Mother knows best: maternal egg-clutch size predicts larval group size in pine sawflies (genus *Neodiprion*)

John W. Terbot II¹

Catherine R. Linnen¹

¹ Department of Biology, University of Kentucky, Lexington, KY, USA

Keywords: parent-offspring conflict, social behavior, phylogenetic comparative methods, coevolutionary arms race, antagonistic coevolution

Submission Type: Article

Word Count: 4417

Other Elements: “Mother Knows Best Supplemental Information”

Authors for correspondence:

John W Terbot II

email: jwterb2@uky.edu

Catherine R Linnen

email: catherine.linnen@uky.edu

Abstract

Evolutionary conflicts are pervasive in nature and have the potential to drive antagonistic coevolution of conflict-related traits. However, when such conflicts are weak or idiosyncratic, phenotypic signatures of coevolutionary arms races may be absent. Here, we ask whether variation in group-living traits among pine-sawfly species in the genus *Neodiprion* is consistent with a history of parent-offspring conflict. To address this question, we compile data on adult female clutch size, larval aggregation behavior, and larval group size for a monophyletic group of 19 eastern North American *Neodiprion* species from field observations, laboratory assays, and published descriptions. We then evaluate the extent to which each trait exhibits phylogenetic signal and, based on these results, examine correlations between group-size traits both with and without phylogenetic correction. Although female oviposition behavior and larval grouping behavior varies among species and variation in these traits is decoupled from phylogeny, we find no evidence of antagonistic coevolution between these traits. Furthermore, while larvae are physically capable of dispersal, female clutch size is a strong predictor of larval colony size, indicating that larvae do not substantially alter initial group size after hatching. Thus, although theoretical work demonstrates the potential for parent-offspring conflict over group size in animals that lack parental care, our data suggest that this type of conflict is not likely to be a long-term driver of phenotypic evolution.

Introduction

Evolutionary theory predicts that conflict—scenarios in which interacting entities have divergent fitness optima for some shared trait of interest—is widespread in nature (Queller and Strassmann 2008). Conflict manifests in a variety of contexts, including between males and females (sexual conflict; (Chapman et al. 2003; Arnqvist and Rowe 2005), parents and their offspring (parent-offspring conflict; (Trivers 1974; Godfray 1995; Crespi and Semeniuk 2004)), and within the genome of a single individual (intragenomic conflict; (Burt and Trivers 2009; Garder and Úbeda 2017)). Regardless of the context, evolutionary conflicts have the potential to fuel antagonistic coevolution, in which there is reciprocal evolutionary change in the genes and traits that mediate the conflict (Rice 1996; O'Neill et al. 2007; Carmona et al. 2015; Lindholm et al. 2016; Dougherty et al. 2017). When this coevolutionary arms race plays out over the course of lineage diversification, it can give rise to correlated evolution of conflict-related traits (Briskie et al. 1994; Arnqvist and Rowe 2002; Lloyd and Martin 2003; Koene and Schulenburg 2005; Kölliker et al. 2005; Ronn et al. 2007) and elevated rates of diversification (Arnqvist et al. 2000; Zen and Zen 2000; Kraaijeveld et al. 2011; Crespi and Nosil 2013). Thus, a comparative approach is a potentially powerful tool for making inferences about the strength and long-term evolutionary consequences of conflict.

One type of conflict that has received theoretical attention, but minimal comparative study, is conflict between parents and offspring over offspring group size. Whenever siblings compete for limited resources, a female's optimal clutch size can differ from that of her offspring (Godfray 1987; Parker and Mock 1987; Godfray and Ives 1988; Damman 1991; Godfray et al. 1991; Desouhand et al. 2000). This type of parent-offspring conflict could occur even in the absence of any parental care (Costa 2018). For example, siblicide among parasitoid larvae may constrain females to produce clutches smaller than would be otherwise optimal (Godfray 1987; Parker and Mock 1987; Rosenheim 1993). Similarly,

competition among herbivorous, gregarious insect larvae may favor a reduction in egg-clutch size of ovipositing females (Godfray and Parker 1992). Conversely, when larvae disperse readily—as is the case in many grazing insects—egg clustering or dumping may be favored (Roitberg and Mangel 1993). Under this scenario, there can be parent-offspring conflict over larval dispersal tendencies (Roitberg and Mangel 1993; Sjerps and Haccou 1994). Thus, across a wide range of invertebrate life histories, parent-offspring conflict has the potential to drive coevolution between female oviposition behavior (clutch size) and offspring behaviors that mediate group dynamics (e.g., siblicide, non-lethal aggression, and dispersal tendency).

Following Arnqvist and Rowe (2002), who described coevolutionary dynamics between traits that mediate sexual conflict, we can make three predictions regarding the evolution of traits that mediate group-size conflict. First, because antagonistic coevolution can produce rapid evolutionary change, parent-offspring conflict over group size should generate extensive interspecific variation in group-living traits. Second, because coevolutionary arms races are expected to have bouts of escalation and de-escalation (Parker 1983; Härdling 1999), trait evolution should be decoupled from phylogenetic history (minimal “phylogenetic inertia”, (Losos 1999; Arnqvist and Rowe 2002)). Third, assuming that the female optimum clutch size consistently exceeds the offspring optimum clutch size (Godfray 1987; Parker and Mock 1987; Godfray and Parker 1992; Roitberg and Mangel 1993; Godfray 1995), increases in female egg-clutch size should favor offspring behaviors that either increase competitive ability or decrease colony size (e.g., via dispersal) and vice versa, generating a negative correlation between these traits among species. Although analogous predictions have been confirmed in lineages experiencing sexual conflict (Arnqvist and Rowe 2002), they remain untested in the context of group-size conflict (but see: Mayhew 1998).

To test these predictions, we take advantage of a group of herbivorous insects for which extensive ecological data are available. The sawfly genus *Neodiprion* (order: Hymenoptera; family:

Diprionidae) is a Holarctic group of approximately 50 species specialized on host plants in the family Pinaceae. Within this genus, the “*Lecontei* clade” is a monophyletic lineage of 21 eastern North American species well studied from taxonomic (Ross 1955; Ross 1961; Linnen and Smith 2012), phylogenetic (Linnen and Farrell 2007; Linnen and Farrell 2008a; Linnen and Farrell 2008b; Linnen and Farrell 2010), and life history and behavioral perspectives (Coppel and Benjamin 1965; Knerer and Atwood 1973; Knerer 1993; Costa and Louque 2001; Fowers and Costa 2003; Terbot II et al. 2017). Importantly, eastern North American *Neodiprion* have documented variation in female egg-laying behavior (Supplemental Table 1) and larval grouping behavior (Terbot II et al. 2017, Supplemental Table 1). A more detailed summary of relevant life history and ecology of *Neodiprion* sawflies can be found in the supplemental materials.

If parent-offspring conflict over group size has shaped the evolution of clutch-size traits, trait variation should match the three predictions outlined above: extensive interspecific variation, minimal phylogenetic signal, and a negative correlation between female egg-clutch size and larval grouping behavior among species. To evaluate these predictions, we combined our own observations from the field and the lab with published descriptions of female and larval behavior from 19 of the 21 eastern North American *Neodiprion* species. To gain additional insight into our data, we also examined correlations between female and larval behavior and larval colony size. If larval behaviors tend to modify initial egg-clutch size, we would expect positive correlations between larval grouping behaviors and larval colony size. Conversely, if there is minimal post-hatching modification of the initial clutch size, we would expect a stronger correlation between female clutch size and larval colony size.

