Confusion of predators does not rely on specialist coordinated behavior

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Antipredatory benefits are generally considered important in the evolution and maintenance of animal aggregations. One such benefit is the confusion effect: the reduced ease of prey capture experienced by some predators resulting from an inability to single out and attack an individual prey from a group as a result of cognitive or sensory limitations. Although widely cited, empirical data that do any more than demonstrate the effect are sparse. Here, we use the artificial system of humans attempting to “capture” images on a computer screen using a computer mouse to explore several hypotheses on the properties of the confusion effect. This system has the advantage that we can control the behavior of the prey and eliminate the risk of confounding factors due to differential prey behavior and/or phenotypes in groups of different sizes. One important result of our study is the demonstration that the confusion effect can occur in the absence of these confounding factors and indeed in the absence of complex coordinated behavior between individuals in the prey group (such as are commonly observed in schooling fish). We also demonstrate for the first time that an individual prey item can still benefit from the confusion effect if it is only loosely associated in space with a larger group of similar prey. Both these results suggest that the confusion effect can arise under less specialist circumstances than previously realized, and so the importance of this mechanism in shaping aggregation by prey and predator–prey interactions may be substantially greater than previously considered.

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confusion is aided by homogeneity in appearance of group members and that the predator can reduce or eliminate the confusion effect by focussing attacks on odd-looking individuals. The empirical basis for the oddity effect rests on the study of Ohguchi (1978) on sticklebacks preying on water fleas and those of Landeau and Terborgh (1986) and Theodorakis (1989) on bass preying on minnows. Each showed that the predator was more successful when a minority of prey group members were visibly distinct from the majority of group members. Because prey are known to modify their behavior according to the visual appearance of group mates, for example, in the context of visible signs of parasitic infection in shoaling fish (e.g., Barber and Huntingford 1996; Barber et al. 1998) or color morph (McRobert and Bradner 1998; Rosenthal and Ryan 2005), this oddity effect may be induced by context-dependent behavioral changes triggered by different group compositions. In order to explore this, we will investigate whether the oddity effect occurs in our model where prey behavior is unaffected by group composition. Secondly, we will explore whether the oddity effect generalizes beyond the fish predators for which it has previously been demonstrated. Also, Landeau and Terborgh (1986) were able to demonstrate that a single odd individual reduced the effect of confusion in prey groups of size 8 but could not demonstrate a similar effect in groups of size 15, suggesting that the oddity effect may only be a feature of small groups. In our experiment, we will use a much wider range of group sizes than has been previously possible to further explore this.

Landeau and Terborgh (1986) observed significant reduction in the confusion effect when a group of 8 fish contained 1 or 2 odd-looking individuals but no reduction when the number of odd individuals was 3 or 4. This suggests that the oddity effect requires that phenotype frequencies within the group are very skewed and that more balanced combinations of phenotype frequencies do not produce any diminution of confusion. Krause and Ruxton (2002) comment that “these very interesting results deserve much more widespread exposure and would greatly benefit from empirical exploration of their generality.” In this spirit, we here use another very different predator–prey system and a much wider range of group sizes compared with the study of Landeau and Terborgh (1986).

It is generally considered that predators can mitigate any effects of confusion by targeting individuals that are peripheral to the group and/or by attempting to isolate one individual from the rest of the group. Although the logic of this is appealing, empirical demonstrations are lacking. In surveying the empirical support for the confusion effect, Krause and Ruxton (2002) concluded that there are numerous suggestions that predators attempt to disrupt aggregations in order to isolate potential targets (Schaller 1972, Major 1978, Schmitt and Strand 1982); however, the extent to which predators benefit from this isolation remains unclear. Hence, again we will use our system to explore whether an individual that is spatially isolated from (but still near) a group of similar individuals gains any protection through predator confusion. Again, our ability to control prey behavior is particularly beneficial to the exploration of this question because in naturally occurring groups there is ample evidence of variation in both underlying phenotype and behavior between central and peripheral group members (for a review, see Krause 1994). Here, we explore the vulnerability of such peripheral individuals in the absence of these confounding factors.

It has commonly been observed that fish shoals become more compact (i.e., interindividual distances decrease) on detection of a nearby predator (Seghers 1974; Magurran and Picher 1987; Domenici et al. 2000) and this has often been interpreted as a behavioral response that improves the efficacy of the confusion effect (e.g., Krakauer 1995). However, despite the plausibility of this suggestion, there is currently no empirical evidence that more compact shoaling induces a stronger confusion effect; indeed, this question has never been addressed empirically before. Hence, the final aim of this study will be to provide the first empirical test of this conjecture.

