeding facilitation (reviewed in Costa, 2006, 2018). On the other hand, siblings in many animal species compete for resources or exclude each other from access to them [e.g. favoured spots for feeding or for thermoregulation (Mock & Lamey, 1991; Godfray & Parker, 1992; Neuenschwander *et al.*, 2003; Drummond, 2006)]. Thus, a larger group size can also be detrimental to some group members. Trade-offs of group membership could be expected if, for example, large group sizes increase survivorship, but negatively affect body size due to competition for resources.

Animals that live in aggregations as young often do not all reach adulthood simultaneously (Drummond, 2006; Lihoreau & Rivault, 2008); with the noticeable exception of gregarious lepidopterans, which mostly emerge synchronously as adults (Costa, 2006; Allen, 2010). In fact, the rank order, relative to others in the same cohort, in which individuals pass through development is often associated with social dominance and access to food and other resources in many taxa (Fujioka, 1984; Drummond *et al.*, 1986; Nilsson & Svensson, 1996; Cook *et al.*, 2000; Dey *et al.*, 2014). Both the size of the group and the order of maturation (within the group) are potentially associated with profound life-long effects. Surprisingly, little is known about how the timing of the adult moult within a sibling group affects adult phenotypes in any arthropod (but see Cobb & Tamm, 1975; Lihoreau & Rivault, 2008). In most of the insect research looking into the effects of density or group size on individuals, order of maturation or development speed within the

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experimental unit is largely or completely ignored (Gimnig *et al.*, 2002; Ireland & Turner, 2006; Alto *et al.*, 2008; Saenz *et al.*, 2014), which is an important omission (see Schrader *et al.*, 2018). Detailed studies on the combined effects of group size and within-group developmental rates can provide us with a better ecological context of the costs and benefits of group living for juveniles. Aggregations of hemimetabolous insects can provide an excellent opportunity to study the effects of group size and the order of maturation. Juveniles of many of these species acquire food on their own and receive no direct help from parents (e.g. protection, thermoregulation).

In group-living hemipterans, several fitness benefits have been attributed to aggregation vs. isolation during the development period. Bed bugs (*Cimex lectularius* Linnaeus; Cimicidae) grow faster in groups than in isolation (Saenz *et al.*, 2014); southern green shield bugs (*Nezara virdula* Linnaeus; Pentatomidae) also develop faster and suffer less predation when in groups (Lockwood & Story, 1986). Furthermore, first to third instar nymphs of the soapberry bug (*Jadera haematoloma* Herrich-Schaeffer; Rhopalidae) have higher survival and development rates when raised in groups, rather than isolated (Ribeiro, 1989). Feeding facilitation has also been reported for adult hemipterans. *Leptoglossus occidentalis* Heidemann (Coreidae) can feed from the very tough seeds of the stone pine; experimentally, groups of adult bugs were more likely to cooperatively make a single hole through the hard seed coat from which all feed (Farinha *et al.*, 2018). Nevertheless, the consequences of group living on sibling competition and adult phenotypes have received little attention in this diverse insect order (Costa, 2006). The need to better understand insect societies that form juvenile aggregations was recently highlighted (Costa, 2018) as it can provide novel insight into the importance of ecology for promoting group living, the early evolution of sociality, and the role of sibling interactions in shaping adult phenotypes. A deeper understanding of the effect of aggregation size on trait expression can lead us to a better integration of ecological and evolutionary processes (Costa, 2006, 2018).

Our goal in this study was to gain insights on the consequences of juvenile social environments on development rates and resulting adult phenotypes. We used the sexually dimorphic leaf-footed cactus bug *Narnia femorata* Stål (Hemiptera: Coreidae); in this species body size has important fitness consequences for both sexes (Gillespie *et al.*, 2014; Nolen *et al.*, 2017; Wilner *et al.*, 2020). Females are on average the larger sex, but males have enlarged hind femurs used as weapons in male-male contests (Procter *et al.*, 2012; Nolen *et al.*, 2017). These hind legs are disproportionately larger on bigger males and their phenotypic expression has been found to be highly sensitive to environmental quality (Miller *et al.*, 2016; Allen & Miller, 2017a). We tested the effects of group size during nymphal development and within-group moulting speed on body size and the size of the male weapon (and female homologous trait), and the effect of group size on development rates. As a group living insect during the juvenile stages (Fig. 1), we expected young *N. femorata* to perform better (fitness related traits, e.g. survivorship, overall size, development rate) at higher densities (Costa, 2006, 2018). Nonetheless, we recognized that larger group sizes could negatively affect the size of *N. femorata* if siblings compete for resources or exclude each other from them. We also predicted that larger body sizes would be associated with longer development times as this is the general pattern observed for insects when raised under similar environmental conditions (Rantala & Roff, 2005; Nijhout *et al.*, 2010; Teder *et al.*, 2014). Thus, large, slow developing males would be expected in a high competition scenario (large group size), and *vice versa* (Kasumovic & Brooks, 2011), unless social dominance is at play.

