



## Prey swarming: which predators become confused and why?

JONATHAN M. JESCHKE\* & RALPH TOLLRIAN†

\*Department of Biology II, Section of Evolutionary Ecology,  
Ludwig-Maximilians-Universität München

†Department of Animal Ecology, Evolution and Biodiversity,  
Biological Sciences and Biotechnology, Ruhr-Universität Bochum

(Received 31 March 2006; initial acceptance 5 June 2006;  
final acceptance 14 August 2006; published online 16 August 2007; MS. number: 8901)

When confronted with a swarm of their prey, many predators become confused and are less successful in their attacks. Despite the general notion that this confusion effect is a major reason for prey swarm formation, it is largely unknown how widespread it is and which predator or prey traits facilitate or impede it. We carried out experiments with four predator–prey systems: *Aeshna* and *Chaoborus* larvae, but not *Libellula* and *Triturus* larvae, became confused when confronted with high *Daphnia* densities. When combining this result with literature data, we found that predators became confused in 16 of the 25 predator–prey systems studied to date. Tactile predators appear to be generally susceptible, whereas visual predators are susceptible mainly when their prey is highly agile. This difference probably results from the superiority of the visual sensory system. However, while our study is an important step towards the mechanistic understanding of predator confusion, it also reveals how poor this understanding currently is.

© 2007 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

**Keywords:** *Aeshna cyanea*; attack efficiency; *Chaoborus obscuripes*; confusion effect; *Daphnia magna*; *Daphnia obtusa*; gregariousness; *Libellula depressa*; swarming effect; *Triturus alpestris*

The formation of animal swarms, where sometimes tons of biomass accumulate in a small space, is a spectacular phenomenon that attracted the attention of early ecologists and has remained important to ecological research (Allen 1920; Miller 1922). Animals form swarms because of foraging, energetic, defensive and other benefits: for example, they find food faster when they search together, they save energy when they move together, and they are better defended when they are together. Defence functions of gregariousness can be subdivided into the dilution effect (Hamilton 1971; Treisman 1975; Foster & Treherne 1981; Treherne & Foster 1982) on the one hand and effects that decrease predator hunting success on the other.

*Correspondence:* R. Tollrian, Department of Animal Ecology, Evolution and Biodiversity, Biological Sciences and Biotechnology, Ruhr-University Bochum, Universitätsstr. 150/ND05, D-44780 Bochum, Germany (email: [tollrian@rub.de](mailto:tollrian@rub.de)). J. M. Jeschke is at the Department of Biology II, Section of Evolutionary Ecology, Ludwig-Maximilians-Universität München, Grosshaderner Str. 2, D-82152 Planegg-Martinsried, Germany.

Examples of these latter effects are early warning (Miller 1922; Eibl-Eibesfeldt 1962; Pulliam 1973; Treisman 1975; Kenward 1978; Treherne & Foster 1981), a reduced detection probability by the predator (Treisman 1975; Inman & Krebs 1987), the potential for active defence (Bertram 1978), and the confusion effect which is the focus of this study.

The confusion effect is present if predators that are confronted with a swarm of their prey are restricted by their neuronal abilities, causing them to be less successful in their attacks. We thereby follow the definition of Krause & Ruxton (2002, page 19): 'The confusion effect describes the reduced attack-to-kill ratio experienced by a predator resulting from an inability to single out and attack individual prey'. Some researchers have defined the confusion effect more broadly and also included cases where the predator launches fewer attacks because of the decreased expectation of success (Miller 1922). However, it is hard to validate this reduction in attack rate empirically because attack rate also declines in the absence of confusion for the same reasons that lead to a type II functional

response (Jeschke et al. 2002, 2004). Furthermore, confusion does not necessarily influence the shape of a functional response, so it cannot be detected in this way either (Jeschke & Tollrian 2005). We therefore focus here on the confusion effect *sensu stricto* as defined above (for further information and references, see the Appendix and Bertram 1978).

Experimental work investigating whether a certain predator suffers from confusion is rare compared to the popularity of this concept and has mainly been restricted to two biological taxa, fish and birds (Appendix). To broaden our taxonomic perspective of predator confusion, we carried out experiments on the predator–prey systems *Aeshna cyanea* Müller (Odonata) – *Daphnia magna* Straus (Crustacea), *Libellula depressa* Linnaeus (Odonata) – *D. magna*, *Chaoborus obscuripes* van der Wulp (Diptera) – *Daphnia obtusa* Kurz, and *Triturus alpestris* Laurenti (Amphibia; Alpine newt) – *D. obtusa*.