In summary, we plan to explore the following 5 questions:

A: Is there a confusion effect in the absence of specialized grouping behavior?
B: Are odd-looking individuals more easily captured?
C: Does the oddity effect disappear for more balanced groups?
D: Is the confusion effect reduced if isolated individuals are targeted?
E: Does group compaction strengthen the confusion effect?

METHODS

The interactive computer program, implemented as a graphical user interface in Matlab (Mathworks 2004), tasked 88 human subjects with attacking moving tadpole-like objects by clicking on them with the mouse cursor.

The start of each screen presentation was signaled by a 3-s text countdown just above the middle of the 142 × 142-mm white clickable arena while the circular mouse cursor was frozen in the exact center. The cursor was then placed under user control, the attack is considered to begin at this point, and a group of tadpoles (each comprising a circular head 1.2-mm diameter and a 3-mm tail) emerged from a randomly chosen side and proceeded across the arena with the tail beating in a swimming fashion at 35.5 mm s⁻¹ and off the opposite side of the arena from where they originated. The tadpole group was initialized according to the treatment group (see The 5 Treatments) just outside the bounds of the arena prior to moving into view. A large red arrow was displayed for the first 0.5 s of the simulation that highlighted the target tadpole appropriate to each treatment, which the user should attack (Figure 1a).

The attack continued until either all the tadpoles had left the arena or a successful attack on the target tadpole was registered by placing the circular cursor around the tadpole (using the mouse) and left-clicking with the mouse after which the target tadpole turned green and the word “Hit” was displayed to the user in the center of the arena. Users were allowed multiple clicks during the simulation; neither clicks on non-target tadpoles nor miss clicks on the arena had any effect on the simulation. Although tadpoles tended to move directly across the arena perpendicular to the side from where they came, some random fluctuations (drawn independently for each individual) were added such that they changed the direction by \( \theta \sim N(0, 0.05) \) (mean and standard deviation) with probability per iteration \( P_{\text{turn}} = 0.3 \). Thus, although individuals moved in the same long-term average direction, their paths had a random component and the exact paths chosen by individuals were independent. They tended to return to their original cross-arena direction with probability \( 1 - P_{\text{turn}} = 0.7 \) by adopting the average vector between their previous iteration and original directions. This independence of paths between individuals meant that 2 individuals could occupy the same space momentarily but would inevitably quickly separate again due to the independence and stochasticity of their paths.

Each user was presented with 15 tadpole group sizes (1, 5, 10, 15, 20, 25, 30, 35, 40, 50, 60, 70, 80, 90, and 100) for each of 5 treatments as detailed below, presented in random order for each user. In order to retain user motivation, trials were terminated after 10 min, even if the user had not completed all 75 screens. We recorded the time in seconds taken to attack the target prey if successful for each screen presentation.
The 5 treatments

(1) Control group for determination of baseline confusion effect
These compact shoals contained identical tadpoles with black-colored head parts and black tails. They were initially uniformly-randomly located within a circular shoal shape (off screen as explained above) at a density of 1 tadpole per 3.55 mm$^2$. The target prey was determined by uniform-randomly choosing one of the tadpoles in each shoal.

(2) Oddity effect
We explored the effect of making the target prey odd looking compared with its shoal mates by coloring its head light gray (RGB color = [0.8 0.8 0.8]) and rendering all the other tadpoles black, as in the control (Figure 1a—this screen shot also shows the red arrow that is present for the first 0.5 s). The shoal was initialized as in the control with a density of 1 tadpole per 3.55 mm$^2$. The target prey was always the gray odd-looking tadpole.

(3) Heterogeneous distracters
This treatment was identical in all respects to the control group except that half of the tadpoles’ heads in the group were drawn black and half light gray. The target prey was drawn randomly from the set of black tadpoles such that the other black members acted as homogeneous distractors and the light gray ones the heterogeneous distractors. For odd group sizes, the number of black tadpoles was rounded up to the nearest integer so that there was always one more black than gray tadpole in these groups.