Materials and Methods

Characterizing variation in group-size traits

We compiled data on female egg-clutch size, larval grouping behavior (aggregative tendency), and larval colony size for 19 of 21 eastern North American *Neodiprion* species (Linnen and Farrell 2008a, b). The only two species for which we were unable to obtain data were *N. cubensis* and *N. insularis*, both endemic to Cuba. Here, we briefly describe how we compiled data for each trait. Additional details are provided in the Supplemental Tables 1-4.

To estimate egg-clutch size for each species, we combined field observations, laboratory assays, and published descriptions. Field observations took place in 2002, 2015, and 2016 and consisted of counts of egg scars on needles found in close proximity to early instar larvae that were collected and reared to later instars or adults for identification. Clutch sizes were estimated from the number of egg scars found on individual branch termini. To supplement our field observations, we used laboratory assays to obtain clutch-size estimates for several species. In each assay, we released a lab-reared, virgin female into a mesh cage (35.6 x 35.6cm x 61cm) containing four *Pinus* seedlings. To obtain an average clutch size for each female, we recorded the number of eggs laid in each discrete clutch (i.e., a single branch terminus on a single seedling). For these assays, females were reared via methods described elsewhere (Harper et al. 2016) and provided seedlings from the *Pinus* species on which they (or their wild-caught progenitors) were originally collected. Finally, to supplement our own clutch-size data, we surveyed the literature and included published data from which we could infer mean clutch size. In total, we obtained clutch-size data for 16 of the 19 *Neodiprion* species included in our study (Supplemental Tables 1-2).

To measure larval aggregative tendency, we used a behavioral assay described in Terbot II et al. 2017. Briefly, we spaced five larvae of a particular species equidistantly along the perimeter of a 14.5 cm

diameter petri dish and recorded their behavior for 90 minutes using a Lenovo Ideapad laptop and either a Logitech or Microsoft webcam. We then used the program Video Image Master Pro (A4Video 2016) to extract individual video frames and a custom Java application to extract one image still per every 3 minutes of video (Terbot II et al. 2017). For each extracted image, we measured all pairwise distances between each of the five larval heads. To provide an acclimation period for the larvae to adjust to the petri dish arena, we excluded the first 12 images (36 minutes) of each video (Terbot II et al. 2017) using Microsoft Excel 2013 (Microsoft 2012) and a custom Perl script. This processing pipeline produced a single mean pairwise larval distance measure for each video. Larger mean pairwise distances correspond to a greater average distance between larvae and therefore a lower “larval aggregative tendency” (i.e., a greater tendency to leave the group); smaller values correspond to a smaller average distance and a higher “larval aggregative tendency”. All larvae used in these assays were collected in the field, then reared in the lab on their natal host species via standard rearing protocols until they reached a suitable size for videotaping. To reduce developmental noise in aggregative behavior, only late-instar, feeding larvae were assayed (Terbot II et al. 2017). Collection information and other details regarding the aggregative tendency assays are included in Supplemental Tables 3-4. In total, we measured larval aggregative tendency in 19 eastern North American *Neodiprion* species.

To obtain estimates of larval colony size for each species, we combined our own field observations with published descriptions of *Neodiprion* colony size. Field observations, which were recorded between 2002-2004 and 2013-2016, consisted of approximate counts of the number of larvae found in each collected colony. Colonies were located in the field via a combination of visual searching and the use of beating sheets (i.e., tapping on branches and catching dislodged larvae on a large, square piece of fabric). With this combination of methods, we were able to collect both large, conspicuous colonies and isolated individuals. We considered sawflies to be in the same colony if they formed a distinct cluster of larvae (e.g., on the same branch tip) that was spatially isolated from other such

groups. We also noted when larvae were collected as isolated individuals (i.e., colony size = 1). To supplement these field data, we included observations from published papers. In total, we obtained group-size data for 19 *Neodiprion* species.

To ensure that our data were normally distributed prior to statistical analysis, we applied a van der Waerden rank-based inverse normal transformation to all three datasets. We also multiplied each value in the aggregative tendency dataset by -1 to ensure that for all three datasets, higher values always corresponded to “large group size” phenotypes (larger egg-clutches, higher aggregative tendency, larger larval colony sizes). We used Microsoft Excel 2013 for all transformations. To determine whether species differed in trait values after accounting for variation within species, we used JMP 12 (SAS Institute 2016) to perform an analysis of variance (ANOVA) on each of the three datasets. Finally, for use in regression analyses, we calculated mean values for each species and trait. The final data set used in the analysis can be found in [REMOVED FOR DOUBLE BLIND REVIEW].

Evaluating phylogenetic signal for group-size traits

To evaluate the extent to which each group-size trait exhibits phylogenetic signal, we estimated Pagel’s λ for each trait using BayesTraits v 3.0 (Meade and Pagel 2017). Pagel’s λ is a scaling parameter that describes how well phylogenetic relationships predict trait covariance among species, with $\lambda=1$ corresponding to a model in which a trait evolves via Brownian motion along a phylogeny (i.e., strong phylogenetic signal) and $\lambda=0$ corresponding to a star-phylogeny model in which a trait evolves independently for each species (Pagel 1999). For each trait, we used BayesTraits to estimate the likelihood of our data under the “Continuous: Random Walk (Model A)” and three different λ values ($\lambda=0$, $\lambda=1$, estimated λ). Then, to evaluate the significance of the observed phylogenetic signal, we performed likelihood ratio tests (LRTs; $LR = -2\Delta\ln L$; LR is χ^2 -distributed with 1 d.f.) in which we compared the likelihood of models in which Pagel’s λ was fixed ($\lambda=1$ or $\lambda=0$) to more complex models in which λ

was estimated from the data. To account for phylogenetic uncertainty, we performed LRTs for each tree in sample of 15,000 trees from the posterior distribution of a Bayesian analysis described in Linnen and Farrell 2008a. Prior to analysis, branch lengths on each tree were scaled to time using r8s version 1.71 [58], as described in Linnen and Farrell 2010. To account for variation in sample size among traits (N = 16 for egg-clutch size, N = 19 for aggregative tendency and larval colony size), we repeated this analysis on reduced (N = 16) aggregative-tendency and larval-group-size datasets.

Evaluating relationships between group-size traits

Because evidence for phylogenetic signal was mixed (see results), we evaluated correlations between group-size traits both with and without phylogenetic correction. For uncorrected analyses, we performed correlation analyses and linear regressions in JMP 12. To test the prediction that conflict generates correlated evolution between parent and offspring traits, we estimated Pearson's correlation coefficient r and evaluated its significance via comparison to Student's t -distribution. To determine which traits contribute to larval colony size, we used linear regression to model the relationship between larval colony size (dependent variable) and different combinations of explanatory variables (egg-clutch size, larval aggregative tendency, and their interaction). To compare these models, we calculated the Akaike information criteria (AIC_c) for all possible models. We then calculated the AIC_c difference between each model and the model with the lowest AIC_c score. We also calculated Akaike weights and evidence ratios for each model and for the subset of models that had AIC_c differences less than or equal to 5. We used JMP 12 to calculate the AIC_c scores, generate model parameter values, evaluate significance of specific model parameters, and calculate model significance compared to a null model. To calculate AIC_c differences, Akaike weights, and evidence ratios, we used Microsoft Excel 2013.