We combined our results with data available from the literature to investigate, first, whether predator confusion is a widespread phenomenon and, second, which predator or prey traits facilitate or impede it. The first question has not, to our knowledge, been addressed before. Regarding the second question, it has long been supposed that erratic escape movements by prey might enhance predator confusion (Eibl-Eibesfeldt 1962; Humphries & Driver 1970), but the validity of this supposition has not been tested. The same is true for suggestions that predator confusion is related to disordered movements among the prey individuals forming a swarm, or to rapid changes in light reflected from the bodies of prey (Humphries & Driver 1970; Treherne & Foster 1981; Nishimura 2002). We have empirical data for only two predator or prey traits that indicate an effect on predator confusion. First, the confusion of predators is more severe if the prey individuals forming a swarm are morphologically more similar to each other (Ohguchi 1981; Landeau & Terborgh 1986; Tosh et al. 2006). Second, three-spined sticklebacks, *Gasterosteus aculeatus*, apparently become more confused if their prey is swimming faster (Ohguchi 1981). We generalized the latter finding and looked for further predator or prey traits affecting confusion.

## METHODS

### Experiment

In each of our four predator–prey systems, we transferred single predators to beakers containing defined numbers of *Daphnia*, thereby confronting the predators with a gradient of prey densities, up to those occurring naturally in swarms (Malone & McQueen 1983; Davies 1985; Kvam & Kleiven 1995). This direct confrontation precluded complications arising from predators avoiding swarms (Milinski 1979). The predators were caught in southern Bavarian ponds, and the prey came from laboratory cultures that originated from such ponds. The odonate and newt larvae were kept in separate tanks (40 × 60 cm, filled with water 5 cm deep) which contained plants (*Elodea*) and stones, in a room with natural

daylight at 21°C. They were fed *Daphnia* from our cultures *ad libitum* every day. After the experiment (after being kept for approximately 6 weeks), they were released into their native ponds. The *Chaoborus* larvae were kept in quantities of 10 individuals in 1.5-litre beakers. Each larva was fed with approximately 10 small *Daphnia* per day. The *Daphnia* were reared in 1.5-litre beakers in an artificial medium based on ultrapure water, trace elements and phosphate buffer (Jeschke & Tollrian 2000) in a climate-controlled room (20 ± 1°C) at room light (16:8 h day:night rhythm). They were fed the unicellular green alga *Scenedesmus obliquus* *ad libitum* every day. The medium was changed weekly. All predators had long experience with the prey but were hungry at the beginning of a trial (last fed on the previous day). The *Chaoborus* trials were carried out in autumn 1997 and the others in summer 1998 in the laboratory at room temperature (21°C). Experimental time began with the first attack of the predator. We carried out short trials to prevent satiation of the predators influencing their behaviour. Except for *T. alpestris* – *D. obtusa*, we did not replace eaten prey, to avoid disturbing the predators and because the numbers of prey eaten were small compared to the numbers of prey present. In each trial, we counted the attacks and the prey eaten and calculated predator attack efficiency as the ratio of the latter to the former. Since *L. depressa* larvae did not always eat the prey they successfully attacked and killed, we also counted these ‘wasteful kills’ (Johnson et al. 1975) and added them to the number of prey eaten. Wasteful kills were rare, however. Our primary goal was not to compare effects of the same food among predators but to test for confusion, measured as decreasing attack efficiency, in each system. Our predators differed considerably in their preferred prey size and prey-scanning volume. We therefore ran test trials to adjust these two factors as well as density of prey and trial duration to the specific abilities of each predator. In the following, we give additional information on the organisms used and the specific experimental conditions.

### *Aeshna cyanea* (Odonata) – *Daphnia magna* (Crustacea)

Larvae of *A. cyanea* are visual predators with a saltatory search behaviour, i.e. they can switch between an ambush and a cruising foraging tactic (Pritchard 1965). An *Aeshna* attack was defined as a rapid extension of the labium towards a nearby prey. We replicated each of seven prey densities (10, 25, 50, 100, 150, 200, 250) five times except prey density 200 where we had four replicates, i.e. five or four *Aeshna* individuals, respectively, were used at each density. Each trial ran with third- and fourth-juvenile-instar *D. magna* in a volume of 280 ml and lasted 2 min.

