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Aposematism and gregariousness: the combined effect of group size and coloration on signal repellence

Gabriella Gamberale and Birgitta S. Tullberg

Department of Zoology, Stockholm University, S-10691 Stockholm, Sweden (`gabriella.gamberale@zoologi.su.se`)

Many aposematic species have evolved an aggregated lifestyle, and one possible advantage of grouping in warningly coloured prey is that it makes the aposematic signal more effective by generating a greater aversion in predators. Here we investigate the effect of prey group size on predator behaviour, both when prey are aposematic and when they are not aposematic, to separate the effects of warning coloration and prey novelty. Naive domestic chicks (*Gallus gallus domesticus*) were presented with either solitary or groups of 3, 9 or 27 live larvae of the aposematic bug *Tropidothorax leucopterus*. Other naive chicks were presented with larvae of the non-aposematic bug *Graptostethus servus* either solitary or in groups of 27. Attack probability decreased with increasing group size of aposematic prey, both when birds were naive and when they had prior experience, whereas prey gregariousness did not affect the initial attack probability on the *G. servus* larvae. In a separate experiment, groups of mealworms were shown to be even more attractive than solitary mealworms to naive chicks. We conclude that the aversiveness of prey grouping in this study can be explained as increased signal repellence of specific prey coloration, in this case a classical warning coloration. These experiments thus support the idea of gregariousness increasing the signalling effect of warning coloration.

Keywords: aposematism; aggregation; predation; defence; Heteroptera; Lygaeidae

1. INTRODUCTION

Many animals use warning coloration to signal their unprofitability to potential predators (Cott 1940; Guilford 1990). Warning coloration decreases the initial attack probability of naive predators, which could be an effect of prey novelty *per se* (Coppinger 1969, 1970), of specific colours or other prey aspects (Roper & Cook 1989; Gamberale & Tullberg 1996*a*,*b*), or possibly a combination of novelty and specific colours (Wiklund & Järvi 1982; Sillén-Tullberg 1985*a*). Warning coloration also increases the speed and memorability of avoidance learning (Gittleman & Harvey 1980; Sillén-Tullberg 1985*a*; Roper & Redston 1987; Roper 1994). In insects, aposematism often occurs together with gregariousness (Edmunds 1974), and phylogenetic investigations show that the evolution of unprofitability and/or warning coloration generally precedes that of egg clustering and larval gregariousness in lepidopteran larvae (Sillén-Tullberg 1988, 1993; Tullberg & Hunter 1995). Thus, it appears that unprofitability and/or warning coloration somehow facilitate the evolution of gregariousness.

One suggested benefit of being aggregated is that gregariousness increases the effect of the aposematic signal (Poulton 1890; Beddard 1895; Cott 1940; Wilson 1975). A typical warning coloration is conspicuous and consists of bright colours of red, yellow or white, often in combination with black, whereas cryptic colorations mimic the background and often consist of greenish or brownish colours that sometimes work disruptively (Cott 1940). Thus, if gregariousness functions to increase a warning signal one would expect warningly coloured, but not cryptic prey, to increase predator aversion when in a group, even when the cryptic prey is novel to the predator. Moreover, one would expect predator aversion to increase with increasing group size of aposematic prey.

An increase in signal efficiency with gregariousness could influence both the initial unconditioned aversion of naive predators and the speed and memorability of avoidance learning. There is empirical evidence that gregariousness increases the initial unconditioned aversion, in that naive chicks are more reluctant to attack groups than solitary live aposematic prey (Gamberale & Tullberg 1996*a*). It has also been shown empirically that predator avoidance learning can be faster and more durable when prey is gregarious (Gagliardo & Guilford 1993). Interestingly, this effect was not due to the aggregation *per se*, but to the possibility of seeing warningly coloured prey items simultaneously or immediately after perceiving the noxious stimulus. However, the initial aposematic effect was not tested, as the prey were not novel to the predators.

Here we use domestic chicks as predators on live aposematic prey, presented solitarily or in groups of different sizes, to investigate how an increase in group size, and thereby an increase in the amount of warning coloration, affects the repellent properties of the aposematic signal. We also study initial predator behaviour towards solitary and gregarious novel prey that lack warning coloration, to separate effects of prey novelty from effects of coloration.

