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Predator hunting mode and host plant quality shape attack-abatement patterns of predation risk in an insect herbivore

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Abstract. Group formation reduces individual predation risk when the proportion of prey taken per predator encounter declines faster than the increase in group encounter rate (attack-abatement). Despite attack-abatement being an important component of group formation ecology, several key aspects have not been empirically studied, that is, interactions with the hunting mode of the predator and how these relationships are modified by local habitat quality. In 79 cage trials, we examined individual egg predation risk in different-sized egg clutches from the blue willow beetle *Phratora vulgatissima* for two predators with different hunting modes (consumption of full group [*Orthotylus marginalis*] vs. part group [*Anthocoris nemorum*]). Because these predators also take nutrients from plant sap, we could examine how the quality of alternative food sources (high- vs. low-quality host plant sap) influenced attack-abatement patterns in the presence of different hunting strategies. For the *O. marginalis* predator, individual egg predation risk was largely independent of group size. For *A. nemorum*, egg predation risk clearly declined with increasing group size. However, approximately one-third of the grouping benefit was lost to an increase in group detectability. There were clear differences in attack-abatement patterns between plants with high- vs. low-quality sap. When *O. marginalis* was the predator, there was no clear change in attack-abatement in relation to host plant quality. However, for *A. nemorum* there was a clear reduction in overall predation risk and a stronger attack-abatement pattern with increasing group size when plant sap quality increased. This implies that the relative benefits of prey grouping behavior for any species might show diurnal or seasonal changes as other aspects of resource/habitat quality change for the focal predator. Modulation of attack-abatement by bottom-up effects such as plant-based food resources is yet to be incorporated into general theory, despite the ubiquity of omnivorous predators and with omnivory being important for shaping food webs, ecosystem functions, and in biological control. Thus, ongoing refinement of attack-abatement theory by focusing on bottom-up vs. top-down processes could have significant impacts on many important contemporary fields of study.

Key words: aggregation; avoidance; clutch size; conspicuousness; dilution; group structure; habitat quality; omnivore; prey detection; searching strategy; selfish herd; tritrophic interaction.

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INTRODUCTION

Prey species have evolved many behaviors to reduce predation risk (Hendrichs et al. 1991, Cocroft 1999), with one of the most important being group living (Ebensperger 2001, Krause and Ruxton 2002, Pollard and Blumstein 2008). A primary benefit of prey grouping behavior results from group-size-related changes between the predator encounter rate and the proportion of the group preyed upon during each encounter (i.e., numerical "dilution"): the so-called "attack-abatement" (Turner and Pitcher 1986; see Fig. 1 and Appendix S1 for an expanded definition).