### *Libellula depressa* (Odonata) – *Daphnia magna*

Larvae of *L. depressa* are ambush predators that select their prey visually (Pritchard 1965). We defined an attack as a rapid extension of the labium towards a nearby prey. We replicated each of eight prey densities (1, 2, 3, 5, 10, 20, 50, 100) six times, except prey density 100 where we

had five replicates. Each trial ran with small *L. depressa* larvae (mean length = 13 mm) and first-adult-instar *D. magna* in a volume of 200 ml and lasted 10 min.

#### *Chaoborus obscuripes* (Diptera) – *Daphnia obtusa* (Crustacea)

*Chaoborus* larvae are tactile hunting ambush predators (Duhr 1955). Kvam & Kleiven (1995) suggested that daphnids sometimes form swarms to defend themselves against *Chaoborus* larvae. An attack was defined as a jerky movement directed to a nearby prey (Swift & Fedorenko 1975). We had 10 replicates for each of eight prey densities (5, 10, 15, 20, 25, 35, 50, 70). We used fourth-instar *Chaoborus* larvae (mean length = 11.6 mm). To standardize the many *Daphnia* to an equal size, we sieved them and used those that passed a 500- $\mu$ m gauze but were retained by a 200- $\mu$ m one. The experimental volume was 40 ml and the duration 30 min.

#### *Triturus alpestris* (Amphibia; Alpine newt) – *Daphnia obtusa*

*Triturus alpestris* larvae hunt visually. Similarly to *A. cyanea*, they switch between an ambush and a cruising foraging tactic (R. Tollrian, personal observation). A *Triturus* attack was defined as snapping at a nearby prey, which usually followed an orientation into the direction of the prey. We had six replicates for each of 10 prey densities (1, 2, 3, 5, 7, 10, 20, 40, 60, 100), except prey densities 60 and 100 where we had five replicates. Each trial ran with small *T. alpestris* larvae (mean length = 25.8 mm) and fourth-juvenile-instar *D. obtusa* in a volume of 400 ml and lasted 10 min.

### Comparative Analysis

To investigate whether predator confusion is a widespread phenomenon and which predator or prey traits facilitate or impede it, we combined the results of our experiment with those of previous studies, for which we searched the databases BIOSIS and ISI Web of Science. In these studies, together with those cited therein, we found data from 24 predator–prey systems, in addition to our four making a total of 28 systems (Appendix). To test for publication bias, we compared the presence/absence of a confusion effect with the impact factor of the journal where the results were published (Leimu & Koricheva 2004; Thomson ISI 2004).

Since predator confusion might correlate with the degree of prey agility (Eibl-Eibesfeldt 1962; Humphries & Driver 1970; Ohguchi 1981), we tried to quantify this trait. It must be related to the agility of the predator's prey-catching organ and should ideally include speed, acceleration and manoeuvrability (see also Howland 1974). The degree of prey position predictability (where a prey item will be in the next moment) is partly included in prey manoeuvrability because these should be negatively correlated. Also important are the movements of the prey items relative to each other. If they all flee in the same direction, it is easier for the predator to predict the position of a certain individual for the next moment

(Humphries & Driver 1970; Treherne & Foster 1981; Nishimura 2002). Since information on these flight patterns is rare, we did not consider them for our analysis and focused instead on prey agility for which data are more frequent but still scarce, especially for manoeuvrability. When possible, we calculated relative prey agility as relative prey speed (i.e. prey escape speed divided by predator attack speed) or relative prey acceleration (i.e. prey escape acceleration divided by predator attack acceleration). When no such data were available, we estimated whether the agility of prey is much lower than that of the predator or roughly similar.

### Statistical Analyses

For statistical analyses, we used SPSS for Windows version 12.0.1 (SPSS Inc., Chicago, IL, U.S.A.).