To account for possible phylogenetic constraints on trait evolution, we repeated correlation and regression analyses in BayesTraits v3.0. First, to evaluate the relationship between egg-clutch size and aggregative tendency, we computed the likelihood of the data under the “Continuous: Random Walk (Model A)” model with correlation either assumed or set to zero. To evaluate the significance of the correlation, we used a LRT to compare the models with and without the correlation. Second, to evaluate the contribution of egg-clutch size and aggregative tendency to larval colony size, we used the “Continuous: Regression” model (Organ et al. 2007), with colony size as the dependent variable and egg-clutch size, larval aggregative tendency, and egg-clutch size + larval aggregative tendency as the explanatory variables. To evaluate the significance of the regression models, we performed LRTs that compared models with and without the explanatory variables. For all correlation and regression analyses, we set $\lambda=1$. As described above, we accounted for phylogenetic uncertainty by performing all analyses on a set of 15,000 ultrametric trees sampled from the posterior distribution of a previous MCMC analysis (Linnen and Farrell, 2008a; Linnen and Farrell 2010).

210 Results

211 Variation in group-size traits

212 Egg-clutch size, larval aggregative tendency, and larval colony size varied both between and
 213 within species (Fig. 1). Although there was substantial intraspecific variation in some traits/species,
 214 ANOVAs revealed significant interspecific variation in all three traits (egg-clutch size: $F_{15, 59} = 4.8850$, $p <$
 215 0.0001 ; larval aggregative tendency: $F_{18, 377} = 5.3260$, $p < 0.0001$; larval colony size: $F_{18, 360} = 17.5712$, $p <$
 216 0.0001 ;))

217 **Figure 1. *Neodiprion* species vary in multiple group-size traits.** Phylogenetic
 218 relationships for 19 eastern North American *Neodiprion* are from (Linnen and Farrell
 219 2008a; Linnen and Farrell 2010). Box plots depict intraspecific variation for egg-clutch
 220 size, larval aggregative tendency, and larval colony size. For all three traits, there is
 221 significant interspecific variation (ANOVAs, $P < 0.001$).

Phylogenetic signal in group-size traits

Overall, we found strong evidence of phylogenetic signal for larval colony size, weak evidence for egg-clutch size, and no evidence for larval aggregative tendency. For larval colony size, the mean estimated λ across 15,000 trees was close to 1 ($\lambda=0.96 \pm 0.05$ s.d.; Fig. 2). Moreover, while 58% of the trees rejected the model in which $\lambda=0$ (at $\alpha=0.05$), only 0.03% of the trees rejected the $\lambda=1$ model. Although λ estimates for egg-clutch size were also high (mean estimated $\lambda=0.83 \pm 0.37$ s.d.; Fig. 2), none of the trees rejected any of the fixed- λ models (0% for both $\lambda=1$ and $\lambda=0$). This difference may be attributable, in part, to the smaller sample size for egg-clutch size ($N = 16$). In support of this interpretation, we also failed to reject fixed- λ models when we repeated the larval colony size analysis using only those taxa present in the female clutch size analysis (estimated $\lambda=0.84 \pm 0.10$ s.d. , 0% reject

$\lambda=1$, 0.17% reject $\lambda=0$). In contrast, aggregative tendency consistently rejected models in which $\lambda=1$ (100%), but not $\lambda=0$ (0%), regardless of sample size. For this trait, the mean estimated λ was 0 ($\pm$ 0.00 s.d.; Fig. 2).

Figure 2. Egg-clutch size has a weak phylogenetic signal; aggregative tendency has no evidence of a phylogenetic signal; and larval colony size has a strong phylogenetic signal. Histograms of estimated lambda values across 15,000 trees sampled from the posterior distribution of a Bayesian analysis (Linnen and Farrell 2008a; Linnen and Farrell 2010) for the three traits of interest: egg-clutch size, aggregative tendency, and colony size. Noted on each histogram is the percentage of trees that rejected the fixed lambda models of $\lambda=0$ and $\lambda=1$.

Relationships between group-size traits

Regardless of whether or not we corrected for phylogeny, we found no evidence of a correlation between egg-clutch size and aggregative tendency (non-phylogenetic: $r = 0.0255$, $p = 0.5547$, Fig. 3A; phylogenetic: estimated $r = -0.0733 \pm 0.0495$ s.d., 0% reject null, Fig. 3D). Likewise, we found no evidence that larval aggregative tendency predicted larval colony size across species (non-phylogenetic: $F_{1,17} = 0.0216$, $R^2 = 0.0013$, $p = 0.8850$, Fig. 3C; phylogenetic: estimated $R^2 = 0.0870 \pm 0.0289$, 0.005% reject null, Fig. 3F). In contrast, our regression analyses consistently indicated a relationship between

egg-clutch size and larval colony size (non-phylogenetic: $F_{1,14} = 13.8751$, $R^2 = 0.4978$, $p = 0.0023$, Fig. 3B; phylogenetic: estimated $R^2 = 0.4997 \pm 0.0356$, 100% reject null, Fig. 3E). Importantly, these relationships were in the predicted direction: larger egg-clutches consistently produced larger larval groups.

Figure 3. Larval aggregative tendency is not correlated with egg-clutch size and does not influence larval colony size; however, egg-clutch size predicts larval colony size.

Panels **A-C** represent analyses lacking phylogenetic correction: egg-clutch size vs. larval aggregative tendency (correlation test, A), egg-clutch size vs. larval colony size (regression analysis, B), and aggregative tendency vs. larval colony size (regression analysis, C). Panels D-F are histograms of phylogenetically corrected correlation coefficients between traits estimated for 15,000 trees from the posterior distribution of a Bayesian analysis (Linnen and Farrell 2008a; Linnen and Farrell 2010): egg-clutch size vs. larval aggregative tendency (correlation test, D), egg-clutch size vs. larval colony size (regression analysis, E), and aggregative tendency vs. larval colony size (regression analysis, F).

Of the eight possible statistical models incorporating some combination of the explanatory traits, egg-clutch size and aggregative tendency, and their interaction; the best fitting model with the lowest AIC_C score was egg-clutch size alone ($AIC_C = 23.77864$; $p = 0.0023$ compared to a null model). The next most likely model used egg-clutch size and the interaction between egg-clutch size and aggregative tendency as explanatory variables ($AIC_C = 25.92652$, $p = 0.0062$ compared to a null model). The third most likely model used egg-clutch size and aggregative tendency as explanatory variables ($AIC_C = 27.41347$, $p = 0.0114$ compared to a null model). All other statistical models had ΔAIC_C scores greater than 5. The p-values for comparisons to a null model, AIC_C scores, ΔAIC_C scores, Aikake weights and evidence ratios for all statistical models are available in Table 1.