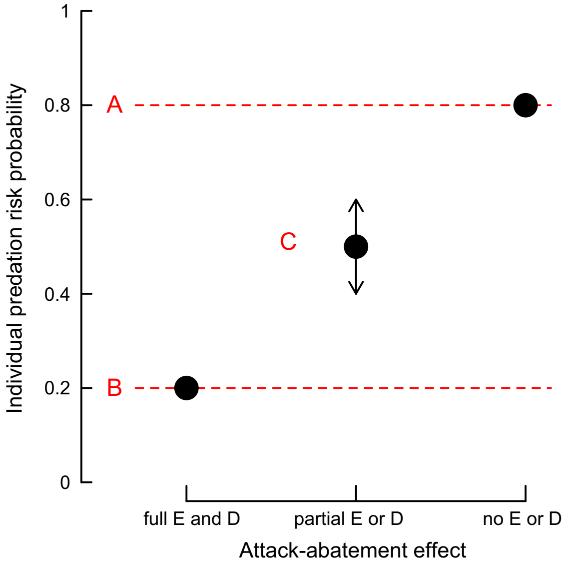

Fig. 1. Individual predation risk probability relative to group size is determined by the multiplicative combination of the encounter (E) and dilution (D) effects relative to a solitary animal (or the smallest group size). In this example, a solitary animal with predation risk "A" joins a group of size *N*. If the group encounter rate is the same for all groups (i.e., full encounter effect) and the proportion of prey taken per group is 1/*N* (i.e., full dilution effect), then group formation results in an *N*-fold reduction in predation risk ("B"). If there is no encounter or dilution effect, predation risk does not change with group size ("A"). If the predation risk of the smallest group is known, then observed predation risk of any group size can be compared relative to A (no attack-abatement) and B (full attack-abatement). Thus, the group formation benefit of "C" can be calculated in absolute terms (A–C) or in terms relative to the potential for full attack-abatement (A–C)/(A–B). In our study where the dilution effect is held constant, if (A–C)/(A–B) < 1, this indicates encounter rates increasing with group size, with this ratio being an estimate of how much the encounter rate changes with group size.

Despite the central role attack-abatement has in explaining the advantages of prey group living (Krause and Ruxton 2002, Davies et al. 2012), few studies have successfully disentangled the relative contribution of encounter and dilution (but see Foster and Treherne 1981, Wrona and Dixon 1991). In addition, studies of attack-abatement have not quantified how other processes potentially important in influencing predator or prey behavior, for example, bottom-up effects relating to resource quality and distribution and structural differences of the foraging, may interact with these top-down group formation benefits.

Although the attack-abatement model is often illustrated using a single idealized prey species under the full range of possible predatory conditions of encounter and dilution (Turner and Pitcher 1986, Inman and Krebs 1987), empirical support comes instead from comparisons of different prey species operating under specific fixed predator conditions. In such cases, the proportion of prey taken universally declines with increasing group size (Calvert et al. 1979, Foster and Treherne 1981, Wrona and Dixon 1991, Uetz and Hieber 1994). This is because the dilution effect in these studies is always complete (Foster and Treherne 1981) or partial (Wrona and Dixon 1991), meaning that the relationship between group size and predation risk under some conditions predicted by theory have never been tested—when the dilution effect is zero because all prey in a group are consumed upon encounter (Fig. 1).

Determining the extent to which attack-abatement contributes to reducing individual predation risk is difficult because attack-abatement may covary with other group-size-related effects such as predator confusion (Schradin 2000), alarm signaling (Maschwitz 1966), group defense (Cocroft 1999), evasion (Weihs and Webb 1984), vigilance (Roberts 1996), disaggregation (Creel and Winnie 2005), and group structure (Hamilton 1971) including predator detection and information spread (Bednekoff and Lima 1998). One solution has been to study sessile organisms (Wrona and Dixon 1991); however, these may still include group structure effects if individuals display non-random settlement. To account for these issues, we used an experimental approach to study egg predation risk related to clutch (i.e., group) size in the blue willow beetle *Phratora vulgatissima* (Coleoptera: Chrysomelidae; hereafter: leaf beetle), because this well-studied system has characteristics that are ideal for studying attack-abatement. First, eggs are grouped into clutches that naturally vary in size from 1 to 50 that can be easily manipulated into specific group sizes with little variation in egg quality. Second, eggs are sessile and do not display any confounding antipredator behaviors. Also, because egg clutches come from a single female and can be assumed to have an equal fitness value, there are no group structure effects complicating dilution calculations (e.g., "selfish herd" where individuals try to minimize their domain of danger by moving closer to conspecifics or placing conspecifics between themselves and the predator; Hamilton 1971). Third, the two primary natural predators of the leaf beetle's eggs have different hunting behaviors (Björkman et al. 2003) that correspond to the extremes of the dilution effect range: *Anthocoris nemorum* takes a certain number of eggs per attack, meaning that the proportion of prey taken is inversely related to group size, and *Orthotylus marginalis* consumes all eggs, meaning that the proportion of prey taken is constant regardless of group size. Thus, by comparing egg survival relative to group size for these two active hunting predators (Miller et al. 2014), the attack-abatement theory can be empirically tested for the first time at the full range of dilution effects within the same prey species. Finally, bottom-up (Godfray 1986, Kagata and Ohgushi 2002) and top-down processes (Subinprasert and Svensson 1988) are important clutch size determinants for herbivorous insects. In this system, the leaf beetles and the omnivorous egg predator *A. nemorum*'s fecundity are clearly influenced by the plant resistance and the sap quality of different willow *Salix* species, respectively (Stenberg et al. 2010, 2011). This has potential consequences for predator behavior as predators consume both leaf beetle eggs and plant sap. In addition, different host plant species may differ with respect to plant architecture that could influence foraging behavior of both omnivorous predators (Gingras et al. 2008). Thus, by examining how attack-abatement relationships change with respect to plant species, we can examine for the first time how bottom-up processes may interact with top-down attack-abatement effects.