## RESULTS

### Experiment

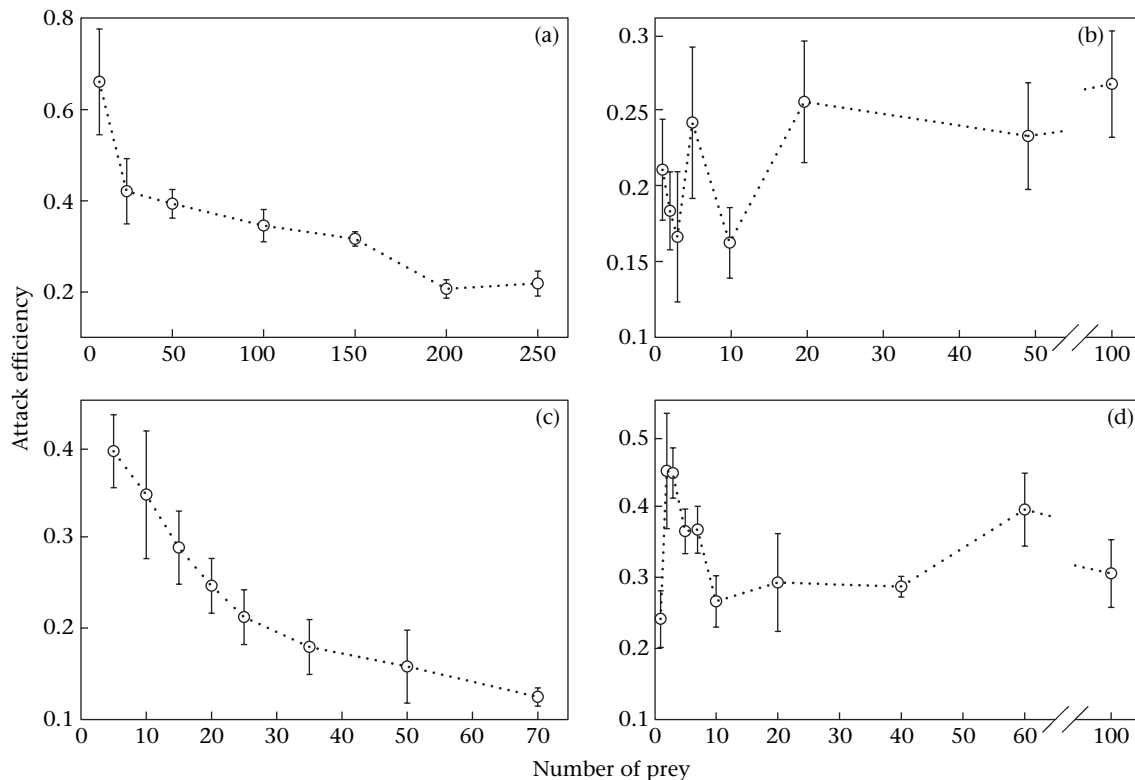
We found a confusion effect for *A. cyanea* preying on *D. magna* (two-tailed Spearman rank correlation:  $r_s = -0.784$ ,  $N = 34$ ,  $P < 0.001$ ) and for *C. obscuripes* preying on *D. obtusa* ( $r_s = -0.630$ ,  $N = 80$ ,  $P < 0.001$ ) but not for either *L. depressa* preying on *D. magna* ( $r_s = 0.242$ ,  $N = 47$ , i.e. no negative correlation between attack efficiency and prey density) or *T. alpestris* preying on *D. obtusa* ( $r_s = -0.108$ ,  $N = 58$ ,  $P = 0.420$ ; Fig. 1).

### Comparative Analysis

Three of the 28 predator–prey systems summarized in the Appendix were excluded from our analysis because of ambiguous results (see Appendix for details). In the remaining 25 systems, the overall frequency of confusion was 64%. The median impact factor of journals in which an absence of confusion was published was 2.14 compared to 2.56 for journals in which the presence of confusion was published. However, this slight publication bias is not significant (two-tailed exact median test:  $N = 21$ ,  $P = 0.361$ ), suggesting that studies reporting the presence of confusion are not significantly less likely to be published than those reporting the absence of confusion. The correlation is small as well ( $r_s = 0.042$ ). Thus, predator confusion can be expected to be similarly common in systems other than the ones summarized in the Appendix.

The results do not indicate a strong influence of taxonomy on confusion. The frequency of confusion was 60% for invertebrates ( $N = 10$ ) and 67% for vertebrates ( $N = 15$ ; fish: 75%,  $N = 8$ ; birds: 80%,  $N = 5$ ). However, the scarcity of data does not allow a definitive answer here.