MATERIAL AND METHODS

STUDY ORGANISM

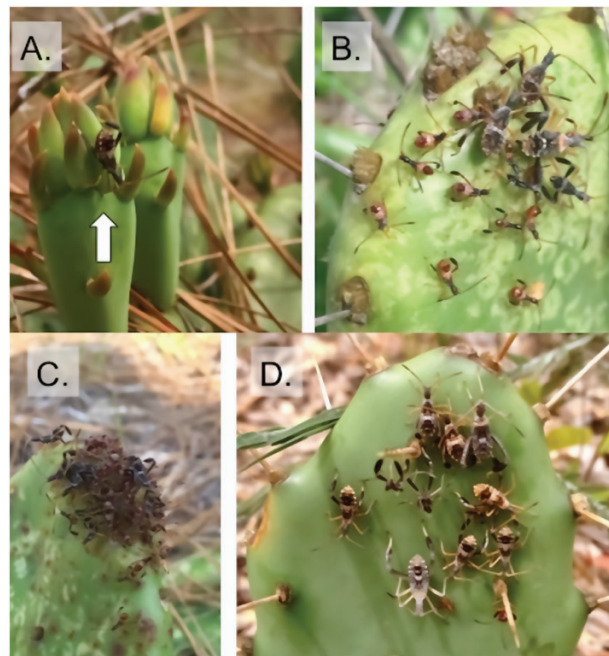The cactus feeding leaf-footed bug, *N. femorata*, has established a population in north-central Florida

Figure 1. *N. femorata* undisturbed and in the wild, in north-central Florida. A, a nymph found alone. B-D, natural nymphal aggregations.

(Baranowski & Slater, 1986) where it has been primarily feeding off the native prickly pear *Opuntia mesacantha* [formerly known as *Opuntia humifusa* (Majure, 2014); Caryophyllales: Cactaceae] for over 70 years. Adult males establish territories on *O. mesacantha* and defend their territories against other conspecifics using their hind legs as weapons. Adult body size is heavily influenced by diet during the juvenile stages (Gillespie *et al.*, 2014; Miller *et al.*, 2016); bigger males are more likely to possess disproportionately larger hind legs (Miller *et al.*, 2016; Allen & Miller, 2017a) and to be dominant over smaller males in territory defence (Procter *et al.*, 2012; Nolen *et al.*, 2017). Additionally, both sexes are less likely to mate with small individuals (Gillespie *et al.*, 2014), and female body size has also been found to correlate positively with egg production (Miller *et al.*, 2013); thus, body size and hind leg size have important fitness consequences in this species.

Females lay clutches of eggs [range = 1–46 eggs, mean ± SD = 7.70 ± 5.40 eggs per clutch, *N* = 804 clutches (75 females); L. Cirino, pers. comm.] on cactus spines and offspring can develop to sexual maturity on a single cactus. In the wild, nymphs are commonly found in variable-sized aggregations (of unknown relatedness) (Fig. 1). Thus, we predicted that developing in groups would have a positive effect on adult body size for this bug, as it has for other insects (Gage, 1995; Allen, 2010), including hemimetabolous species (Costa, 2006; Kasumovic *et al.*, 2011). In parallel with group size, moulting order per se (i.e. 1st, 2nd) provides rough information on the ranking order (development rate and nymph size) within each sibling group in this species (P. Allen, pers. obs.) and may also be predictive of adult phenotypes. Nymphs are constantly interacting with each other (Fig. 1), feeding, basking and hiding together; it is therefore likely that these interactions influence their development.

SOURCE POPULATION

Adults were collected from the UF/IFAS Ordway-Swisher Biological Station (Melrose, FL, USA) in mid-September 2014. Males and females were randomly paired, forming 36 families. Pairs were kept in plastic deli containers (top diameter 118 mm, bottom diameter 85 mm, height 148 mm), with a 30 mm layer of topsoil, and a cactus pad (*O. mesacantha*) with ripe fruit attached to it (one per cup). These parental pairs were allowed to mate freely. We obtained up to 40 eggs from each female (4-week period) and placed them in separate containers in a large greenhouse. Over this time period (September-November) greenhouse temperatures ranged from 24-30 °C.

EXPERIMENTAL NYMPHS

Once the eggs hatched and nymphs reached the 2nd instar, they were split into the three group size treatments. For each parental female we separated 35 offspring as follows: one cup with ten nymphs, three cups with five nymphs, and five cups with two nymphs. Within each cup, nymphs originated from the same egg clutch (laid within minutes of each other) and reached the 2nd instar in the same 24-h period (7–8 days after hatching in this experiment). Only 24 families produced enough nymphs to field at least one cup per treatment (17 complete sets), and therefore only these families were used in this study. Ten-nymph cups were supplied with four ripe cactus fruit each, five-nymph cups were supplied with two ripe fruit, and two-nymph cups with one ripe fruit; fruits were replaced when they deteriorated. We aimed to keep food availability similar across treatments, so that food abundance would be less likely to be a factor influencing differences across densities. The number of days each nymph took to develop from 2nd instar to adulthood (adult moult) was recorded; this was our measure of developmental time. This procedure also allowed us to keep track of the moulting order to adulthood within every cup. Nonetheless, to be able to make comparisons across group size treatments we used the number of days in reaching the adult stage within each cup, instead of moulting order. Another reason to use this method was the considerable variation in the time over which nymphs in the same aggregation moulted, which is not captured in the moulting order (e.g. orders 1st and 2nd might be separated by one day or five). Thus, the number of days since the first sibling moulted in the same cup is a better proxy for comparing within-group developmental rates. This was done by assigning the first nymph(s) to moult to adult within each cup a value of 0 (= days since first sibling moulted). The next, and subsequent, nymphs to moult were assigned a value corresponding to the number of days that they moulted after the first nymph moulted. For purposes of simplified analyses, individuals that moulted to adulthood after five or more days were all assigned a value of 5 (this category accounted for 21% of all individuals; with a maximum value of 35 days).