Table 1. Egg-clutch size is a better predictor of larval colony size than larval

aggregative tendency. Results for non-phylogenetically corrected model comparisons.

In the “Model” column, “C” refers to “colony size”, “E” to “egg-clutch size”, and “A” to “aggregative tendency”. The columns contain the p-values for each model compared to the null model (colony size alone), AICc are the Akaike information criteria corrected for sample size, $\Delta AICc$ are the differences between AIC scores from the best model ($C \sim E$), w_i are the Akaike weights for each model, and ER_i are the evidence ratios of each model compared to the best model ($C \sim E$).

Model	p-value	AICc	$\Delta AICc$	w_i	ER_i
$C \sim E + A + E * A$	0.0196	30.097	6.318	0.027	23.552
$C \sim E + A$	0.0114	27.413	3.635	0.103	6.156
$C \sim E + E * A$	0.0062	25.927	2.148	0.216	2.927
$C \sim A + E * A$	0.4044	36.205	12.427	0.001	499.326
$C \sim E * A$	0.1707	32.575	8.797	0.008	81.315
$C \sim E$	0.0023	23.779	0	0.631	1
$C \sim A$	0.6593	34.567	10.789	0.003	220.151
C	.	31.721	7.942	0.012	53.036

Discussion

Comparative data across diverse systems suggest that antagonistic coevolution stemming from evolutionary conflicts can fuel rapid diversification of traits and species (Crespi and Nosil 2013; Carmona et al. 2015; Queller and Strassmann 2018). Such dynamics have been confirmed in the context of parent-offspring conflict in organisms providing substantial parental care (Briskie et al. 1994; Lloyd and Martin 2003). Although conflicts are also expected even in the absence of parental care (Godfray and Parker 1987; Parker and Mock 1987; Godfray and Parkre 1992; Roitbeerg and Mangel 1993; Rosenheim 1993;

Sjerps and Haccou 1994), comparative studies examining such systems are lacking (but see Mayhew 1998). In this study, we have taken advantage of a genus of herbivorous insects with well-documented interspecific variation in traits that mediate group size to ask whether evolutionary dynamics are consistent with parent-offspring conflict. While we find extensive interspecific variation in all three traits and some decoupling from phylogeny, there is no evidence of coevolution between adult female oviposition behavior and larval grouping behavior. Furthermore, while larvae have the physical capacity to disperse (Benjamin 1955; Smirnov 1960; Codella and Raffa 1995), the close correspondence between egg-clutch size and larval colony size suggests that variable aggregative behavior in the larvae does not substantially alter the initial clutch size. A discussion of possible limitations of our phenotypic datasets can be found in the supplemental materials. Here, we consider possible biological explanations for the apparent lack of strong parent-offspring conflict over group size and propose alternative explanations for interspecific variation in group-living traits.

One potential explanation for the apparent lack of correlated evolution between female clutch-size and larval grouping behavior is that populations often lack heritable variation in grouping traits that mediate conflicts over group size. However, this explanation seems unlikely because we have detected considerable interspecific variation in both oviposition traits and larval aggregative tendency, even when measured under uniform laboratory conditions (Fig. 1). Although non-genetic sources (e.g., plasticity) may explain some of this variation, experimental crosses have confirmed that some of this behavioral variation is attributable to genetic differences between populations and species (Knerer and Atwood 1972; Bendall et al 2017). That said, even with genetic variation for adult and larval behaviors, physiological limits on some traits could constrain trait evolution in response to parent-offspring conflict over group size. For example, sawfly females typically emerge from cocoons with their full complements of eggs (Coppel and Benjamin 1965), placing an upper limit on maximum clutch size. This upper limit

could prevent egg-clutch sizes from becoming large enough to generate strong selection on dispersal tendencies, thereby limiting the potential for repeated bouts of reciprocal evolutionary change.

Assuming that populations could respond to selection stemming from parent-offspring conflict, another explanation for a lack of correlated evolution is that conflict is too weak or idiosyncratic to produce such a pattern. For example, many theoretical studies on group-size conflict assume that larval fitness is optimized at a group size of $n = 1$ (Parker and Mock 1987; Godfray and Parker 1992; Roitberg and Mangel 1993; but see Godfray and Ives 1988), ignoring possible advantages to larval grouping (e.g., an Allee effect (Courchamp et al. 1999)). By contrast, potential benefits of group-living are well documented (Seymour 1974; Bertram 1978; Young and Moffett 1979; Tsubaki and Shiotsu 1982; Pulliam and Caraco 1984; Joos et al. 1988; Stamp and Bowers 1990; Codella and Raffa 1993; Klok and Chown 1999; Despland and Le Huu 2007; Fletcher 2009; McClure et al. 2011a; McClure et al. 2011b; McClure et al. 2013; Campbell and Stastny 2015). In *Neodiprion*, it has been hypothesized that group-living helps larvae overcome host defenses (Ghent 1960, but see Kalin and Knerer 1977). If benefits of group-living consistently outweigh costs in *Neodiprion*, parent-offspring conflict over group size could be minimal.

Overall, our data suggest that parent-offspring conflict is not the predominant force shaping interspecific variation in female clutch size and larval grouping behavior. Another potential explanation for among-species variation in these traits is that it accumulated via genetic drift as species diverged from common ancestors. Under this scenario, however, we would expect a strong phylogenetic signal for grouping traits. By contrast, our data indicate that traits are at least partially (female clutch-size) or completely (larval aggregative tendency) decoupled from phylogeny. Therefore, we now consider other possible selection pressures that may shape intra- and interspecific variation in these traits. Ultimately, testing these hypotheses will require a combination of experiments that verify targets and agents of selection and comparative analyses that evaluate the contribution of different selective mechanisms to genus-wide variation.

For an adult female, optimal clutch size depends on the distribution and quality of available host plants, the physiological condition of the female, and the relationship between clutch size and offspring survival (Skinner 1985; Mangel 1987; Tostowaryk 1972). Variation in any of these factors could favor different oviposition strategies in different species. For example, *Neodiprion* species vary in their preferred oviposition hosts (Knerer and Atwood 1972; Knerer and Atwood 1973; Linnen and Farrell 2010; Bendall et al. 2017). If preferred hosts differ in their patchiness, different oviposition strategies may be favored. Interspecific variation in clutch size may also arise if the relationship between clutch size and larval survival varies among species. For example, some *Neodiprion* species have aposematic coloration (Tostowaryk 1972; Linnen et al. 2018). When aposematic signals are used, group-living can enhance the efficacy of those signals (Gamberale and Tullberg 1998; Hatle and Salazar 2001; Riipi et al. 2001). Anecdotally, *Neodiprion* with brighter coloration (e.g., *Neodiprion lecontei*) tend to have larger colony sizes than more cryptically colored species (e.g., *N. compar*). However, additional comparative work is needed to determine whether group-living correlates with conspicuousness in *Neodiprion*.