The occurrence of predator confusion does appear to be influenced by both the mode of prey detection and the degree of prey agility. Predators that do not actively detect their prey should not become confused at all. This agrees with empirical data from both the carnivorous plant *Utricularia vulgaris*, where an attack is triggered by direct contact with the prey, and from the passively filter-feeding



**Figure 1.** An empirical test of the presence of predator confusion in four predator–prey systems. (a) *Aeshna cyanea* – *Daphnia magna*, (b) *Libellula depressa* – *D. magna*, (c) *Chaoborus obscuripes* – *Daphnia obtusa* and (d) *Triturus alpestris* – *D. obtusa*. Means  $\pm$  SE are given. Attack efficiency is the ratio of number of prey eaten to the number of attacks.

copepod *Acartia tonsa*. Conversely, all three tactile predators investigated so far showed a confusion effect. In visual predators, finally, confusion seems to correlate with the degree of prey agility. If we classify prey agility as high for values larger than 0.3 in the Appendix, the frequency of confusion is 79% for highly agile prey ( $N = 14$ ) but only 33% for prey of low agility ( $N = 6$ ), and the correlation between the occurrence of confusion in visual predators and the degree of prey agility (low or high) is significant (one-tailed Spearman rank correlation:  $r_s = 0.435$ ,  $N = 20$ ,  $P = 0.028$ ; we used a one-tailed test because a negative correlation between confusion and agility is not reasonable). We can conceptually summarize the Appendix as follows. (1) Visual predators tend to become confused if they are confronted with highly agile prey. (2) Tactile predators usually show confusion. (3) Predators without a sensory system for detecting prey do not show confusion. This conceptual summary is correct for 20 of the 25 predator–prey systems (80%).

## DISCUSSION

Predator confusion appears to be a widespread phenomenon, as it has been observed in 64% of the predator–prey systems investigated to date. This figure is not hampered by a strong publication bias.

We found that tactile predators seem generally susceptible to confusion. In contrast, visual predators seem susceptible mainly if their prey is highly agile (Eibl-Eibesfeldt 1962; Humphries & Driver 1970; Ohguchi

1981). The suggestion that tactile predators are generally susceptible to confusion is challenged by a small sample size and the fact that prey of only a single genus, *Daphnia*, were used in all but one study. If we none the less assume the validity of this suggestion, we may ask why tactile and visual predators differ. Confusion has been empirically and theoretically shown to decrease if a prey swarm includes odd individuals (Ohguchi 1981; Landeau & Terborgh 1986; Krakauer 1995; Tosh et al. 2006). Thus, confusion appears to decrease if it is easier for a predator to single out individual prey. This ability to single out individuals includes the ability to concentrate on individuals at the edge of a swarm and to reduce the field of attack. It surely differs between predators, and our comparative analysis suggests that visual predators are better able than tactile predators to single out individuals. This is admittedly conjecture but makes sense because singling out an individual means to detect one or more differences between this and other members of the swarm (Milinski 1979), which requires a high spatial resolution, and eyes have a higher resolution than mechanoreceptors (Dusenbery 1992). Our results imply that predators as well as prey have coevolutionary options to avoid or enhance confusion, respectively. From the predators' perspective, the crucial point in avoiding confusion seems to be the ability to single out individual prey. From the prey's perspective, swarm formation should be an especially effective defence against tactile predators.

This study is an important step towards the mechanistic understanding of predator confusion. However, it also



reveals how little is known about this classical concept, thereby hopefully motivating researchers to address the many important open questions. Specifically, the taxonomic bias in the data calls for studies in further predator–prey systems. Second, since our finding that tactile predators seem especially susceptible to confusion is challenged by a small sample size, its validity should be tested for other tactile predators. Third, our comparison of the influence of the mode of prey detection and the degree of prey agility on the occurrence of predator confusion needs more measured data on prey agility. Fourth, this comparison may be extended by considering further potentially important animal traits, such as the size of the prey relative to the predator's prey-catching organ (relatively smaller prey might allow less precise attacks), the visibility of the prey, or the amount of light reflected from the bodies of prey (Treherne & Foster 1981). Finally, data on the relation between the probability of attack and swarm density, as well as on attack rate and swarm density, would be helpful to test the suggestion that singling out individual prey is a mechanism that allows predators to overcome confusion.

### Acknowledgments

We appreciate funding from the DFG and thank Sonja Hübner, Mechthild Kredler and Eric Röttinger for their help with the experiment. We are also grateful to Wilfried Gabriel for discussions and to Sebastian Diehl, Knut Helge Jensen, Michael Kopp, Burt Kotler, Piers Napper, Andrew Sih and three anonymous referees for their comments on the manuscript.