We experimentally manipulated clutch sizes in the leaf beetle in the presence of two different predation strategies on two plants of differing host plant quality and asked the following questions. First, does egg predation risk relative to group size follow expectations from attack-abatement theory as the dilution effect varies from being complete (*A. nemorum*) to zero (*O. marginalis*) for a single prey species? Second, to what extent does group size influence the group encounter rate for an egg predator, and is the effect similar between group size categories? Finally, we investigate how these patterns of egg predation risk relative to group size vary on host plants differing in food quality and architecture. Omnivorous predators may alter their predatory behavior relative to how well their plant-based dietary needs are satisfied (Vasseur and Fox 2011) or due to the structure of the foraging area (Grevstad and Klepetka 1992).

MATERIALS AND METHODS

Study species

The adults and larvae of the blue willow beetle (*Phratora vulgatissima*) skeletonize the leaves of their host plants. This pest species is the most important specialist herbivore on willow (*Salix* spp.) in Europe, and it frequently outbreaks in plantations and in natural willow stands (Dalin et al. 2009). Adults emerge in April after overwintering, mate after feeding for two weeks, and lay hundreds of eggs on the underside of leaves. *Orthotylus marginalis* (Heteroptera: Miridae; dark green apple capsid) is important in regulating leaf beetle population dynamics (Björkman et al. 2004) and is, together with *Anthocoris nemorum* (Heteroptera: Anthocoridae; common flower bug), the most common natural enemies of the leaf beetle in willow plantations (Björkman et al. 2003). Although *A. nemorum* and *O. marginalis* are generally regarded as predators of the leaf beetle's eggs, both are omnivorous and also require host plant sap as part of their diet (Lehman 1932). As Heteropterans, both predators have piercing and sucking feeding behavior; however, they have distinctly different egg hunting modes (Björkman et al. 2003). *Anthocoris nemorum* preferentially forages in the upper part of the plant and displays an "eat and run" predator feeding strategy where it only takes a certain number of eggs from a clutch before seeking out plant-based nutrients. On average, it spends only 22 min at a particular prey grouping and is described as "restless" (Sigsgaard 2010). Although it may prefer leaf edges (Lauenstein 1980), we observed that both species search whole leaves. The less mobile *O. marginalis* preferentially forages in the lower part of the plant and has a "find and stay" predation strategy, where it consumes all eggs in a clutch before moving on. Thus, from attack-abatement theory, increasing group size should benefit the leaf beetle in the presence of *A. nemorum* (assuming the encounter rate does not increase in direct proportion to group size), but not in the presence of *O. marginalis*.

Different *Salix* species vary in their quality as host plants for this leaf beetle (Lehrman et al. 2012) and their omnivorous predator *A. nemorum* (Stenberg et al. 2010, 2011). Leaf beetles have a much higher fecundity on genotypes of *Salix viminalis* (78183, 78021) than *Salix dasyclados* (Loden, Gudrun). The predator *A. nemorum* has a higher fecundity on *S. dasyclados* over *S. viminalis* in the absence of leaf beetle prey; however, this difference in host plant quality disappears when leaf beetle eggs are present (Stenberg et al. 2011). This suggests that *A. nemorum* has less need for leaf beetle eggs on *S. dasyclados* with the host plant potentially influencing egg predation rates and attack-abatement patterns. For the other predator, *O. marginalis*, no such specific information is available, although a similar effect could be assumed. Neither of the predator's behavior is affected by leaf trichomes (Björkman and Ahrne 2005); however, the two plant species also differ in leaf morphology and plant architecture, with *S. dasyclados* ("simpler" architecture) having roughly half as many leaves that are approximately twice as large as *S. viminalis* ("complex" architecture). Thus, the predator search areas on each plant was similar (comparable cumulative leaf areas; same shoot height), but with different plant structures that conceivably could influence foraging behavior (Gingras et al. 2008).