For larvae, although aggregative tendency does not appear to impact larval group size, it may nevertheless play an important role in larval survival. By controlling the density of larvae within groups, variation in aggregative tendency can impact disease transmission rates, microclimate, and host physical and chemical defenses. First, because disease transmission occurs primarily through physical contact, reduced disease transmission is one possible advantage of having a diffuse larval group (i.e., low aggregative tendency). Notably, nucleopolyhedrovirus and other infectious diseases can be a major source of mortality for sawfly larvae and gregarious larvae of ecologically similar species (Bird 1955; Mohamed et al 1985; Young and Yearian 1987; Hochberg 1991; Fletcher 2009). Second, through managing the larval group's density, larval aggregative tendency could also be a mechanism through which group-living species optimize their micro-environment (Seymour 1974; Joos et al. 1988; Codella and Raffa 1993; Klok and Chown 1999; Fletcher 2009; McClure et al. 2011a). For example, compared to

warm and wet environments, cold or dry environments may favor tighter clustering of larval groups. Third, variation in pine needle morphology and defensive chemistry among pine species may favor different larval densities. When feeding in groups, sawfly larvae form a characteristic “ring” around a needle near the tip and, as a group, consume the needle tissue down to the fascicle (Ghent 1960). However, the ability to form a stable feeding ring may decrease on thin- and long-needed hosts. Reduced aggregative tendency may prevent larvae from overloading thin needles unable to bear their weight. By contrast, thick and resinous needles may favor increased aggregative tendency to ensure a sufficient number of larvae to establish feeding sites and distribute host resins (Ghent 1960).

Conclusions

Comparative analysis is a powerful tool for testing and honing intuitions derived from evolutionary theory. For example, although theoretical work suggests that small, gregarious broods of parasitoids are evolutionary unstable and transitions from solitary to gregarious states should be rare (Godfray 1987), clutch-size data from parasitoid wasps suggests that such transitions have occurred many times independently (Mayhew 1998). Analogously, although theory demonstrates the potential for parent-offspring conflict over group size in plant-feeding insects (Roitberg and Mangel 1993), our data suggest that this conflict is not sufficiently strong or consistent to drive correlated evolution of adult and larval grouping traits in pine sawflies. To be clear, these findings do not rule out parent-offspring conflict entirely. Rather, they suggest that when parental care is minimal, parent-offspring conflict is not a major driver of long-term patterns of phenotypic change. Although these trends are intriguing, more comparative data are needed to evaluate whether some forms of conflict are more likely than others to leave a detectable phenotypic footprint in phylogenetic comparative analyses.

Works Cited

- A4Video. 2016. Video Image Master Pro.
- Arnqvist, G., and L. Rowe. 2002. Correlated evolution of male and female morphologies in water striders. *Evolution* 56: 936–947. (doi:10.1111/j.0014-3820.2002.tb01406.x)
- Arnqvist, G. and L. Rowe. 2005. Sexual Conflict. Princeton University Press, Princeton, NJ. (doi:10.1515/9781400850600)
- Arnqvist, G., Edvardsson, M., Friberg, U., and T. Nilsson. 2000. Sexual conflict promotes speciation in insects. *Proceedings of the National Academy of Science* 97: 10460–10464. (doi:10.1073/pnas.97.19.10460)
- Bendall, E. E., Vertacnik, K. L., and C. R. Linnen. 2017. Oviposition traits generate extrinsic postzygotic isolation between two pine sawfly species. *BMC Evolutionary Biology* 17: 1–15. (doi:10.1186/s12862-017-0872-8)
- Benjamin, D. M. 1955. The biology and ecology of the red-headed pine sawfly. Tech. Bull. No. 1118. USDA, Washington, D.C.
- Bertram, B. C. R. 1978. Living in Groups: Predators and Prey. Pages 64-96 in J. R. Krebs and N. B. Davis, eds. Behavioural Ecology: An Evolutionary Approach Sinauer Associates, Sunderland, MA.
- Bird, F. T. 1955. Virus Diseases of Sawflies. *Canadian Entomologist* 87: 124–127. (doi:10.4039/Ent87124-3)
- Briskie, J. V., Naugler, C. T., and S. M. Leech. 1994. Begging intensity of nestling birds varies with sibling relatedness. *Proceedings of the Royal Society B* 258: 73–78. (doi:10.1098/rspb.1994.0144)

404 Burt, A., and R. L. Trivers. 2009. Genes in Conflict: the Biology of Selfish Genetic Elements. Harvad
405 University Press, Cambridge, MA.

406 Campbell, S. A., and M. Stastny. 2015. Benefits of gregarious feeding by aposematic caterpillars depend
407 on group age structure. *Oecologia* 177: 715–721. (doi:10.1007/s00442-014-3141-1)

408 Carmona, D., Fitzpatrick, C. R., and M. T. J. Johnson. 2015. Fifty years of co-evolution and beyond:
409 integrating co-evolution from molecules to species. *Molecular Ecology* 24: 5315–5329.
410 (doi:10.1111/mec.13389)

411 Chapman, T., Arnqvist, G., Bangham, J., and L. Rowe. 2003. Sexual conflict. *Trends in Ecology and*
412 *Evolution* 18: 41–47. (doi:10.1016/S0169-5347(02)00004-6)

413 Codella, S. G., and K. F. Raffa. 1993. Defense strategies of folivorous sawflies. Pages 261-294 in M. R.
414 Wagner and K. F. Raffa, eds. Sawfly Life History Adaptations to Woody Plants. Academic Press, San
415 Diego, CA.

416 Codella, S. G., and K. F. Raffa. 1995. Contributions of female oviposition patterns and larval behavior to
417 group defense in conifer sawflies (Hymenoptera: Diprionidae). *Oecologia* 103: 24–33.
418 (doi:10.1007/BF00328421)

419 Coppel, H. C., and D. M. Benjamin. 1965. Bionomics of the Nearctic Pine-Feeding Diprionids. *Annual*
420 *Review of Entomology* 10: 69–96. (doi:10.1146/annurev.en.10.010165.000441)

421 Costa, J. T., and R. W. Louque. 2001. Group Foraging and Trail Following Behavior of the Red-headed
422 Pine Sawfly *Neodiprion lecontei* (Fitch) (Hymenoptera: Symphyta: Diprionidae). *Annals of the*
423 *Entomological Society of America* 94: 480–489. (doi:10.1603/0013-
424 8746(2001)094[0480:GFATFB]2.0.CO;2)