(4) Isolation
The shoal in this treatment group was initialized in an identical manner to the control group, that is, all-black tadpoles in a circular shoal at a density of 1 tadpole per 3.55 mm$^2$. The exception was that the target prey was offset by an arbitrary 35.5 mm from a random position within the shoal either up or down for a shoal moving side-to-side, or left or right for a shoal moving top-to-bottom (Figure 1b). This meant that the target prey was visually isolated from the rest of the shoal. The shoal was located so as both the main group and the isolated individual were rendered within the confines of the arena.

(5) Compaction/dispersion
This treatment group was identical to the control group except that the tadpoles were initially located in a shoal that was more dispersed than the other 4 treatments, at a density of 1 tadpole per 7.10 mm$^2$. The target prey was determined by uniform-randomly choosing one of the tadpoles in each shoal.

We measure the confusion effect both in terms of the frequency with which the prey was successfully hit and the time taken to achieve successful hits. Each screen is considered as an attack, although within a single screen, a human volunteer could make several unsuccessful clicks before a successful one. The software recorded all clicks, and volunteers generally made few unsuccessful clicks, such that our results would be qualitatively unchanged if we defined each click as a separate attack and/or if we censored the results after the first click on each screen. However, we prefer the presented definition of an attack because it captures the idea that the prey are at risk until they reach the safety of the edge of the screen, no matter how many attempts to capture the prey the predator makes during this time.

The frequency data are analyzed using binary logistic regression and the timing data by general linear model with identity of the volunteer predator and group size as explanatory factors. Because we are not interested in studying differences between volunteers, we do not report the variance explained by this factor, although we always include it in the model.

RESULTS

A: Is there a confusion effect in the absence of specialized grouping behavior? (treatment 1)

The 88 subjects experienced a total of 1156 screens of this treatment and failed to capture the target individual on 436 (38%) of occasions. There was no evidence that the probability

Figure 1
Black and white representations of sample screens used in tests for (a) the oddity effect, with 60 prey and with the arrow present for the first half second of each trial indicating the target tadpole, and (b) an isolated individual in a group of 60, immediately after being successfully attacked.
that the target prey was missed was related to group size (logistic regression, \(Wald = 0.40, P = 0.53\)). However, as can be seen from Figure 2, for cases where the target prey was eventually captured, the time to capture was longer when group size was higher (linear regression: \(F_{1,718} = 51.4, P < 0.001\)). Hence, analysis of this treatment suggests that there is a confusion effect, which shows up as an increase in the time taken to capture prey, but not as a decrease in the likelihood that the prey escapes.

B: Are odd-looking individuals more easily captured? (treatment 1 vs. treatment 2)

If there is an oddity effect, then we predict that the odd (gray) target of treatment 2 will be easier to capture than the black target of treatment 1. The 88 subjects experienced 1077 screens of treatment 2 and failed to capture the target prey on 351 (32%) of occasions. Combining the data from treatments 1 and 2, a binary logistic regression did not show a significant effect of group size (Wald = 0.41, \(P = 0.52\)) but did show a significant effect of treatment (Wald = 6.20, \(P = 0.013\)) on the probability of the target prey item being captured. An odd (gray) target in treatment 2 being significantly more likely to be captured than a black target in treatment 1.

If we consider the time to successfully capture the targeted prey item, then analysis of covariance (ANCOVA) with treatment as a fixed factor and group size as a covariate suggests that group size (\(F_{1,1445} = 76.9, P < 0.001\)) affected this time but provided no evidence of an effect of treatment (\(F_{1,1445} = 0.009, P = 0.93\)). Because we were also interested in whether the oddity effect might be influenced by group size, we also tested the interaction between treatment and group size, but this was not significant (\(F_{1,1355} = 0.40, P = 0.53\)).

C: Is group homogeneity needed for the confusion effect? (treatment 1 vs. treatment 3)

By comparing treatment 3 and treatment 1, we can explore whether the target was more likely to survive in the balanced group of 50% gray and 50% black, compared with an all-black group. The probability of the target avoiding capture is similar in the 2 treatments: 37% in treatment 3 and 38% in treatment 1. Logistic regression did not provide evidence that either treatment (Wald = 3.065, \(P = 0.080\) or group size (Wald = 1.69, \(P = 0.194\)) affected the probability that the targeted prey item is captured. If we consider the time to successfully capture the targeted prey item, then ANCOVA with treatment as a fixed factor and group size as a covariate suggests that group size (\(F_{1,1132} = 94.7, P < 0.001\)) affected this time but provides no evidence of an effect of treatment (\(F_{1,1132} = 2.68, P = 0.11\)). Thus, there was no difference between treatments 1 and 3.