Attack-abatement experiments

We measured the relationship between group size and egg predation risk during 79 replicated cage trials. For each trial, we took leaves with egg clutches from the rearing cage, and using forceps under microscopy created fixed clutch sizes of 5, 15, or 45 eggs; this method has been used previously and does not affect the viability of the eggs (Kabir et al. 2014). Each trial consisted of a *Salix* shoot that was divided into 13 equal-sized segments along its length, with several leaves in each segment. Each segment randomly received one clutch by pinning the leaf with the clutch onto the underside of one of the leaves in the segment (Appendix S2). Because predators may use plant volatiles as foraging kairomones for locating prey care was taken that the margins of the pinned leaves/piercing holes had dried out and therefore did not release green leaf volatiles during the experiment (plant sap feeding does not trigger herbivore-induced plant volatiles).

The total number of eggs on each plant and number of eggs in each size class were the same (each plant received 9 × 5, 3 × 15, and 1 × 45 egg clutches); these were typical of egg numbers seen during outbreak years. Egg quality was assumed to be similar for all clutches because variation in the nutritional value of each egg is minimal and independent of the feeding source of the female (mean [mg/g] ± SE: carbon: 492.9 ± 8.4, nitrogen: 85.2 ± 1.2; Björkman et al. 2011), with no systematic differences in egg size within and between clutches (J. Stephan, *unpublished data*). The shoots were placed in cylindrical transparent plastic cages (height 70 cm, diameter 30 cm) covered with a net to allow air convection. In each cage, three *A. nemorum* individuals (43 experiments) or three *O. marginalis* individuals (36 experiments) were released for 72 h. After this time, the numbers of empty eggshells were counted on each shoot and summed for each group size category (i.e., number preyed upon per 45 eggs). With this experimental design, we ensured that (1) the behavior of both predators can be compared because we excluded the possibility of different responses to different prey densities (Wiedenmann and O'Neil 1992), (2) possible differences in predators' satiation point are independent from group size-related predation probability (both have similar consumption rate: around seven eggs per day; the experiment would end when around half the eggs were consumed; here we also assumed that increased energy demand during searching for more scattered clutches is minimal and does not increase the satiation point), and (3) changes in intraspecific interference due to different prey density (Abrams and Ginzburg 2000) were excluded.

For each predator, we compared the relationship between group size and egg predation risk using two *Salix* host plant species known to differ in plant nutrient quality for the omnivorous predator *A. nemorum* (i.e., *S. viminalis* genotypes "78021" and "78183" [low sap quality] and

S. dasyclados genotypes "Gudrun" and "Loden" [high sap quality]; Stenberg et al. 2010). For the 43 experiments with *A. nemorum*, 22 were on *S. viminalis* and 21 on *S. dasyclados*; for the 36 experiments with *O. marginalis*, 18 were on each *Salix* species.

Growth of plant material, insect maintenance, and all trials took place in a glasshouse (23°C, relative humidity 80%, 18:6-h light:dark cycle). All insects were collected from natural populations in the Uppsala region of Sweden (59.85°, 17.64°). The Anthocoridae were collected from stinging nettle (*Urtica dioica*) and the Miridae and the leaf beetles from willow shrubs (mainly *S. cinerea*). The predators were stored without food in vials overnight before usage, while the leaf beetles were allowed to feed in rearing cages on *S. viminalis* genotype 78183 until reproduction started and eggs could be collected for the experiments. *Salix* shoots grown from 20-cm winter cuttings had between 17 and 35 leaves and were prepared by removing the top two to four newly emerged, incompletely unfolded leaves and the lowest old and withering leaves.