- 425 Costa, J. T. 2018. The other insect societies: overview and new directions. *Current Opinion in Insect*
426 *Science* 28: 40–49. (doi:10.1016/j.cois.2018.04.008)
- 427 Courchamp, F., Clutton-Brock, T., and B. Grenfell. 1999. Inverse density dependence and the Allee effect.
428 *Trends in Ecology and Evolution* 14: 405–410. (doi:10.1016/S0169-5347(99)01683-3)
- 429 Crespi, B., and P. Nosil. 2013. Conflictual speciation: species formation via genomic conflict. *Trends in*
430 *Ecology and Evolution* 28: 48–57. (doi:10.1016/j.tree.2012.08.015)
- 431 Crespi, B., and C. Semeniuk. 2004. Parent-Offspring Conflict in the Evolution of Vertebrate Reproductive
432 Mode. *American Naturalist* 163: 635–653. (doi:10.1086/382734)
- 433 Damman, H. 1991. Oviposition behaviour and clutch Size in a group-feeding Pyralid moth, *Omphalocera*
434 *munroei*. *Jornal of Animal Ecology* 60: 193. (doi:10.2307/5454)
- 435 Desouhant, E., Debouzie, D., Ploye, H., and F. Menu. 2000. Clutch size manipulations in the chestnut
436 weevil, *Curculio elephas*: Fitness of oviposition strategies. *Oecologia* 122: 493–499.
437 (doi:10.1007/s004420050971)
- 438 Despland, E., and A. Le Huu. 2007. Pros and cons of group living in the forest tent caterpillar: Separating
439 the roles of silk and of grouping. *Entomologia Experimentalis et Applicata* 122: 181–189.
440 (doi:10.1111/j.1570-7458.2006.00512.x)
- 441 Dougherty, L. R., van Lieshout, E., McNamara, K. B., Moschilla, J. A., Arnqvist, G., and L. W. Simmons.
442 2017. Sexual conflict and correlated evolution between male persistence and female resistance
443 traits in the seed beetle *Callosobruchus maculatus*. *Proceedings of the Royal Society B* 284:
444 20170132. (doi:10.1098/rspb.2017.0132)
- 445 Fletcher, L. E. 2009. Examining potential benefits of group living in a sawfly larva, *Perga affinis*.
446 *Behavioral Ecology* 20: 657–664. (doi:10.1093/beheco/arp048)

447 Flowers, R. W., and J. T. Costa. 2003 Larval Communication and Group Foraging Dynamics in the Red-
448 Headed Pine Sawfly, *Neodiprion lecontei* (Fitch) (Hymenoptera: Symphyta: Diprionidae). *Annals of*
449 *the Entomological Society of America* 96: 336–343. (doi:10.1603/0013-
450 8746(2003)096[0336:LCAGFD]2.0.CO;2)

451 Gamberale, G., and B. S. Tullberg. 1998. Aposematism and gregariousness: the combined effect of group
452 size and coloration on signal repellence. *Proceedings of the Royal Society B* 265: 889–894.
453 (doi:10.1098/rspb.1998.0374)

454 Gardner, A., and F. Úbeda. 2017. The meaning of intragenomic conflict. *Nature Ecology and Evolution* 1:
455 1807–1815. (doi:10.1038/s41559-017-0354-9)

456 Ghent, A. W. 1960. A study of the group-feeding behaviour of larvae of the jack pine sawfly, *Neodiprion*
457 *pratti banksianae* Roh. *Behaviour* 16: 110–147. (doi:10.1163/156853960X00070)

458 Godfray, H. C. J., and A. R. Ives. 1988. Stochasticity in invertebrate clutch-size models. *Theoretical*
459 *Population Biology* 33: 79–101. (doi:10.1016/0040-5809(88)90005-6)

460 Godfray, H. C. J., and G. A. Parker. 1992. Sibling competition, parent-offspring conflict and clutch size.
461 *Animal Behaviour* 43: 473–490. (doi:10.1016/S0003-3472(05)80106-X)

462 Godfray, H. C. J. 1987. The evolution of clutch size in parasitic wasps. *American Naturalist* 129: 221–233.
463 (doi:10.2307/2462001)

464 Godfray, H. C. J. 1995. Evolutionary theory of parent–offspring conflict. *Nature*. 376: 133–138.
465 (doi:10.1038/376133a0)

466 Godfray, H. C. J., Partridge, L., and P. H. Harvey. 1991 Clutch Size. *Annual Review of Ecology and*
467 *Systematics* 22: 409–429. (doi:10.1146/annurev.es.22.110191.002205)

468 Härdling, R. 1999. Arms Races, Conflict Costs and Evolutionary Dynamics. *Journal of Theoretical Biology*
469 196: 163–167. (doi:10.1006/jtbi.1998.0828)

470 Harper, K. E., Bagley, R. K., Thompson, K. L., and C. R. Linnen. 2016. Complementary sex determination,
471 inbreeding depression and inbreeding avoidance in a gregarious sawfly. *Heredity* 117: 326–335.
472 (doi:10.1038/hdy.2016.46)

473 Hatle, J. D., and B. A. Salazar. 2001. Aposematic coloration of gregarious insects can delay predation by
474 an ambush predator. *Environmental Entomology* 30: 51–54. (doi:10.1603/0046-225X-30.1.51)

475 Hochberg, M. E. 1991. Viruses as costs to gregarious feeding behaviour in the Lepidoptera. *Oikos* 61:
476 291–296. (doi:10.2307/3545236)

477 Joos, B., Casey, T. M., Fitzgerald, T. D., and W. A. Buttemer. 1988. Roles of the tent in behavioral
478 thermoregulation of Eastern tent caterpillars. *Ecology* 69: 2004–2011. (doi:10.2307/1941178)

479 Kalin, M., and G. Knerer. 1977. Group and mass effects in diprionid sawflies. *Nature* 267: 427–429.
480 (doi:10.1038/267427a0)

481 Klok, C. J., and S. L. Chown. 1999. Assessing the benefits of aggregation: thermal biology and water
482 relations of anomalous Emperor Moth caterpillars. *Functional Ecology* 13: 417–427.
483 (doi:10.1046/j.1365-2435.1999.00324.x)

484 Knerer, G., and C. E. Atwood. 1972. Evolutionary Trends in the Subsocial Sawflies Belonging to the
485 *Neodiprion abietis* Complex (Hymenoptera: Tenthredinoidea). *American Zoologist* 12: 407–418.
486 (doi:10.1093/icb/12.3.407)

487 Knerer, G., and C. E. Atwood. 1973. Diprionid Sawflies: Polymorphism and Speciation: Changes in
488 diapause and choice of food plants led to new evolutionary units. *Science* 179: 1090–1099.
489 (doi:10.1126/science.179.4078.1090)

490 Knerer, G. 1993. Life History Diversity in Sawflies. Pages 33-60 in M. R. Wagner and K. F. Raffa, eds.
491 Sawfly Life History Adaptations to Woody Plants. Academic Press, San Diego, CA.

492 Koene, J. M., and H. Schulenburg. 2005. Shooting darts: Co-evolution and counter-adaptation in
493 hermaphroditic snails. *BMC Evolutionary Biology* 5: 1–13. (doi:10.1186/1471-2148-5-25)

494 Kölliker, M., Brodie III, E. D., and A. J. Moore. 2005. The coadaptation of parental supply and offspring
495 demand. *American Naturalist* 166: 506–516. (doi:10.1086/491687)

496 Kraaijeveld, K., Kraaijeveld-Smit, F. J. L., and M. E. Maan. 2011. Sexual selection and speciation: The
497 comparative evidence revisited. *Biological Reviews* 86: 367–377. (doi:10.1111/j.1469-
498 185X.2010.00150.x)

499 Lindholm, A. K. et al. 2016. The Ecology and Evolutionary Dynamics of Meiotic Drive. *Trends in Ecology*
500 *and Evolution* 31: 315–326. (doi:10.1016/j.tree.2016.02.001)

501 Linnen, C. R., and B. D. Farrell. 2007 Mitonuclear discordance is caused by rampant mitochondrial
502 introgression in *Neodiprion* (Hymenoptera: Diprionidae) sawflies. *Evolution* 61: 1417–1438.
503 (doi:10.1111/j.1558-5646.2007.00114.x)