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2. MATERIALS AND METHODS

(a) *Predators and prey*

We used domestic chicks (*Gallus gallus domesticus*) as predators. The chicks arrived from the hatchery in batches of 30–40 individuals. On arrival, they were less than 20 h old and had not eaten. Each batch was housed in a 100 cm × 55 cm × 20 cm cage with wooden sides, a steel-net floor, and a roof made partly of wood and partly of chicken wire. The cage was heated with a 60 W carbon light bulb and the floor of the cage was covered with sawdust. All chicks were fed chick starter crumbs and water, and at least from their second day on they were also fed live mealworms (*Tenebrio molitor*). Throughout the experiments birds in each batch were evenly divided among treatment groups.

As prey we used live larvae of the seed bug *Tropidothorax leucopterus* (Heteroptera: Lygaeidae). In this species, all larvae, independent of size and instar, are of the same coloration (at least to the human eye). They are brightly orange–red with a black head, legs and wing buds, and thus can be considered to be warningly coloured. We used larvae of two different sizes: third instar larvae (0.43–0.49 cm, 6.0–6.3 mg) and fourth instar larvae (0.60–0.66 cm, 13.9–14.8 mg). *T. leucopterus* larvae had been used in a previous experiment (Gamberale & Tullberg 1996*b*), from which we know that they are distasteful to chicks. The insects were reared on a diet consisting of seeds and green parts of their toxic host-plant *Vincetoxicum hirundinaria* (Asclepiadaceae), husked sunflower seeds and water.

We also used fourth instar larvae of the related bug *Graptostethus servus* (Heteroptera: Lygaeidae). These larvae have a size in between the third and the fourth instar *T. leucopterus* larvae (0.49–0.58 cm, 9.9–12.5 mg). They resemble *T. leucopterus* larvae in shape, but are greyish-brown with black wing buds, legs and head. The *G. servus* insects were reared on a diet of husked sunflower seeds and water. All larvae were cultured at a temperature of 27 °C on a 17:7 h light:dark regime.

(b) *Experimental arena and procedure*

The experiments took place in an arena of the same kind of cage that the chicks were housed in. Part of the cage was screened off, leaving a testing floor size of 30 cm × 55 cm. The birds always had free access to chick crumbs and water throughout an acclimatization period and during testing. The chicks were tested in pairs consisting of one experimental and one companion chick. Before testing a batch, we fed one chick with as many mealworms as it could eat. This made the chick inactive and not interested in the experimental prey, and it became a companion to the experimental chicks during the experiments. The use of companion chicks was necessary because the chicks became distressed and were not interested in food when alone. The testing started on the birds' third day, when they were less than 60 h old. Chicks were exposed to the prey throughout the trial, and thus allowed to make as many attacks as they wished. We collected data concerning chick attacking behaviour and the mortality of the attacked insects. The risk to the prey was measured as the proportion of individual birds attacking. We also noted the total number of pecks at the prey during the test minute, and if the prey was eaten. An attacked insect was investigated after the trial and was counted as effectively dead even if it was only severely injured.

When presented to the birds, the test insects were arranged in two Petri dishes 5 cm in diameter, that were placed on top of each other and taped together with masking tape so that the contents could only be seen from above. When groups were presented, one accessible prey was placed in the top dish and the rest were enclosed in the bottom dish. This meant that the birds could see a group of prey but only one could be attacked. When a solitary prey was presented it was placed in the top dish, leaving the bottom dish empty. In addition, owing to this Petri dish arrangement, any possible difference in odour between aggregated and solitary treatments was controlled for. This could be important because odour has been shown to have strong interactive effects with prey coloration (Marples & Roper 1996; Rowe & Guilford 1996). A thin layer of Fluon was applied to the rim of the top dish to prevent the insect's escape. To control if the birds were active and interested in attacking live prey, we also presented a mealworm to each bird at the same time as the bugs. It was placed in the same type of double Petri dish arrangement.