In our experimental design we did not change the volume of available space for the nymphs across treatments (same-sized deli cup and pads), and we kept food availability proportional to the number of nymphs. Therefore, an increase in group size also means an increase in density.

EXPERIMENTAL ADULTS AND MEASUREMENTS

As nymphs moulted into adults they were removed from their cups and placed singly or as same-sex pairs

in separate cups with fruit until they were completely sclerotized (2 weeks), then they were frozen. A digital camera (Canon EOS 50D) attached to a dissecting microscope (Leica M165 C) was used to photograph the insects, and the software ImageJ (Schneider *et al.*, 2012) was used for the linear measurement of pronotum width and hind femur width (average of both left and right hind legs). We used pronotum width as a proxy for body size, because in this species it is highly correlated with overall body size (Procter *et al.*, 2012; Gillespie *et al.*, 2014). The environmental sensitivity of the hind femurs relative to the rest of the body illustrates that they have heightened condition-dependence (Miller *et al.*, 2016; Allen & Miller, 2017a); thus, we hypothesized that if group size during development had any kind of effect on morphological traits it would show up on these environmentally sensitive appendages. We used hind femur width as our measurement of male sexually selected weapon as it is a simple measurement that is strongly correlated with other hind femur metrics (Allen & Miller, 2017a, b).

STATISTICAL ANALYSIS

All the analyses were conducted using R (R Core Team, 2017). We examined survivorship differences across the three developmental group size treatments (fixed factor) using a binary logistic regression. We did not separate our survivorship analysis by sex, as it is not possible to tell the sex of the nymphs. Each individual nymph was assigned either a '0' if it died before reaching adulthood or a '1' if it survived.

In our following analyses we only looked at those insects that survived to adulthood (see *Notes on sample sizes*). We used univariate Generalized Linear Mixed Models (GLMMs) to test for nymphal group size (fixed factor), sex (fixed factor), and family (random factor) effects on developmental time (measured as the number of days needed to reach adulthood from the beginning of the 2nd instar), body size (= pronotum width) and hind femur width. This was done using the R-package *nlme*. Family (sibling groups distributed across the different group sizes) was included in all the models to account for genetic and shared-environment contribution to overall trait variation, but otherwise not examined/reported.

We used an Analysis of Covariance (ANCOVA) to test for sex (fixed factor), group size (fixed factor), and their interaction on the scaling relationships of hind femur width with body size as the covariate. We used the $\log_{10}$-$\log_{10}$ Ordinary Least Squares (OLS) regression method to compare allometric slopes and intercepts (Warton *et al.*, 2006; Smith, 2009; Kilmer & Rodriguez, 2017). Family was included in the models as a random factor. Next, we used two-way ANOVAs on

each sex separately to test for group size (fixed factor), days since first sibling (in the same cup) to moult to adulthood (fixed factor), and their interaction effects on body size and hind femur width.

Lastly, to test for the relationship between time to adulthood (our metric of developmental time) and the morphological traits (pronotum width and hind femur width), at a population level, we used ANCOVAs to test for the effect of group size (fixed factor) on the slope and intercept of these relationships. In these analyses developmental time was used as the covariate. We included sex (fixed factor) on the analyses expecting to find sex differences on the intercepts (as females are overall larger than males), but not on the slopes. Family was included in the models as a random factor.

NOTES ON SAMPLE SIZES

Since nymph mortality directly affected group size, we did not include cups in which the number of nymphs that achieved adulthood was deemed too low to obtain relevant data for development time and trait size analyses. In the two-nymph treatment we only used cups in which both nymphs achieved adulthood. In the five-nymph treatment we only used cups where three or more adults were obtained, and in the ten-nymph treatment only cups where we got six or more adults. Furthermore, we obtained at least one female and one male from each treatment for 19 families.

RESULTS

LIFE HISTORY TRAITS

In total, we obtained 619 adults from 848 initial nymphs, across all treatments. Survivorship was 62.6% (SE = 3.82, N = 99) in the two-nymph treatment and 79.0% (SE = 3.85, N = 30) in the ten-nymph treatment (Fig. 2A); survivorship was significantly lower in smallest group size treatment (logistic regression; X^2 = 14.0, df = 2, P = 0.001). Developmental time did not differ across group sizes ($F_{2,411}$ = 0.634, P = 0.53; Fig. 2B) or sexes ($F_{1,411}$ = 2.87, P = 0.091), and there were no statistically significant interactions between factors ($F_{2,411}$ = 0.326, P = 0.722).