504 Linnen, C. R., and B. D. Farrell. 2008a. Comparison of methods for species-tree inference in the Sawfly
505 Genus *Neodiprion* (Hymenoptera: Diprionidae). *Systematic Biology* 57: 876–890. (doi:
506 10.1080/10635150802580949)

507 Linnen, C. R., and B. D. Farrell. 2008b. Phylogenetic analysis of nuclear and mitochondrial genes reveals
508 evolutionary relationships and mitochondrial introgression in the *sertifer* species group of the genus
509 *Neodiprion* (Hymenoptera: Diprionidae). *Molecular Phylogenetics and Evolution* 48: 240–257.
510 (doi:10.1016/j.ympev.2008.03.021)

511 Linnen, C. R., and B. D. Farrell. 2010. A test of the sympatric host race formation hypothesis in
512 *Neodiprion* (Hymenoptera: Diprionidae). *Proceedings of the Royal Society B* 277: 3131–3138.
513 (doi:10.1098/rspb.2010.0577)

514 Linnen, C. R., and D. R. Smith. 2012. Recognition of Two Additional Pine-Feeding *Neodiprion* Species
515 (Hymenoptera: Diprionidae) in the Eastern United States. *Proceedings of the Entomological Society*
516 *of Washington* 114: 492–500. (doi:10.4289/0013-8797.114.4.492)

517 Linnen, C. R., O’Quin, C. T., Shackleford, T., Sears, C. R., and C. Lindstedt. 2018. Genetic Basis of Body
518 Color and Spotting Pattern in Redheaded Pine Sawfly Larvae (*Neodiprion lecontei*). *Genetics* 209:
519 291–305. (doi:10.1534/genetics.118.300793)

520 Lloyd, J. D., and T. E. Martin. 2003. Sibling competition and the evolution of prenatal development rates.
521 *Proceedings of the Royal Society B* 270: 735–740. (doi:10.1098/rspb.2002.2289)

522 Losos, J. B. 1999. Uncertainty in the reconstruction of ancestral character states and limitations on the
523 use of phylogenetic comparative methods. *Animal Behaviour* 58: 1319–1324.
524 (doi:10.1006/anbe.1999.1261)

525 Mangel, M. 1987. Opposition site selection and clutch size in insects. *Journal of Mathematical Biology*
526 25: 1–22. (doi:10.1007/BF00275885)

527 Mayhew, P. J. 1998. The evolution of gregariousness in parasitoid wasps. *Proceedings of the Royal*
528 *Society B* 265: 383–389. (doi:10.1098/rspb.1998.0306)

529 McClure, M., Cannell, E., and E. Despland. 2011a. Thermal ecology and behaviour of the nomadic social
530 forager *Malacosoma disstria*. *Physiological Entomology* 36: 120–127. (doi:10.1111/j.1365-
531 3032.2010.00770.x)

532 McClure, M., Ralph, M., and E. Despland. 2011b. Group leadership depends on energetic state in a
533 nomadic collective foraging caterpillar. *Behavioral Ecology and Sociobiology* 65: 1573–1579.
534 (doi:10.1007/s00265-011-1167-5)

535 McClure, M., Morcos, L., and E. Despland. 2013. Collective choice of a higher-protein food source by
536 gregarious caterpillars occurs through differences in exploration. *Behavioral Ecology* 24: 113–118.
537 (doi:10.1093/beheco/ars141)

538 Meade, A., and M. Pagel. "BayesTraits V3. 0." (2017).

539 Microsoft. 2012. Microsoft Excel 2013.

540 Mohamed, M. A., Coppel, H. C., and J. D. Podgwaite. 1985. Temperature and crowding effects on virus
541 manifestation in *Neodiprion sertifer* (Hymenoptera: Diprionidae) larvae. *Great Lakes Entomologist*
542 18: 115–118.

543 O'Neill, M. J., Lawton, B. R., Mateos, M., Carone, D. M., Ferreri, G. C., Hrbek, T., Meredith, R. W., Reznick,
544 D. N., and R. J. O'Neill. 2007. Ancient and continuing Darwinian selection on insulin-like growth
545 factor II in placental fishes. *Proceedings of the National Academy of Sciences* 104: 12404–12409.
546 (doi:10.1073/pnas.0705048104)

547 Organ, C. L., Shedlock, A. M., Meade, A., Pagel, M., and S. V. Edwards. 2007. Origin of avian genome size
548 and structure in non-avian dinosaurs. *Nature* 446: 180–184. (doi:10.1038/nature05621)

549 Pagel, M. 1999. Inferring the historical patterns of biological evolution. *Nature* 401, 877–884.
550 (doi:10.1038/44766)

551 Parker, G. A. & Mock, D. W. 1987. Parent-offspring conflict over clutch size. *Evolutionary Ecology* 1: 161–
552 174. (doi:10.1007/BF02067398)

553 Parker, G. A. 1983. Arms races in evolution-An ESS to the opponent-independent costs game. *Journal of*
554 *Theoretical Biology* 101: 619–648. (doi:10.1016/0022-5193(83)90019-X)

555 Pulliam, H. R., and T. Caraco. 1984. Living in Groups: Is There an Optimal Group Size?. Pages 122-147 in J.
556 R. Krebs and N. B. Davies, eds. *Behavioural Ecology: An Evolutionary Approach*. Sinauer Associates,
557 Sunderland, MA.

558 Queller, D. C., J. E. Strassmann. 2018. Evolutionary Conflict. *Annual Review of Ecology, Evolution, and*
559 *Systematics* 49: 73–93. (doi:10.1146/annurev-ecolsys-110617-062527)

560 Rice, W. R. 1996. Sexually antagonistic male adaptation triggered by experimental arrest of female
561 evolution. *Nature* 381: 232–234. (doi:10.1038/381232a0)

562 Riipi, M., Alatalo, R. V, Lindström, L., and J. Mappes. 2001. Multiple benefits of gregariousness cover
563 detectability costs in aposematic aggregations. *Nature* 413: 512–514. (doi:10.1038/35097061)

564 Roitberg, B. D., and M. Mangel. 1993. Parent-offspring conflict and life-history consequences in
565 herbivorous insects. *American Naturalist* 142: 443–456. (doi:10.1016/j.jfluchem.2013.03.019)

566 Ronn, J., Katvala, M., and G. Arnqvist. 2007. Coevolution between harmful male genitalia and female
567 resistance in seed beetles. *Proceedings of the National Academy of Sciences* 104: 10921–10925.
568 (doi:10.1073/pnas.0701170104)

569 Rosenheim, J. 1993. Single-sex broods and the evolution of nonsiblicidal parasitoid wasps. *American*
570 *Naturalist* 141: 90–104. (doi:10.1086/285462)

571 Ross, H. H. 1955. The Taxonomy and Evolution of the Sawfly Genus *Neopdirion*. *Forest Science* 1: 196–
572 209. (doi:10.1093/forestscience/1.3.196)

573 Ross, H. H. 1961. Two New Species of Neodiprion from Southeastern North America (Hymenoptera:
574 Diprionidae). *Annals of the Entomological Society of America* 54: 451–453.
575 (doi:10.1093/aesa/54.3.451)