Analysis

The relationship between group size and egg predation risk was analyzed separately for each predator type using a generalized linear mixed model (GLMM) framework with a binomial logit-link distribution in R (R Development Core Team 2015). For this, the response variable was the number of eggs preyed upon from the 45 eggs within each group size category (i.e., number of "successes" for a given number of "trials"), with the individual plant ID as a random effect (Appendix S3: Table S1). This was first implemented with group size treated as a categorical variable, thus providing separate estimates for each group size category. We used the predation risk per egg for the smallest group (clutch size = 5) as the baseline for calculations of attack-abatement for the other group sizes (Wrona and Dixon 1991), where this level of predation risk would indicate no attack-abatement effect for larger groups (Fig. 1). From this, we calculated the expected full attack-abatement effect on predation risk for each group size by dividing the baseline risk by the relative increase in group size (i.e., three or nine for group sizes of 15 and 45, respectively; Turner and Pitcher 1986). From these two reference points, we could determine the proportion of the observed reduction in predation risk relative to the total possible reduction in predation risk (Fig. 1; Appendix S3: Table S2). For *A. nemorum*, because the proportion of prey taken per encounter is inversely related to group size (i.e., full dilution effect), if the observed attack-abatement is smaller than predicted, this would indicate that increases in group size result in increased group encounters, with the proportionate increase being a direct measure of the change in the encounter effect relative to group size. For *O. marginalis*, because the proportion of prey taken is 1 (i.e., no dilution effect), we expect the observed predation risk to remain at a similar level regardless of group size. Because each group size represented a threefold increase in clutch size (5, 15, and 45), we also modeled the GLMM using group size coded as a continuous variable (0, 1, 2) to compare between-predator differences in intercepts (i.e., was there a baseline between-predator difference in predation risk for the smallest group size) and slopes (i.e., was there a between-predator difference in attack-abatement). We then extended these GLMM analyses to include plant sap quality/plant architecture (Appendix S3: Table S3), by including host plant species as a two-category variable with interactions at the group level. From this, we wanted to examine how the quality of an additional food source or the plant architecture changed attack-abatement patterns depending on the degree of dilution in the predator hunting mode.

We estimated parameters and derived variables from the GLMMs using Bayesian hierarchical models implemented in JAGS (an MCMC Gibb's sampler; Plummer 2003) called from R. We used a Bayesian framework primarily because we could generate posterior distributions for any derived variables of interest. This means that any variable calculated from the models (e.g., differences between predicted and observed values or proportions) has its own probability distribution from which the mean, standard deviation, and 95% credible intervals can be calculated. This allows us to assign exact probabilities on whether things differ, rather than simply using point estimates that do not allow such interpretation. We used vague priors in all models, and sampled the MCMC chains 50,000 times once

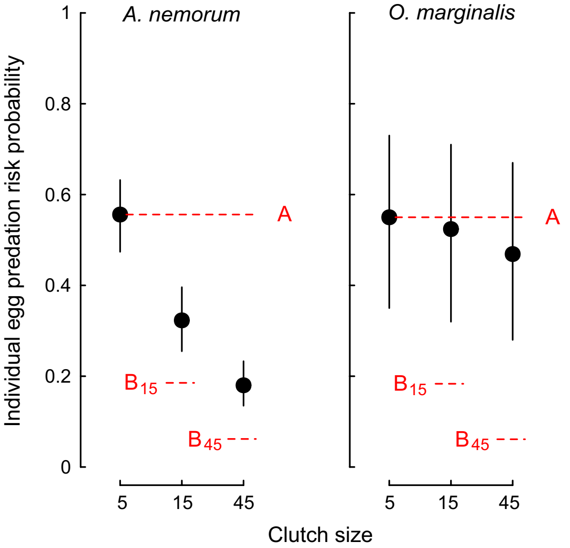

Fig. 2. The attack-abatement effect for leaf beetle eggs relative to two different predator hunting strategies (*Anthocoris nemorum* = "eat and run" vs. *Orthotylus marginalis* = "find and stay"). Points show the median and 95% CIs of the posterior distributions of predation risk probability estimated from experimental observations for clutch sizes 5, 15, and 45 eggs (Appendix S3: Table S2). The advantage of grouping is calculated relative to the smallest group size (A) as the baseline, and the full potential advantage from attack-abatement for each group size (B_{15} and B_{45}).

the chains had stabilized (for *A. nemorum* chains stabilized after 50,000 iterations; for *O. marginalis* chains took ~1 million iterations to stabilize). Convergence was checked by visually inspecting the chains and confirmed using the Gelman and Rubin diagnostic.