In conclusion, we find that the confusion effect occurs if the phenotype of the target is common within the group, even if that phenotype does not dominate the group.

D: Are isolated individuals more vulnerable? (treatment 1 vs. treatment 4)

Treatment 4 differs from treatment 1 only in that the targeted individual was spatially isolated from the rest of the group. In treatment 4, 285 out of 1031 (28%) of target prey survived; this is noticeably lower than the 38% of treatment 1. Combining the data from the 2 treatments, logistic regression suggests that treatment (Wald = 24.44, \(P < 0.001\)) affected the probability that the targeted prey item is captured but provides no evidence of an effect of group size (Wald = 1.095, \(P = 0.295\)). Time to successful capture was affected by group size (\(F_{1,1280} = 63.305, P < 0.001\)), but there was no evidence of an effect of treatment (\(F_{1,1280} = 1.15, P = 0.252\)). The fact that there still is a group size effect for time to successful capture in treatment 4 suggests that although isolated individuals are more vulnerable than those individuals integrated into the group, they still gain some protection from the group and are less vulnerable than a lone individual (see Figure 3).

E: The effect of shoal compaction (treatment 1 vs. treatment 5)

Whereas treatment 1 is a compact shoal, treatment 5 is similar in all other respects but is a more dispered shoal. For treatment 5, 368 out of 983 prey (37%) survived attack; this is very similar to the 38% of treatment 1. Combining the data from the 2 treatments, logistic regression provides no evidence that
either treatment (Wald = 0.08, P = 0.93) or group size (Wald = 0.281, P = 0.59) affected the probability that the target prey is captured. The incremental capture was affected by group size (F(9,32) = 45.4, P < 0.001), but there was no evidence of an effect of treatment (F(1,32) = 0.93, P = 0.34). Hence, we find no evidence that shoal compaction affects prey capture in our system.

**DISCUSSION**

In our experiment, we used 2 measures of the confusion effect: the fraction of targeted prey that are successfully captured before disappearing from the edge of the screen and the time taken to successfully capture targeted prey. Both of these have ecological and evolutionary relevance. Our subjects only have a finite time to capture prey before they leave the screen; this may equate to predators only having a finite time to capture prey before, for example, the prey reaches protective shelter, or accelerates away from the predator, or the predator’s stamina is exhausted. However, even before this finite interval, there may be a fitness benefit to the predator in capturing prey as quickly as possible if this minimizes energetic expenditure by the predator, or the chance of alerting the focal predator’s own predators to its presence, or the risk of alerting conspecifics that may attempt to kleptoparasitize captured prey. Additionally, speed of capture may increase the ultimate success of attacks, if attacks can be interrupted during the attack process by, for example, other predators, and such interruptions lead to prey escape. Hence, although both are measures of predatory success, the most relevant measure will differ between systems. This is particularly important to note in situations where the 2 measures make different predictions. For example, our results in (A) suggest a confusion effect when predators get a fitness benefit from rapidly capturing the prey, but not if the predators are less time pressured.

Despite our artificial prey purposefully being designed to show no special coordinated behaviors that might influence predator confusion, we find a strong effect of predator confusion in our experimental system: with our human volunteers taking approximately 50% longer to catch their target in the largest groups compared with that same target presented on the screen; this may equate to predators only having a finite time to capture prey before they leave the screen (without a common preferred direction). Effectively, the group in the previous study the prey started at one side of the screen and all individuals moved in the same long-term average direction taking them across the screen, in the previous study the prey started at the center of the screen and all individuals took different random paths to the edge of the screen (without a common preferred direction). Effectively, the group in the previous study burst away from the initial predator position, in a similar way to the fountain effect that has been reported in some fish shoals (Hall et al. 1986).

Thus, the difference in distribution of behaviors within the prey group (in this study individuals had a similar long-term average direction; in Tosh et al. (2006) these directions where very different) is likely to explain the difference in the relationships between group size and strength of confusion effect. This suggests that although we have demonstrated that coordination of behaviors between group members is not required for the confusion effect, the distribution of behaviors within the group is likely to influence the strength of the predator’s confusion.