576 Sanderson, M. J. 2003. Evolution and Divergence Times in the Absence of a Molecular Clock. *Evolution*
577 19: 301–302. (doi:10.1093/bioinformatics/19.2.301)

578 SAS Institute. 2016. JMP, Version 12.

579 Seymour, R. S. 1974. Convective and evaporative cooling in sawfly larvae. *Journal of Insect Physiology*
580 20: 2447–2457. (doi:10.1016/0022-1910(74)90030-4)

581 Sjerps, M., and P. Haccou. 1994. A war of attrition between larvae on the same host plant: Stay and
582 starve or leave and be eaten?. *Evolutionary Ecology* 8: 269–287. (doi:10.1007/BF01238278)

583 Skinner, S. W. 1985. Clutch size as an optimal foraging problem for insects. *Behavioral Ecology and*
584 *Sociobiology* 17: 231–238. (doi:10.1007/BF00300141)

585 Smirnov, W. A. 1960. Observations on the Migration of Larvae of *Neodiprion swainei* Midd.
586 (Hymenoptera: Tenthredinidae). *Canadian Entomologist* 92: 957–958. (doi:10.4039/Ent92957-12)

587 Stamp, N. E., and M. D. Bowers. 1990. Variation in food quality and temperature constrain foraging of
588 gregarious caterpillars. *Ecology* 71: 1031–1039. (doi:10.2307/1937371)

589 Terbot II, J. W., Gaynor, R. L., and C. R. Linnen. 2017. Gregariousness does not vary with geography,
590 developmental stage, or group relatedness in feeding redheaded pine sawfly larvae. *Ecology and*
591 *Evolution* 7: 3689–3702. (doi:10.1002/ece3.2952)

592 Tostowaryk, W. 1972. The effect of prey defense on the functional response of *Podisus modestus*
593 (Hemiptera: Pentatomidae) to densities of the sawflies *Neodiprion swainei* and *N. pratti banksianae*
594 (Hymenoptera: Neodiprionidea). *Canadian Entomologist* 104: 61–69. (doi:10.4039/Ent10461-1)

595 Trivers, R. L. 1974. Parent-offspring conflict. *American Zoologist* 14: 249–264. (doi:10.1093/icb/14.1.249)

596 Tsubaki, Y., and Y. Shiotsu. 1982. Group feeding as a strategy for exploiting food resources in the burnet
597 moth *Pryeria sinica*. *Oecologia* 55: 12–20. (doi:10.1007/BF00386712)

598 Young, A. M., and M. W. Moffett. 1979. Studies on the Population Biology of the Tropical Butterfly
599 *Mechanitis isthmia* in Costa Rica. *American Midland Naturalist* 101: 309. (doi:10.2307/2424596)

600 Young, S. Y., and W. C. Yearian. 1987. Intra- and inter-colony transmission of a nuclear polyhedrosis virus
601 of the loblolly pine sawfly, *Neodiprion taedae linearis* Ross, on Pine. *Journal of Entomological Science*
602 22: 29–34. (doi:10.18474/0749-8004-22.1.29)

603 Zeh, D. W., and J. A. Zeh. 2000. Reproductive mode and speciation: The viviparity-driven conflict
604 hypothesis. *BioEssays* 22: 938–946. (doi:10.1002/1521-1878(200010)22:10<938::AID-
605 BIES9>3.0.CO;2-9)

Figures and Tables

Figure 1. *Neodiprion* species vary in multiple group-size traits. Phylogenetic relationships for 19 eastern North American *Neodiprion* are from (Linnen and Farrell 2008a; Linnen and Farrell 2010). Box plots depict intraspecific variation for egg-clutch size, larval aggregative tendency, and larval colony size. For all three traits, there is significant interspecific variation (ANOVAs, $P < 0.001$).

Figure 2. Egg-clutch size has a weak phylogenetic signal; aggregative tendency has no evidence of a phylogenetic signal; and larval colony size has a strong phylogenetic signal. Histograms of estimated lambda values across 15,000 trees sampled from the posterior distribution of a Bayesian analysis (Linnen and Farrell 2008a; Linnen and Farrell 2010) for the three traits of interest: egg-clutch size, aggregative tendency, and colony size. Noted on each histogram is the percentage of trees that rejected the fixed lambda models of $\lambda=0$ and $\lambda=1$.

Figure 3. Larval aggregative tendency is not correlated with egg-clutch size and does not influence larval colony size; however, egg-clutch size predicts larval colony size. Panels A-C represent analyses lacking phylogenetic correction: egg-clutch size vs. larval aggregative tendency (correlation test, A), egg-clutch size vs. larval colony size (regression analysis, B), and aggregative tendency vs. larval colony size (regression analysis, C). Panels D-F are histograms of phylogenetically corrected correlation coefficients between traits estimated for 15,000 trees from the posterior distribution of a Bayesian analysis (Linnen and Farrell 2008a; Linnen and Farrell 2010): egg-clutch size vs. larval aggregative tendency (correlation test, D), egg-clutch size vs. larval colony size (regression analysis, E), and aggregative tendency vs. larval colony size (regression analysis, F).

Table 1. Egg-clutch size is a better predictor of larval colony size than larval aggregative tendency.

Results for non-phylogenetically corrected model comparisons. In the “Model” column, “C” refers to “colony size”, “E” to “egg-clutch size”, and “A” to “aggregative tendency”. The columns contain the p-values for each model compared to the null model (colony size alone), AICc are the Akaike information criteria corrected for sample size, $\Delta AICc$ are the differences between AIC scores from the best model ($C \sim E$), w_i are the Akaike weights for each model, and ER_i are the evidence ratios of each model compared to the best model ($C \sim E$).

Model	p-value	AICc	$\Delta AICc$	w_i	ER_i
$C \sim E + A + E * A$	0.0196	30.097	6.318	0.027	23.552
$C \sim E + A$	0.0114	27.413	3.635	0.103	6.156
$C \sim E + E * A$	0.0062	25.927	2.148	0.216	2.927
$C \sim A + E * A$	0.4044	36.205	12.427	0.001	499.326
$C \sim E * A$	0.1707	32.575	8.797	0.008	81.315
$C \sim E$	0.0023	23.779	0	0.631	1
$C \sim A$	0.6593	34.567	10.789	0.003	220.151
C	.	31.721	7.942	0.012	53.036

Egg Clutch Size

Aggregative Tendency

Colony Size

Aggregative Tendency $\propto$ Egg Clutch Size

Colony Size $\propto$ Egg Clutch Size

Colony Size $\propto$ Aggregative Tendency

Model	p-value	AICc	Δ AICc	w_i	ER_i
$C \sim E + A + E * A$	0.0196	30.097	6.318	0.027	23.552
$C \sim E + A$	0.0114	27.413	3.635	0.103	6.156
$C \sim E + E * A$	0.0062	25.927	2.148	0.216	2.927
$C \sim A + E * A$	0.4044	36.205	12.427	0.001	499.326
$C \sim E * A$	0.1707	32.575	8.797	0.008	81.315
$C \sim E$	0.0023	23.779	0	0.631	1
$C \sim A$	0.6593	34.567	10.789	0.003	220.151
C	.	31.721	7.942	0.012	53.036