RESULTS

Egg predation risk relative to group size and predator strategy

As predicted by attack-abatement theory, there was a clear negative relationship between group size and egg predation risk when *Anthocoris nemorum* was the predator, while egg predation risk was largely independent of group size for *Orthotylus marginalis* (Fig. 2; Appendix S3: Table S2). For *A. nemorum,* there was strong evidence that larger groups were more likely to be encountered than smaller groups (45 > 15 > 5) because predation risk for larger groups was higher than predicted if encounter rate was independent of group size (Fig. 2); however, this higher encounter probability was too small to eliminate the benefits from the dilution effect. For intermediate-sized groups (15 eggs), attack-abatement was 63% of the expected effect if encounter rate was group size independent, and for the largest group (45 eggs), it was 76% of the expected full effect (Appendix S3: Table S2).

Host plant identity and attack-abatement patterns

Attack-abatement patterns varied in relation to host plant species. Although the decline in predation risk relative to group size was largely similar on both *Salix* species, there was a clear difference in the absolute predation risk between *S. dasyclados* (higher quality sap for predators/simpler plant architecture = lower egg predation risk) and *S. viminalis* (lower quality sap/complex plant architecture = higher egg predation risk; Fig. 3). For *A. nemorum,* there was strong evidence for differences in attack-abatement between *S. dasyclados* and *S. viminalis* based on a linear decline in predation risk relative to group size (Appendix S3: Table S3). Here there was a 98% probability that *S. dasyclados* had a lower intercept than *S. viminalis* (difference between intercepts [logit mean ± SD] = 0.62 ± 0.30; 95% CI = 0.03, 1.22), and a 99% probability that the attack-abatement effect was stronger on *S. dasyclados* (difference between slopes [logit] = 0.20 ± 0.08, 95% CI = 0.05, 0.36). For *O. marginalis,* the magnitude of the estimated mean difference between intercepts on the different *Salix* species was similar to *A. nemorum* (0.60 ± 0.87); however, there was much greater uncertainty in the estimates (only 75% probability that *S. dasyclados* < *S. viminalis* intercept; 95% CI = −1.1, 2.4; Fig. 3; Appendix S3: Table S3). There was no difference between the slopes for the two *Salix* species with *O. marginalis* (mean ± SD = 0.007 ± 0.09; 95% CI = −0.18, 0.17).

DISCUSSION

Using a model prey system with two predators at the extreme ends of the dilution effect range, and an experimental design with the same total number of sessile prey in each group size category, we could tease apart the contribution of the

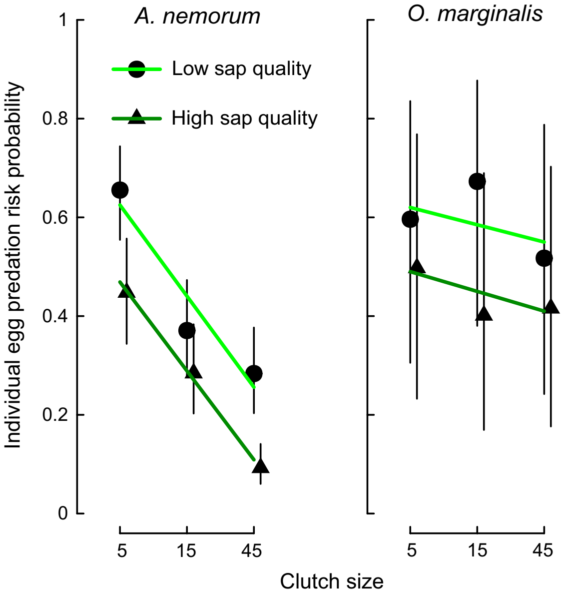

Fig. 3. The attack-abatement effect for leaf beetle eggs relative to predator type (*Anthocoris nemorum* vs. *Orthotylus marginalis*) and plant genotype (lower sap quality = *Salix viminalis*; higher sap quality = *Salix dasyclados*) based on the derived variable estimates (Appendix S3: Table S3). Points show the median and 95% CIs of the posterior distributions estimated from models where clutch size is a categorical variable; lines show the predicted median of models where clutch size was treated as a continuous variable (mind that for *A. nemorum*, our analysis showed that the slope of high sap quality is steeper than that of low sap quality).

encounter and dilution effects to attack-abatement in unusual detail. In addition, because we used two different host plant species to represent different impacts of habitat quality and complexity as the experimental arena we could show for the first time how top-down (hunting modes) and bottom-up (different suitability of plant species to the omnivorous predators; different complex foraging areas) processes interacted to generate attack-abatement patterns.