GROUP SIZE AND MORPHOLOGICAL TRAITS

Group size during development did not result in mean differences for adult body size ($F_{2,411}$ = 0.740, P = 0.478; Fig. 2C). We did find sexual size dimorphism, as expected, with larger female body sizes ($F_{1,411}$ = 101.9, P < 0.0001), but no group size-by-sex interactions ($F_{2,411}$ = 0.096, P = 0.91). Hind femur size was also
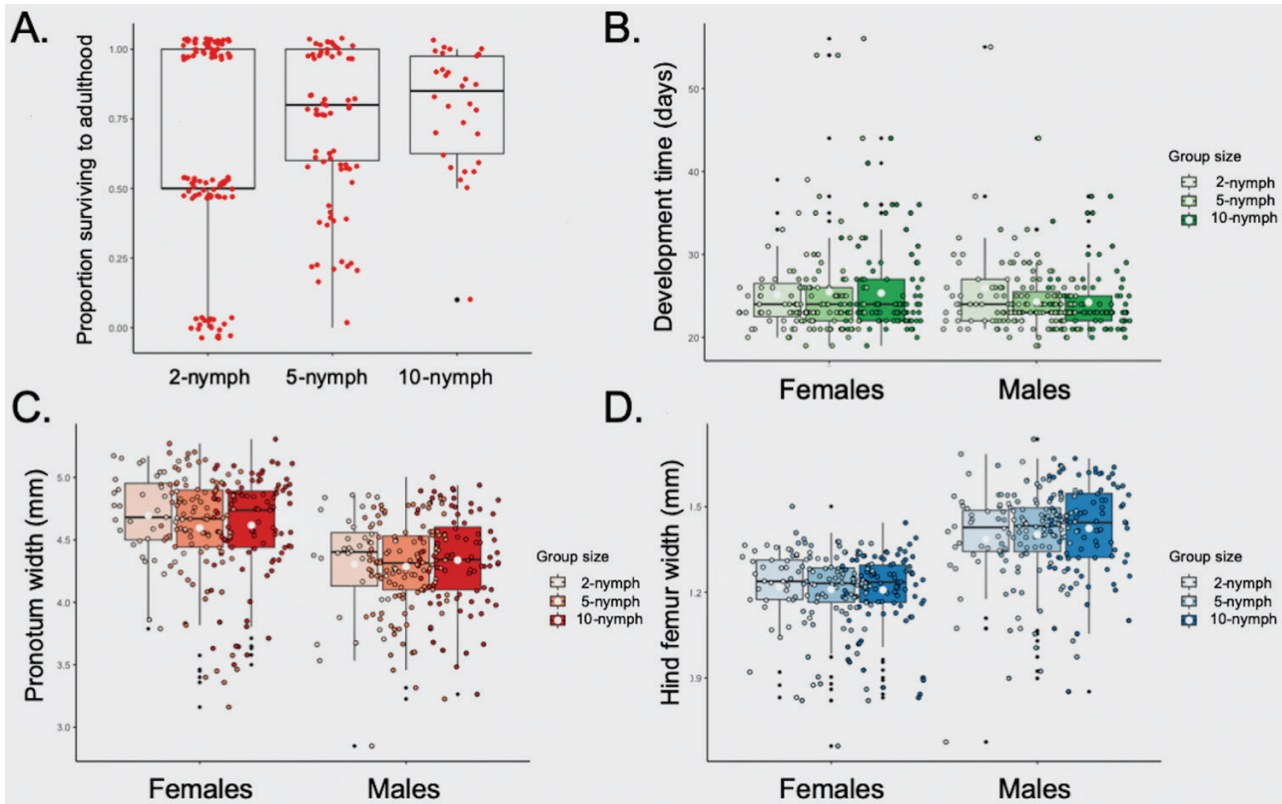
Figure 2. For *N. femorata* small group size during development, from 2nd instar to adulthood, had a negative effect on survival (A), but no effect on developmental time (B), body size (= pronotum width, C) or absolute hind femur size (D). A, boxplots and raw data of the proportion of nymphs per cup that survived to adulthood under the three group size treatments. B-D, box plots and means (white dots) of number of days to complete development to adulthood from beginning of 2nd instar (B), pronotum width (C) and hind femur width (D), separated by sex. Samples sizes (B-D): females 39 two-cup nymphs, 87 five-cup nymphs and 93 ten-cup nymphs; males 36 two-cup nymphs, 107 five-cup nymphs and 84 ten-cup nymphs, respectively.

sexually dimorphic, with males possessing larger femurs ($F_{1,411} = 219.2$, $P < 0.0001$; Fig. 2D). Group size during development did not have a detectable effect on adult hind femur size ($F_{2,411} = 0.224$, $P = 0.80$), with no significant interaction between factors ($F_{2,411} = 0.122$, $P = 0.885$).