Our results demonstrate that the oddity effect that has previously been demonstrated using fish predators may well have greater generality, and thus, we should assume that the confusion effect should have a strong influence in driving assortative aggregation of prey and selection of prey individuals within groups (and indeed groups of prey) by predators on the basis of oddity. Our results do not support the suggestion of Landeau and Terborgh (1986) that the effect of oddity in reducing the confusion effect only occurs in smaller groups, and we found no evidence that the increased vulnerability of odd individuals within a group was confined to smaller group sizes. However, we were able to confirm the suggestion of these authors that the oddity effect disappears if the phenotype of the target is common within the group, even if that phenotype does not dominate the group. Specifically, we found that a targeted individual in a group of a given size was no more vulnerable if its phenotype made up only 50% of the group than if that phenotype made up 100% of the group. Now that we have demonstrated this effect, study of the fine detail of the relationship between group composition and vulnerability to predation in specific systems could be interesting.
It is no surprise that the isolated individual in treatment 4 does not receive the same protection from predation through the confusion effect as an individual that is part of a compact group. What is interesting is that this individual still benefits from confusion at all, despite being really quite spatially separate from the main group. As Figure 1b shows, the target individual is generally approximately as far from any other individual as the distance from one extreme of the group to the opposite extreme. Despite this, the time to capture this individual when paired with a large group is over 50% longer than when alone or paired with a small group. This suggests the hitherto unrecognized possibility that individuals that are not tightly bunched with others can still obtain some protection from confusion, and predators that split an individual from a group may lessen the confusion effect but not entirely destroy it. However, such benefits may be tempered if the close proximity of a large group attracts predators from afar: a phenomenon which our system could not evaluate.

We find no evidence that shoal compaction enhances the confusion effect, despite previous speculations that the compactness of fish groups often seen in response to a nearby predator leads to such a benefit to prey. However, there is no other empirical evidence that compaction enhances confusion, and indeed, the most comprehensive theoretical treatment on confusion (Tosh et al. 2006) explicitly explored the effect of compaction and found no evidence of enhanced confusion. Hence, based on current evidence, speculations that compaction enhances predator confusion should be treated with caution. It is possible that compaction of fish shoals occurs through a selfish-herd effect, with individual prey seeking to “hide behind” other group members (Hamilton 1971). However, it is premature to reject the possibility that group compaction may enhance confusion if compaction is combined with special coordinated behaviors that are seen in schooling fish but which were deliberately omitted from our investigations. In exploring the function of predator-induced compaction in fish, it would be useful to explore under what circumstances (if any) similar compaction is observed in other prey groups, such as ungulate herds or avian flocks.

Although our results add to the growing evidence for the confusion effects across a range of taxa, we do not mean to imply that we would expect either our results or the confusion effect in general to apply ubiquitously to predator–prey interactions. Firstly, of course, vision is not the primary sensory modality of all predators, and there is currently no empirical evidence of the confusion effect acting through nonvisual sensory systems. Turning to our experiments in particular, we would expect them to have more relevance to situations such as fish attacking small aggregations of invertebrates where all the prey can be seen simultaneously, rather than say lion attacking a herd of wildebeest, where the whole herd cannot be viewed simultaneously when the lion is close enough to attack.

In our simulations, prey behavior remained unchanged during each attack. It may be that some predator–prey systems show prey behavior that changes characteristically during an attack, for example, with the prey group gradually fragmenting. Such behaviors were not explored in our model but could impact on the effectiveness of any confusion effect. Studies of such phenomenon would need to be much more system specific than was our intention here.

In this study, we have been able to study a wider range of group sizes than has been possible in previous studies and been able to use orders of magnitude more predators to improve the power of our statistical tests. Further, we have been able to control the behavior of individual prey and avoid confounding effects of behavioral changes induced by the presence, behavior, or phenotype of other group members. This study has been effective in producing a considerable number of new insights about the working of the confusion effect. However, there is no denying that our predator–prey system is highly artificial, and the next challenge to empiricists interested in the confusion effect will be to find a more realistic system that preserves at least some of the powerful qualities of our system and allows the generality and applicability of our conclusions to be explored. Our demonstrations that the confusion effect does not require any specialist coordinated behavior between individuals beyond aggregating into a group and that individuals that appear significantly spatially separated from others can still benefit from confusion suggest that the confusion effect may well be much more prevalent and important in the natural world than is currently acknowledged. Thus, further work in this field would be particularly valuable.

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REFERENCES