(c) *The effect of group size in aposematic bugs*

We tested a total of 208 birds, which we divided into eight treatment groups of 26. Birds in the treatment groups were presented with either third or fourth instar aposematic *T. leucopterus* larvae, that were either solitary or in groups of 3, 9 or 27. The group sizes were chosen so that they would increase by a multiple of three; this produced manageable groups that differed visibly in size. The chicks were tested with one trial (duration 1 min) on each of two consecutive days. If a chick did not attack the prey during a trial, the presentation was repeated twice more after intervals of 10 min. On the first day we investigated the chicks' unconditioned aversion to the different larval and group sizes. Only birds that attacked the prey were tested again on the second day with the same type of prey arrangement and in the same manner as on the first day.

(d) *The effect of group size in non-aposematic bugs*

One hundred and eighteen chicks, divided into two treatment groups, were given either a solitary ($N=58$) or an aggregation of 27 ($N=60$) fourth instar *G. servus* larvae. Only the unconditioned aversion of the chicks to these novel non-aposematic prey could be investigated, because the prey were not distasteful enough for studying avoidance learning. The procedure was as described above (§ 2*c*), except that the trial was only repeated once with each chick because we had seen that if a chick attacked the prey, it did so during the first two trials.

To investigate how chicks with prior experience of the non-aposematic bugs, which were thus not naive with respect to the shape of the prey, would react to warningly coloured prey, we tested attacking birds from three of the batches with fourth instar *T. leucopterus* larvae. The birds were tested the day after being tested with *G. servus* larvae, with the same treatment as before, except for the prey species ($N=29$). Thus, a bird tested with a solitary *G. servus* larva was tested with a solitary *T. leucopterus* larva the day after (on its fourth day). The birds were also tested again in the same way with *G. servus* larvae on its fifth day to control for avoidance effects from the first *G. servus* experience.

(e) *The effect of group size in mealworms*

In a separate experiment, using birds with no prior experience of live prey whatsoever, we investigated the effect of gregariousness on attack behaviour towards mealworms (*Tenebrio molitor*). Mealworms are usually found to be very attractive and eagerly devoured by chicks. Birds from three batches were tested in pairs receiving solitary ($N=30$ pairs) or aggregations of 27 ($N=30$ pairs) live mealworms in the same manner as described for the above experiment. The experiment took place on the chicks' second day, when they were less than 36 h old.

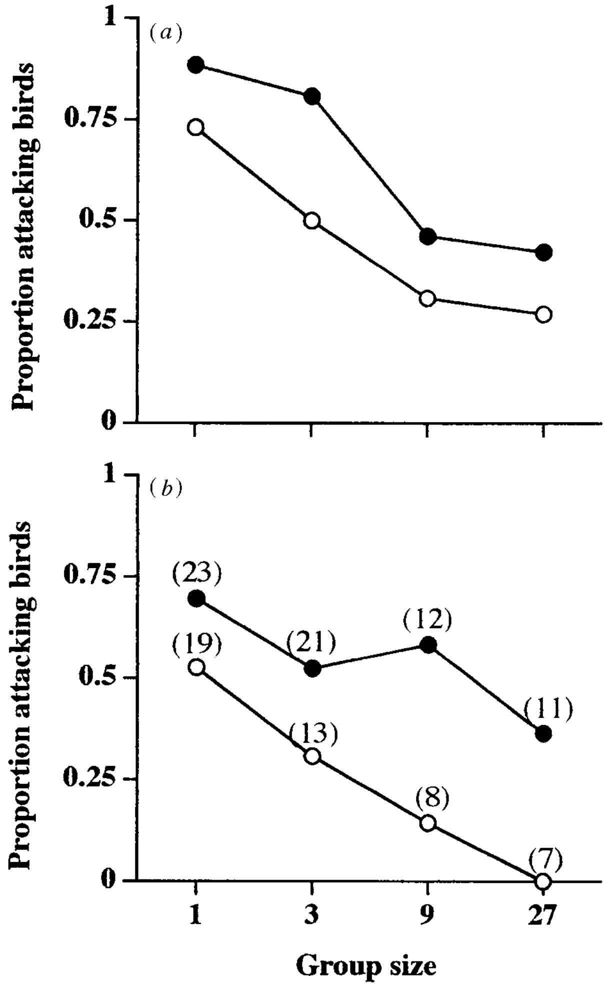

Figure 1. (*a*) The proportion of naive birds attacking solitary and groups of 3, 9 and 27 third (closed circles) and fourth (open circles) instar larvae of the aposematic bug *T. leucopterus*. In all eight *T. leucopterus* treatments the sample size is 26. (*b*) The attack probability of chicks with prior experience of the same presentation of either solitary or groups of 3, 9 or 27 third or fourth instar larvae of the aposematic bug *T. leucopterus*. The numbers in parentheses are sample sizes.