Regarding the allometric slopes of the linear relationships between body size and hind femur size, we found no significant interaction between body size (log pronotum width), sex and group size ($F_{2,423} = 1.22$, $P = 0.30$; see complete test results in Table 1). Slopes across all sex and group size treatment combinations ranged between 1.1 and 1.3 (Fig. 3). Therefore, we carried out a single two-way ANCOVA to test for the effects of group size, sex and their interaction on the allometric intercepts, including family as a random factor in the analysis. We found that hind femur size relative to body size differed between the sexes ($F_{1,410} = 2037.7$, $P < 0.0001$), with a clear male-biased sexual dimorphism (Fig. 3). There was no effect of group size treatment on relative hind femur size

within each sex ($F_{2,410} = 0.474$, $P = 0.623$), and we found no evidence of a sex-by-group size interaction ($F_{2,410} = 0.462$, $P = 0.630$).

EFFECT OF WITHIN-GROUP DEVELOPMENTAL RATES ON TRAIT SIZE

The within-group speed (days since first sibling to moult in the same cup) in which individuals developed into adults had a positive effect on the two morphological traits' sizes for both sexes (Table 2; Fig. 4). Across group size treatments the fastest insects to moult within a cup developed larger body sizes and bigger hind femurs (Fig. 4); this led to large variation in both body and weapon size across treatments for males and females. Nonetheless, we did not find mean differences in trait size between groups size treatments for either trait or sex (Table 2; Fig. 4). There were no significant interactions between within-group speed to moult and group size treatment for either trait or sex (Table 2).

Table 1. ANCOVA result (slope homogeneity) testing for the effects of group size, sex and their interactions on the allometric slope of hind femur width, with pronotum width (PW) as a covariate (Fig. 3). Significant effects are highlighted in bold

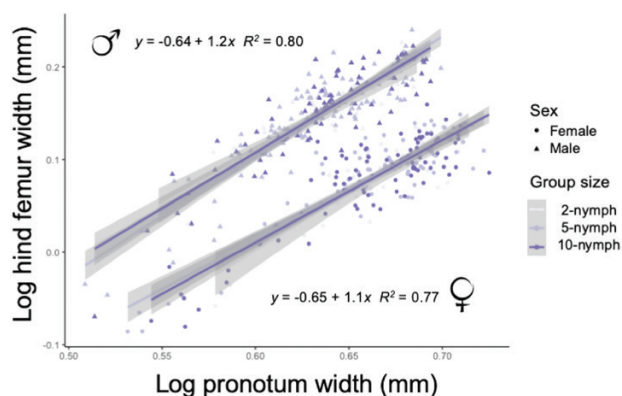| Factors	df	F	P
Body size (PW)	1, 423	1555.9	**< 0.0001**
Sex	1, 423	1756.0	**< 0.0001**
Group size (Grp)	2, 423	0.236	0.790
Sex × Grp	1, 423	0.084	0.920
PW × Sex	1, 423	4.948	**0.027**
PW × Grp	2, 423	0.120	0.887
PW × Sex × Grp	2, 423	1.216	0.297

Figure 3. Scaling relationships (static allometry – $\log_{10}$-$\log_{10}$ scale) of hind femur width (male weapons) for adults of both sexes reared at three juvenile group sizes, in *N. femorata*. Regression lines with 95% confidence intervals illustrate the allometries for each group size treatment, separated by sex. The allometric slopes did not differ across sexes or group size treatments (Table 1). Across sexes, the allometric intercepts differed indicating that males have larger hind femurs relative to body size (= pronotum width). There were no differences in intercepts across group sizes within each sex; thus, the linear regression equations in the figure incorporate all treatments for each sex.

RELATIONSHIP BETWEEN INDIVIDUAL SIZE AND DEVELOPMENT TIME AT THE POPULATION LEVEL

Across both sexes and all group size treatments, the fastest individuals to develop achieved the largest body sizes with the biggest hind femurs (Fig. 5). For both morphological traits, the slopes of these linear relationships were found to be uniform, even across sexes (Table 3). When comparing slopes, we found no significant interaction between developmental time, sex and group size for body size ($F_{2,423} = 0.43$, $P = 0.65$; see complete test results in Table 3), or for

hind femur size ($F_{2,423} = 0.08$, $P = 0.92$). The slopes for the linear regressions between development time (DT) and body size (PW) for both sexes ranged between -0.041 and -0.064 (Fig. 5A-B). The slopes for the linear regressions between DT and hind femur size (HFW) for both sexes ranged between -0.016 and -0.024 (Fig. 5C-D). The ANCOVAs, which included family as a random factor, did reveal significant sexual differences on the intercepts of the linear relationships between developmental time and both traits (Fig. 5), because females have larger body sizes ($F_{1,410} = 181.1$, $P < 0.0001$) and because males have bigger hind femurs ($F_{1,410} = 279.0$, $P < 0.0001$). Within each sex, the intercepts of the group size treatments did not differ for body size ($F_{2,410} = 2.46$, $P = 0.090$) or hind femur size ($F_{2,410} = 1.039$, $P = 0.355$). We did not detect any sex-by-group size interactions for either trait (PW – $F_{2,410} = 0.05$, $P = 0.950$; HFW – $F_{2,410} = 0.341$, $P = 0.711$).