Attack-abatement predictions relating to variation in the dilution effect on a single prey species (Fig. 1; Turner and Pitcher 1986, Inman and Krebs 1987) were largely supported. Differences between observed predation risk and the predation risk expected if group encounter rates are the same regardless of group size, should accurately reflect the proportionate increase in group encounters that directly result from a larger group size. Thus, a threefold group size increase from 5 to 15 does not result in a reduction in predation risk of 0.37 ± 0.03 as predicted against *Anthocoris nemorum*, but rather 0.23 ± 0.02 (Fig. 2; Appendix S3: Table S1). This indicates that approximately one-third of the expected benefit of grouping is lost because of the increase in detectability/conspicuousness or group encounter rate. Interestingly, a further threefold increase in group size from 15 to 45 shows the same pattern; a reduction in predation risk with one-third of the expected benefit lost. Thus, the benefits of the encounter effect as group size increased remained relatively constant within the range of natural clutch sizes for the leaf beetle in these experiments.

Although it is widely accepted that bottom-up effects may influence prey aggregations (Jensen and Larsson 2002), we show for the first time how the benefits of attack-abatement are modified when the focal predator can switch to feeding on the same trophic level as the prey. Here, the probability of group encounter was lower when the quality of the alternative food source was higher. This suggests that predators are less motivated to seek out prey if they can more easily satisfy their nutritional needs via other means. Although parallels exist to decreasing predation rate for one prey if another prey is provided (apparent mutualism; Colton 1987), our results could imply a more general phenomenon with important implications. Namely, that the relative benefits of prey grouping behavior for any species via attack-abatement could be expected to show diurnal or seasonal changes as other aspects of resource/habitat quality change for the focal predator. Therefore, such qualitative changes can act on the attack-abatement mechanism, not only on more complex behaviors overlaying it (e.g., grass cover [Schaller 1968] or light level [Metcalfe and Ure 1995] affecting predator detection).

We also found evidence that the slope of the regression describing the decline in predation risk with group size was steeper when alternative resources for the predator *A. nemorum* were of higher quality. Thus, additional benefits of grouping may occur when predators are less motivated to hunt, with attack-abatement being less effective during periods when predators must satisfy their needs by hunting the focal prey.

These "bottom-up" effects most likely result from differences in the quality of plant sap rather than plant architecture because (1) the patterns fit with what is known about plant sap quality for the omnivorous predators, (2) both predators are agile and had enough time to visit every leaf on the shoot several times (eggs were consumed on every vertical position), with both species observed searching whole leaves, (3) the leaf/foraging area on both plant species was similar, and (4) egg encounter rate should be greater for simple plant structures (Gingras et al. 2008), which would increase egg predation pressure, rather than lowering it on *S. dasyclados* as we observed.

Our experiment has likely removed some cues important for guiding insect predators like olfactometric cues from plant volatiles (Dicke and Baldwin 2010, Lehrman et al. 2013) and prey pheromones and feces (Fernandez and Hilker 2007), resulting in attack-abatement patterns that might look different under natural conditions. Thus, the increased encounter of larger groups in our study likely resulted from increased visual detection (Hénaut et al. 1999) and olfactometric detection of eggs (Bin et al. 1993). Although this potentially complicates the interpretation of natural selection pressures on clutch size determination in these insects, one advantage of having removed these cues is that our results can be generalized to systems where predators mainly use vision (such as avian predators). Also, different selection pressures on groups, in the form of optimal clutch size (Godfray et al. 1991) and larval aggregation (explained with, e.g., thermoregulation, Klok and Chown 1999; overcoming plant defenses, Clark and Faeth 1997) have been addressed in insects. However, we directly emphasized the parallels to classical group formation ecology for the first time.