### References

- Alerstam, T. 1987. Radar observations of the stoop of the peregrine falcon *Falco peregrinus* and the goshawk *Accipiter gentilis*. *Ibis*, **129**, 267–273.
- Allen, W. E. 1920. Behavior of loon and sardines. *Ecology*, **1**, 309–310.
- Bertram, B. C. R. 1978. Living in groups: predators and prey. In: *Behavioural Ecology* (Ed. by J. R. Krebs & N. B. Davies), pp. 64–96. Oxford: Blackwell Scientific.
- Brewer, M. C., Dawidowicz, P. & Dodson, S. I. 1999. Interactive effects of fish kairomone and light on *Daphnia* escape behavior. *Journal of Plankton Research*, **21**, 1317–1335.
- Caldow, R. W. G. & Furness, R. W. 2001. Does Holling's disc equation explain the functional response of a kleptoparasite? *Journal of Animal Ecology*, **70**, 650–662.
- Cresswell, W. 1994. Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. *Animal Behaviour*, **47**, 433–442.
- Davies, J. 1985. Evidence for a diurnal horizontal migration in *Daphnia hyalina lacustris* Sars. *Hydrobiologia*, **120**, 103–105.
- Davies, N. B. 1977. Prey selection and social behaviour in wagtails (Aves: Motacillidae). *Journal of Animal Ecology*, **46**, 37–57.
- Duhr, B. 1955. Über Bewegung, Orientierung und Beutefang der Corethralarve (*Chaoborus crystallinus* de Geer). *Zoologische Jahrbücher Physiologie*, **65**, 378–429.
- Dusenbery, D. B. 1992. *Sensory Ecology: How Organisms Acquire and Respond to Information*. New York: W. H. Freeman.
- Eibl-Eibesfeldt, I. 1962. Freiwasserbeobachtungen zur Deutung des Schwarmverhaltens verschiedener Fische. *Zeitschrift für Tierpsychologie*, **19**, 165–182.
- Elliott, J. P., McTaggart Cowan, I. & Holling, C. S. 1977. Prey capture by the African lion. *Canadian Journal of Zoology*, **55**, 1811–1828.
- Englund, G. & Harms, S. 2001. The functional response of a predatory plant preying on swarming zooplankton. *Oikos*, **94**, 175–181.
- Foster, W. A. & Treherne, J. E. 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature*, **293**, 466–467.
- Garland, T., Jr. 1983. The relation between maximal running speed and body mass in terrestrial mammals. *Journal of Zoology*, **199**, 157–170.
- Hamilton, W. D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology*, **31**, 295–311.
- Harper, D. G. & Blake, R. W. 1990. Fast-start performance of rainbow trout *Salmo gairdneri* and northern pike *Esox lucius*. *Journal of Experimental Biology*, **150**, 321–342.
- Hirvonen, H. & Ranta, E. 1996. Prey to predator size ratio influences foraging efficiency of larval *Aeshna juncea* dragonflies. *Oecologia*, **106**, 407–415.
- Howland, H. C. 1974. Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. *Journal of Theoretical Biology*, **47**, 333–350.
- Humphries, D. A. & Driver, P. M. 1970. Protean defence by prey animals. *Oecologia*, **5**, 285–302.
- Inman, A. J. & Krebs, J. 1987. Predation and group living. *Trends in Ecology & Evolution*, **2**, 31–32.
- Jensen, K. H. & Larsson, P. 2002. Predator evasion in *Daphnia*: the adaptive value of aggregation associated with attack abatement. *Oecologia*, **132**, 461–467. doi:10.1007/s00442-002-0979-4.
- Jeschke, J. M. & Tollrian, R. 2000. Density-dependent effects of prey defences. *Oecologia*, **123**, 391–396.
- Jeschke, J. M. & Tollrian, R. 2005. Effects of predator confusion on functional responses. *Oikos*, **111**, 547–555.
- Jeschke, J. M., Kopp, M. & Tollrian, R. 2002. Predator functional responses: discriminating between handling and digesting prey. *Ecological Monographs*, **72**, 95–112.
- Jeschke, J. M., Kopp, M. & Tollrian, R. 2004. Consumer-food systems: why type I functional responses are exclusive to filter feeders. *Biological Reviews*, **79**, 337–349. doi:10.1017/s1464793103006286.
- Johnson, D. M., Akre, B. G. & Crowley, P. H. 1975. Modeling arthropod predation: wasteful killing by damselfly naiads. *Ecology*, **56**, 1081–1093.
- Kenward, R. E. 1978. Hawks and doves: factors affecting success and selection in goshawk attacks on woodpigeons. *Journal of Animal Ecology*, **47**, 449–460.
- Krakauer, D. C. 1995. Groups confuse predators by exploiting perceptual bottlenecks: a connectionist model of the confusion effect. *Behavioral Ecology and Sociobiology*, **36**, 421–429.
- Krause, J. & Godin, J.-G. J. 1995. Predator preferences for attacking particular group sizes: consequences for predator hunting success and prey predation risk. *Animal Behaviour*, **50**, 465–473.
- Krause, J. & Ruxton, G. D. 2002. *Living in Groups*. Oxford: Oxford University Press.
- Krause, J., Ruxton, G. D. & Rubenstein, D. 1998. Is there always an influence of shoal size on predator hunting success? *Journal of Fish Biology*, **52**, 494–501.
- Kvam, O. V. & Kleiven, O. T. 1995. Diel horizontal migration and swarm formation in *Daphnia* in response to *Chaoborus*. *Hydrobiologia*, **307**, 177–184.
- Landeau, L. & Terborgh, J. 1986. Oddity and the 'confusion effect' in predation. *Animal Behaviour*, **34**, 1372–1380.