DISCUSSION

As predicted, insects raised at the highest density had the lowest mortality, a pattern that suggests developing in groups has advantages for this insect, even in the absence of predation. Other results were unanticipated. We found that nymph developmental group size did not have a detectable effect on mean adult body size or hind femur size for either sex. Yet, that pattern belies the interesting phenomenon we detected; individual developmental speed (days to achieve adulthood) within a sibling group had significant effects on body and hind leg size for both sexes. Eggs were laid at approximately the same time and all the nymphs in a cup moulted to the 2nd instar within the same 24 h; however, adult emergence differed by 6.34 ± 7.1 days (mean ± SD, $N = 104$) between first and last nymph to moult to adult within each cup. The first individuals to mature into adults were larger, and the last were small; this meant that the fastest males to develop grew bigger and developed disproportionately larger weapons (Figs 3–4; Miller *et al.*, 2016; Allen & Miller, 2017a). Our data highlights that when studying group size or density effects, individual developmental speed (e.g. moulting order, emergence date) must be considered as it provides additional biologically relevant information.

Group living species are often conferred important benefits from their social interactions (Costa, 2006, 2018). Increased survival at the higher densities in *N. femorata* may be the result of feeding facilitation, or better thermal regulation, and thus requires further inquiry. Thermoregulation benefits of group living have been described for multiple species of Lepidoptera during the caterpillar stages (Klok & Chown, 1999; Costa, 2006; McClure *et al.*, 2011). However, the fact

Table 2. Four two-way ANOVA results testing for the effects of group size, within-group developmental speed (day since first in cup to moult), and their interaction on pronotum width (PW) and hind femur width (HFW). Significant effects are highlighted in bold

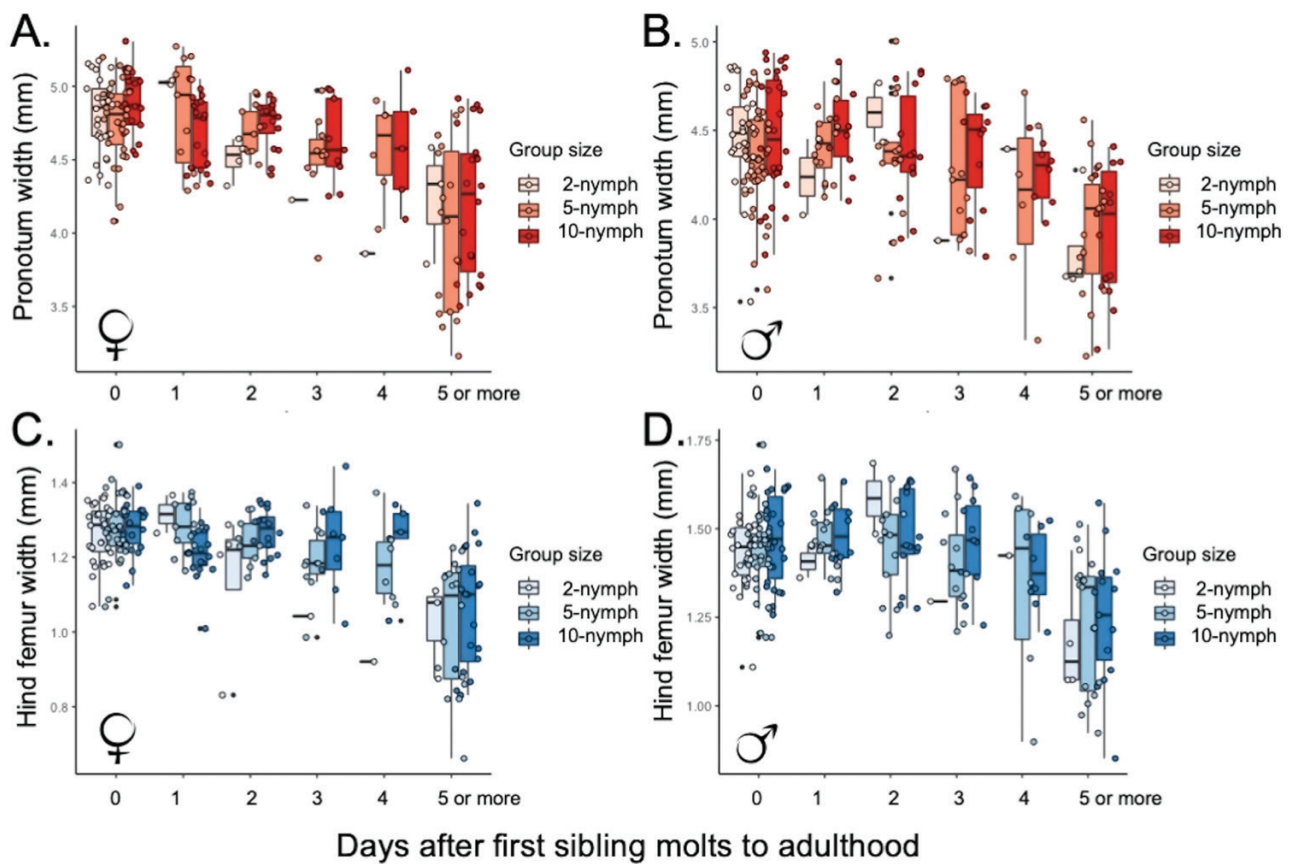|	Trait	Factors	df	F	P
Females	PW	Days	5, 196	25.33	**< 0.0001**
		Group size (Grp)	2, 196	1.146	0.320
		Days × Grp	10, 196	1.229	0.274
	HFW	Days	5, 194	26.84	**< 0.0001**
		Grp	2, 194	1.730	0.180
		Days × Grp	10, 194	1.807	0.062
Males	PW	Days	5, 205	13.49	**< 0.0001**
		Grp	2, 205	1.526	0.220
		Days × Grp	10, 205	0.618	0.797
	HFW	Days	5, 204	15.14	**< 0.0001**
		Grp	2, 204	1.476	0.231
		Days × Grp	10, 204	0.388	0.951