Table 1. *Log–linear analysis of chick attack probability on aposematic prey*

(Predator attack (yes/no) was the response variable in the analysis, and *T. leucopterus* instar (third/fourth), group size (solitary/3/9/27) and predator prior experience (yes/no) were design variables.)

effects	d.f.	χ^2	p
attack–instar	1	9.557	0.002
attack–group size	3	39.31	<0.0001
attack–experience	1	10.52	0.001

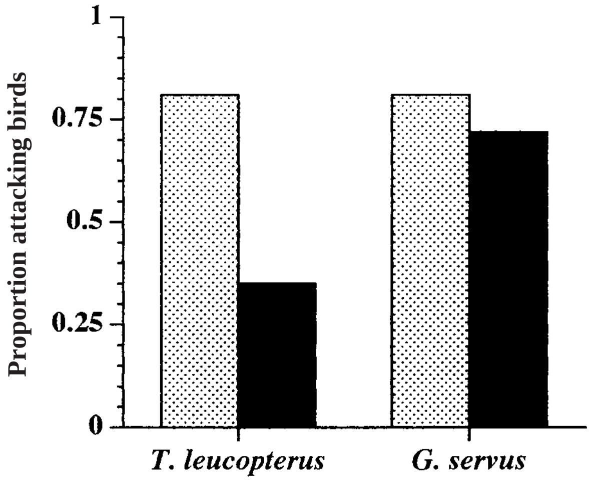

Figure 2. The proportion of naive birds attacking aposematic (third or fourth instar) *T. leucopterus* larvae and cryptic *G. servus* larvae. Dot-filled columns represent birds presented with solitary prey (*T. leucopterus*, $N=52$; *G. servus*, $N=58$) and dark columns represent birds presented with groups of 27 prey (*T. leucopterus*, $N=52$; *G. servus*, $N=60$).

(f) *Statistical analyses*

To investigate the separate effects and interactions between prey size, prey group size and predator experience on the proportion of attacking birds tested with aposematic prey, and to investigate whether there was an interaction between gregariousness and prey coloration, we used log–linear analysis (STATISTICA 4.1). To test further the effects of these factors we used contingency tables. The difference in pecking frequency on solitary and grouped *T. leucopterus* larvae of the two instars was investigated using Kruskal–Wallis ANOVA.

3. RESULTS

(a) *The effect of group size in aposematic bugs*

For chicks presented with aposematic prey the attack probability decreased with increasing prey group size, both when they had no prior experience of the prey (figure 1*a*), and after previous attacks (figure 1*b*). Using log–linear analysis we found a significant effect on attack probability of larval size, group size, and the birds' prior experience of the prey (table 1). However, there was no significant improvement in the model when including higher interactions ($\chi^2=3.10$, d.f.$=10$, $p=0.979$). Thus, fourth instar larvae were more aversive than the smaller third instar larvae. Also, there was a significant increase in aversiveness with group size, but it was proportional for birds with third and fourth instar treatments. In addition, the chicks learned to avoid the prey, but there was no difference in avoidance learning of prey in different group sizes or of prey of different size.

Because the chicks were left with the prey for a fixed trial time of 1 min, the number of pecks delivered at the accessible prey individual, and therefore also the amount of punishment received, could vary between chicks in different treatments and therefore have a confounding effect on the avoidance learning. However, there was no significant difference in pecking frequencies between group sizes on the first experimental day for birds with third instar (Kruskal–Wallis ANOVA, $H=6.34$, $p=0.097$) or fourth instar treatments (Kruskal–Wallis ANOVA, $H=2.49$, $p=0.48$). However, attacking birds pecked less when attacking during the second than they did on the first experimental day (Wilcoxon matched pairs test, $N=53$, $T=130.0$, $p<0.001$). Accordingly, more