- Leimu, R. & Koricheva, J.** 2004. Cumulative meta-analysis: a new tool for detection of temporal trends and publication bias in ecology. *Proceedings of the Royal Society of London, Series B*, **271**, 1961–1966. doi:10.1098/rspb.2004.2828.
- Malone, B. J. & McQueen, D. J.** 1983. Horizontal patchiness in zooplankton populations in two Ontario kettle lakes. *Hydrobiologia*, **99**, 101–124.
- Meinertzhagen, R.** 1955. The speed and altitude of bird flight (with notes on other animals). *Ibis*, **97**, 81–117.
- Milinski, M.** 1979. Can an experienced predator overcome the confusion of swarming prey more easily? *Animal Behaviour*, **27**, 1122–1126.
- Milinski, M.** 1990. Information overload and food selection. *NATO ASI Series*, G20, 721–736.
- Milinski, M. & Curio, E.** 1975. Untersuchungen zur Selektion durch Räuber gegen Vereinzelung der Beute. *Zeitschrift für Tierpsychologie*, **37**, 400–402.
- Milinski, M. & Heller, R.** 1978. Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.). *Nature*, **275**, 642–644.
- Miller, R. C.** 1922. The significance of the gregarious habit. *Ecology*, **3**, 375–382.
- Morgan, M. J. & Godin, J.-G. J.** 1985. Antipredator benefits of schooling behaviour in a cyprinodontid fish, the banded killifish (*Fundulus diaphanus*). *Zeitschrift für Tierpsychologie*, **70**, 236–246.
- Neill, S. R. S. J. & Cullen, J. M.** 1974. Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. *Journal of Zoology*, **172**, 549–569.
- Nelmes, A. J.** 1974. Evaluation of the feeding behaviour of *Prionchulus punctatus* (Cobb), a nematode predator. *Journal of Animal Ecology*, **43**, 553–565.
- Nishimura, S. I.** 2002. A predator's selection of an individual prey from a group. *BioSystems*, **65**, 25–35.
- Ohguchi, O.** 1981. Prey density and selection against oddity by three-spined sticklebacks. *Advances in Ethology*, **23**, 1–79.
- Paffenhöfer, G.-A. & Stearns, D. E.** 1988. Why is *Acartia tonsa* (Copepoda: Calanoida) restricted to nearshore environments? *Marine Ecology Progress Series*, **42**, 33–38.
- Page, G. & Whitacre, D. F.** 1975. Raptor predation on wintering shorebirds. *Condor*, **77**, 73–83.
- Pastorok, R. A.** 1981. Prey vulnerability and size selection by *Chaoborus* larvae. *Ecology*, **62**, 1311–1324.
- Peter, D. & Kestenholz, M.** 1998. Sturzflüge von Wanderfalke *Falco peregrinus* und Wüstenfalke *F. pelegrioides*. *Der Ornithologische Beobachter*, **95**, 107–112.
- Pritchard, G.** 1965. Prey capture by dragonfly larvae (Odonata; Anisoptera). *Canadian Journal of Zoology*, **43**, 271–289.
- Pulliam, H. R.** 1973. On the advantages of flocking. *Journal of Theoretical Biology*, **38**, 419–422.
- Schradin, C.** 2000. Confusion effect in a reptilian and a primate predator. *Ethology*, **106**, 691–700.
- Swift, M. C. & Fedorenko, A.** 1975. Some aspects of prey capture by *Chaoborus* larvae. *Limnology and Oceanography*, **20**, 418–425.
- Thomson ISI.** 2004. *Journal Citation Reports Science Edition 2003*. <http://www.isiwebofknowledge.com>.
- Tosh, C. R., Jackson, A. L. & Ruxton, G. D.** 2006. The confusion effect in predatory neural networks. *American Naturalist*, **167**, E52–E65.
- Treherne, J. E. & Foster, W. A.** 1981. Group transmission of predator avoidance behaviour in a marine insect: the Trafalgar effect. *Animal Behaviour*, **29**, 911–917.
- Treherne, J. E. & Foster, W. A.** 1982. Group size and anti-predator strategies in a marine insect. *Animal Behaviour*, **30**, 536–542.
- Treisman, M.** 1975. Predation and the evolution of gregariousness. I. Models for concealment and evasion. *Animal Behaviour*, **23**, 779–800.
- Turesson, H. & Brönmark, C.** 2004. Foraging behaviour and capture success in perch, pikeperch and pike and the effects of prey density. *Journal of Fish Biology*, **65**, 363–375.
- Van Orsdol, K. G.** 1984. Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda. *African Journal of Ecology*, **22**, 79–99.
- Welty, J. C.** 1934. Experiments in group behaviour of fishes. *Physiological Zoology*, **7**, 85–128.