Figure 4. Effect of developmental group size (two-five-ten nymphs), and days since first sibling in the group (experimental cup) to moult into adulthood (proxy for moulting order), on body size (A-B) and weapon size (C-D) for both sexes of *N. femorata*. The fastest individuals to develop within a sibling group achieved the largest sizes; group size during development did not have an effect on either trait (Table 2). Box plots and raw values are shown in all cases. Within each cup all insects were given the same value (0 to 5 days) if they moulted on the same day. Individuals that moulted 5 or more days after the first nymph were pooled together (value of 5).
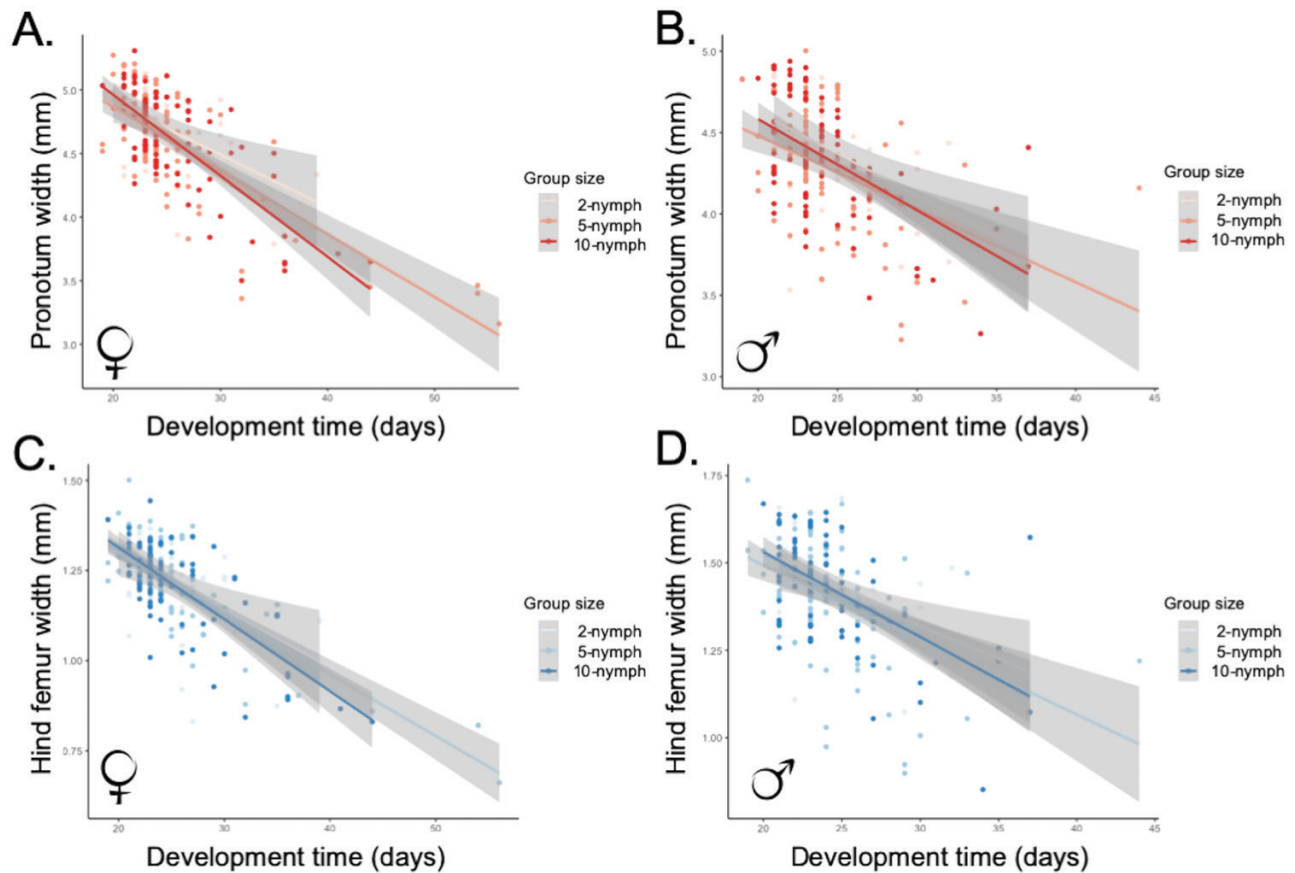
Figure 5. For *N. femorata* body size (pronotum width) and hind femur size decreased with developmental time in all group size treatments and for both females (A, C) and males (B, D), the largest insects developed faster. Lines represent linear regressions with 95% confidence intervals for each group size treatment. Within each sex, we found no differences in slopes or intercepts across juvenile group sizes (Table 3). Each data point corresponds to one individual. Developmental time represents total number of days from the beginning of the 2nd nymphal instar to the adult moult.