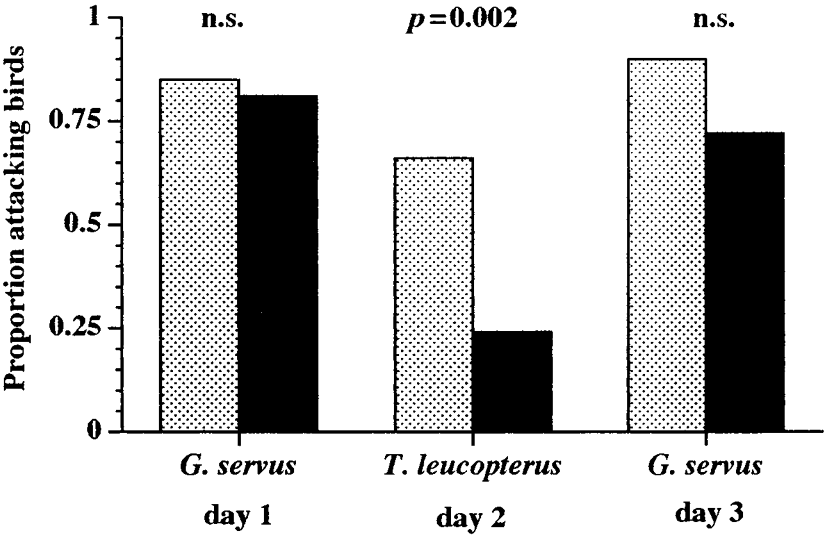

Figure 3. The proportion of birds attacking prey on three consecutive days: fourth instar *G. servus* larvae (solitary, $N=34$; groups, $N=36$) followed by fourth instar *T. leucopterus* larvae, again followed by fourth instar *G. servus* larvae. The same individual birds receive only solitary or aggregated prey during the experiment, and only birds that attacked the *G. servus* prey the first experimental day (solitary, $N=29$; groups, $N=29$) are represented in the following days. Light bars represent birds presented with solitary prey and dark bars represent birds presented with groups of 27 prey.

T. leucopterus larvae died from attacks from naive predators than from predators that had one prior experience ($\chi^2=7.10$, d.f. $=1$, $p<0.01$).

(b) *Interaction between bug group size and coloration*

Gregariousness does not seem to have a negative effect on the chicks' attacking behaviour when prey are not aposematic. There was no significant difference in attack probability for birds presented with solitary and aggregated *G. servus* larvae ($\chi^2=1.43$, d.f. $=1$, $p=0.23$; figure 2). There was no significant difference in attack probability of solitary *G. servus* larvae, as compared with solitary third and fourth instar *T. leucopterus* larvae ($\chi^2=1.99$, d.f. $=2$, $p=0.37$), suggesting that the effect of novelty did not differ between prey types. Furthermore, there was a significant interaction between group size (solitary/group of 27 prey) and prey coloration (aposematic, *T. leucopterus*/ non-aposematic, *G. servus*) on the attack probability of predators in a log–linear analysis ($\chi^2=6.03$, d.f. $=1$, $p=0.014$; figure 2). Thus, the effect of gregariousness differed between prey types.

The pattern of a greater avoidance of gregarious aposematic prey was repeated in the birds tested with aposematic *T. leucopterus* larvae the day after being tested with *G. servus* larvae. These too showed a greater aversion towards the gregarious rather than the solitary aposematic larvae (Fisher exact probability $=0.002$; figure 3). That these results with *T. leucopterus* larvae were not due to a negative experience of the *G. servus* larvae is shown by the fact that when presented with *G. servus* prey again, the attack probability increased for both treatments and there was no significant difference between attack probabilities on solitary and gregarious prey (Fisher exact probability $=0.57$; figure 3). In conclusion, it seems that the major part of the chicks' increased aversiveness to aggregations is due to the increase in the efficiency of the warning signal.

(c) *The effect of group size in mealworms*

In this case, gregariousness increased the attack probability of naive chicks. Twenty-one out of 30 pairs of chicks attacked solitary mealworms, and 28 out of 30 pairs attacked groups of mealworms (Fisher exact probability $=0.02$). This suggests that there is no innate avoidance of aggregated prey *per se*.