We are convinced that the different predator effects result from differences in hunting mode rather than some "species" effect because other studies find consistent evidence for predator hunting mode as an explanation for observed effects on prey survival and behavior (Miller et al. 2014) as we have found here. Although both predators show contrasting vertical preferences on the shoots for egg predation (Stephan 2016), this would not confound hunting mode because (1) the clutch size classes were distributed randomly along the shoot and survival was calculated per class, not clutch; (2) both predators visited all positions on the shoot (data not shown); (3) the alternative food source is not interfering with the predator movement because plant sap quality does not change along the shoot (Siebrecht et al. 2003); and (4) any differences in duration of feeding on plant sources would only alter the total egg consumption, but not the predation risk probability in the different group size categories. Hunting mode can therefore determine prey survival probabilities for passive sessile prey, without more complex behaviors involved, like predator confusion effects (Cresswell and Quinn 2010).

Our results indicate that leaf beetles should, in general, increase clutch size to increase egg survival; however, observations of egg laying in this leaf beetle do not reveal such a clear pattern, as clutch size varies from 1 to 50 eggs and is not affected by predator presence (Stephan 2016). There could be a number of explanations for this variation. First is that by examining the relationship between grouping and predation risk in relation to different natural predators of the leaf beetle, it is obvious that in a system with both *A. nemorum* and *Orthotylus marginalis,* the benefits of attack-abatement would be weakened. For this leaf beetle, it has been shown that it faces several predators in plantations as well as in natural willow stands (Björkman et al. 2003) and the lack of positive effects of larger clutches may be attributed to additive predator affects (Stephan et al. 2016). We now can explain, using predators with large difference in hunting mode, why it is difficult to detect benefits of larger clutches. Second, there are complex interactions between food preferences for the ovipositing leaf beetles (that prefer *S. viminalis*; Stenberg et al. 2011) and those of their predators that result in trade-offs between food quality for the prey and predation risk avoidance. Even more, avoiding competition may also be more important for egg survival than predation avoidance, especially given the synchronized oviposition behavior. This leaf beetle, for example, employs spatial memory to increase between-clutch distance to lower intraspecific exploitative competition (Stephan et al. 2015).

These complex interactions and behaviors highlight an important point that is often not discussed: Most studies to date have focused on a specific predator–prey interaction (e.g., Ioannou et al. 2011). Thus, there has been little consideration of the likely scenario that grouping strategies are not simply a result of the interaction under study but a compromise between several predator–prey interactions with different attack-abatement patterns (but see Morrell et al. 2011 on how different timings of predator attack, which correlates with hunting mode, can affect group formation strategies). There are also implications for tritrophic—predator–prey–plant—interactions in that if the plant can satisfy the predator's nutritional needs with its sap, the predator is less likely to act as the plant's "bodyguard" and hunt leaf beetles. Thus, we should perhaps not be surprised that the leaf beetle does not follow the simple rule of "lay big clutches" when there are so many interactions and selective pressures still unaccounted for.

Although the classic studies on attack-abatement were over 30 years ago (Calvert et al. 1979, Foster and Treherne 1981, Turner and Pitcher 1986, Inman and Krebs 1987), there are still many unexplored aspects of how group formation relates to predation risk in terms of the key components of group encounter rate and numerical dilution. Using a simple system, we have illustrated how the benefits of group living against predation can accrue through these basic mathematical components and how these are modified by hunting mode and local habitat (i.e., plant) quality. Modulation of attack-abatement by bottom-up effects such as plant-based food resources is yet to be incorporated into general theory, despite omnivorous predators being more common than strict carnivores (Rosenheim and Corbett 2003) and omnivory being important for shaping food webs (Holt and Polis 1997), influencing ecosystem functions (Zhang et al. 2004), and in biological control (Wäckers et al. 2005). Refining attack-abatement theory by looking at bottom-up vs. top-down processes, often in a tritrophic interaction perspective, would significantly impact many important contemporary fields of study.

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