that the largest individuals developed faster within sibling groups, and that the last to reach adulthood were substantially smaller (Fig. 4A-B), is suggestive of competition among siblings (e.g. fighting for feeding spots or other resources) and reveals a steep cost of developing in large groups. Being a large adult has important fitness consequences in this species, as it does in many others. In *N. femorata*, big males with larger weapons are more likely to win contests against smaller rivals (Procter *et al.*, 2012; Nolen *et al.*, 2017), and smaller individuals of both sexes are less likely to mate (Gillespie *et al.*, 2014). Thus, group membership trade-offs between survivorship and body size are likely in this species.

Our data indicates that at any group size within-group developmental rates vary widely across individuals (Fig. 4), even in the presence of ample food and under abiotic conditions that resemble their natural setting (e.g. temperature, humidity, light availability). The fastest to develop achieve larger body sizes, and this size advantage likely translates into adult gains (Gillespie *et al.*, 2014; Nolen *et al.*, 2017), with the added benefit of increased survivorship for the larger sibling groups. This pattern could be the result of competitive and/or aggressive interactions between siblings, or alternatively, genetic differences within sibling groups, or both. Further studies are needed. In any case, developmental rate and body size differences were ubiquitous across families and group size treatments, which suggests that the within-group and one-on-one nymphal dynamics (e.g. interactions, behaviours) are common and likely responsible for the observed pattern. A big group size seems to provide developmental/physiological benefits even if an insect is not the fastest to mature (to adult); however, those benefits dwindle as development time in days increases; the runts suffer the most (Fig. 4).

At both group and individual levels development time and body size are strongly negatively correlated

Table 3. ANCOVA results (slope homogeneity) testing for the effects of group size, sex and their interactions on the slopes of the linear relationships between developmental time (DT) and body size (pronotum width – PW), and between DT and hind femur width (HFW). Significant effects are highlighted in bold. See Fig. 5

Factors	PW			HFW		
	df	F	P	df	F	P
DT	1, 423	251.5	**< 0.0001**	1, 423	227.7	**< 0.0001**
Sex	1, 423	160.6	**< 0.0001**	1, 423	274.6	**< 0.0001**
Group size (Grp)	2, 423	1.96	0.140	2, 423	1.05	0.351
Sex × Grp	1, 423	0.16	0.852	1, 423	0.408	0.665
DT × Sex	1, 423	0.30	0.583	1, 423	2.967	0.086
DT × Grp	2, 423	2.02	0.134	2, 423	0.995	0.371
DT × Sex × Grp	2, 423	0.43	0.648	2, 423	0.08	0.923

(Figs 4–5). We know that both traits can have important fitness consequences. Faster development time has been found to reduce predation risk in other taxa (Peckarsky *et al.*, 2001) and the benefits of a larger body and weapon are well documented in this species. Thus, sibling interactions could be driving the faster developing achieve larger size pattern seen in this species. In a separate across population experiment (Allen & Miller, unpublished data) using a Texas population and the same Florida population used in this study, we found genetic differences in the development time vs. body size relationship. Two distinct populations exhibited the same pattern, fast and big, except that one population was faster to adulthood, but with a smaller maximum body size. Hence, it is likely that there has been strong selection for both fast developing and big individuals, to account for the pattern seen in this species. Although we found no body size – time to maturity trade-offs, these may appear in other forms, such as reduced life span or investment in primary sexual traits [e.g. testis size (Gage, 1995; Stockley & Seal, 2001; Joseph *et al.*, 2017)]. Although rare (Nijhout *et al.*, 2010; Teder *et al.*, 2014), this fast and big pattern is not unique among insects (see Klingenberg & Spence, 1997).

To conclude, we found both a benefit and a cost to group living. Group size had a positive effect on survivorship but did not have an effect on the mean body size or the mean hind femur width for either sex. On the other hand, individual developmental speed within sibling groups was strongly associated with size, in a counter-intuitive direction. The fastest developing bugs within a group achieved the largest adult sizes, which is reminiscent of life history accounts for bird broods and mammal litters (Drummond, 2006). Intraspecific competition, social hierarchical interactions, and/or large genetic variation across siblings likely contribute to define adult phenotypes; the understanding of how these factors interact can provide further clues about the early evolution of group living.

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