4. DISCUSSION

In these experiments the aversion of naive chicks increased with group size of the aposematic *T. leucopterus* bugs, but there was no difference between solitary and large groups of non-aposematic *G. servus* bugs. There was no obvious difference in prey novelty, because both prey species were initially attacked to the same degree in solitary presentations. In addition, as only one prey individual was accessible to the birds in both the solitary and the aggregated treatments, we do not except any difference in smell (Marples & Roper 1996; Rowe & Guilford 1996) between treatments with the same species. Therefore, we conclude that the aversiveness of prey grouping in this study can be explained as increased signal repellence of specific prey coloration, in this case a classical warning coloration. The fact that aggregated mealworms were even more attractive to naive chicks than were solitary mealworms supports this conclusion. Thus, one important function of aggregations may indeed be to increase the effect of aposematic signals (Poulton 1890; Beddard 1895; Cott 1940; Wilson 1975).

Aposematic coloration has at least three beneficial properties that have been discussed theoretically and shown experimentally on several occasions. One is the property of looking as different as possible from the cryptic profitable prey that the predators usually hunt (Turner 1975), effecting a neophobic reaction (Coppinger 1969, 1970) or possibly indifference in predators. Another property is contrast against the background (Harvey & Greenwood 1978), which has been shown to be important for avoidance learning in bird predators (Gittleman & Harvey 1980; Roper 1994). The third property is that some colour intensities and hues are more effective than others, regardless of background (Sillén-Tullberg 1985*b*; Roper 1990).

In extensive experiments using chicks as predators, Roper & Cook (1989) and Roper (1990) argued that novelty *per se* is usually too crude a concept to explain predator aversion, because predators often react differently towards equally novel but differently coloured prey. Moreover, they argued that contrast against the background, apart from facilitating avoidance learning, often attracts predators, at least in an initial stage of a predator–prey interaction. They concluded that the most important prey aspect to explain predator aversion is specific colours or colour combinations. The results of the present study lend support to the idea of specific colour being important, as the repellent effect of increasing group size was only significant for the warningly coloured prey.

Attack probability, decreased rather quickly with prey group size. Thus, we have found an unconditioned response gradient along a stimulus dimension consisting of the number of aposematic prey. We have previously shown a similar initial gradient along a dimension of increasing size of aposematic prey (Gamberale & Tullberg 1996*b*), and this finding was supported in the present experiment. It may be that the effects of increasing prey size and group size are based on the same principle, namely that of increasing the amount, or area, of visible warning colour.

Because of the experimental design, we could not separate an additional avoidance due to learning in birds with prior experience from the avoidance due to seeing the groups on the second day. However, the repellent effect of gregariousness is still present to some extent in experienced predators, and this resulted in fewer aggregated individuals being sampled also by experienced predators.

There are several ways in which gregariousness may reduce predation, of which a dilution effect (Bertram 1978; Turner & Pitcher 1986), operating through limited predation (i.e. predator satiation) on distasteful prey (Sillén-Tullberg & Leimar 1988), is perhaps the most important. The model by Sillén-Tullberg & Leimar (1988) showed that prey unprofitability may be sufficient for gregariousness to evolve, providing that the risk of discovery does not increase too much with group size (in addition, see Turner & Pitcher (1986)). However, the model also suggests that it is easier for gregariousness to evolve in already aposematic species. This is so because conspicuous coloration reduces the number of prey needing to be sampled during avoidance learning. Moreover, the increase in detection risk with gregariousness may not be so great when prey are warningly coloured, simply because this risk is already considerable for brightly coloured individuals. Thus, warning coloration is likely to facilitate the evolution of gregariousness by reducing both the cost of detection and the risk of being attacked when discovered.

The present experiment shows that a third factor may facilitate the evolution of gregariousness, namely the repellent effect of aposematic coloration. This effect increases with increasing prey group size and rather markedly reduces the risk of being attacked by both naive and experienced predators. This result is important because larval group size in insects may also be limited for reasons other than predation, e.g. female fecundity and host-plant resource limitations (Stamp 1980; Fitzgerald 1993), which means that the reduction in attack probability that warning coloration entails in an aggregation may sometimes be crucial, because the prey will be protected also in relatively small groups.

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