## Appendix

**Table A1.** Empirical data on the confusion effect

Predator	Prey detection	Prey	Relative prey agility*	Confusion observed? (expected)†
<b>Carnivorous plants</b>				
<i>Utricularia vulgaris</i>	None	<i>Polyphemus pediculus</i> (Crustacea)	—	− <sup>1</sup> (−)
<b>Nematodes</b>				
<i>Prionchulus punctatus</i>	Tactile	<i>Aphelenus avenae</i> (Nematoda)	(ca. 1)	+ <sup>2</sup> (+)
<b>Molluscs: cephalopods</b>				
<i>Loligo vulgaris</i> (squid)	Visual	<i>Atherina</i> spp. (Pisces)	(ca. 1)	+ <sup>3</sup> (+)
<i>Sepia officinalis</i> (cuttlefish)	Visual	<i>Mugil</i> spp. (mullet)	(ca. 1)	+ <sup>3</sup> (+)
<b>Crustaceans</b>				
<i>Acartia tonsa</i>	None (filtering) <sup>4</sup>	<i>Gyrodinium fissum</i> (Flagellata)	(<0.1)	− <sup>4</sup> (−)
<b>Insects</b>				
Odonate larvae				
<i>Aeshna cyanea</i>	Visual <sup>5</sup>	<i>Daphnia magna</i> (Crustacea)	ca. 0.25 <sup>6</sup>	+ <sup>7</sup> (−)
<i>Aeshna juncea</i>	Visual <sup>5</sup>	<i>D. magna</i> (small/medium/large)	ca. 0.25 <sup>6</sup>	+/-/- <sup>8</sup> (−)
<i>Libellula depressa</i>	Visual <sup>5</sup>	<i>D. magna</i>	ca. 0.25 <sup>6</sup>	− <sup>7</sup> (−)
Dipteran larvae				
<i>Chaoborus flavicans</i>	Tactile <sup>9</sup>	<i>Daphnia pulex</i>	ca. 0.02 <sup>10</sup>	+ <sup>11</sup> (+)
<i>Chaoborus obscuripes</i>	Tactile <sup>9</sup>	<i>Daphnia obtusa</i>	ca. 0.02 <sup>10</sup>	+ <sup>7</sup> (+)

Table A1 (continued)

Predator	Prey detection	Prey	Relative prey agility*	Confusion observed? (expected)†
<b>Fish</b>				
<i>Aequidens pulcher</i> (blue acara cichlid)	Visual	<i>Poecilia reticulata</i> (guppy)	(ca. 0.5–1)	+ <sup>12</sup> (+)
<i>Ambloplites rupestris</i> (rock bass)	Visual	<i>Semotilus atromaculatus</i> (creek chub)	(ca. 0.5–1)	? <sup>13</sup> (+)
<i>Esox lucius</i> (pike)	Visual	Cyprinids <sup>14</sup>	(ca. 0.1–0.3) <sup>15</sup>	+ <sup>3</sup> (–)
<i>Esox lucius</i> (pike)	Visual	<i>Rutilus rutilus</i> (roach)	(ca. 0.1–0.3) <sup>15</sup>	– <sup>16</sup> (–)
<i>Micropterus salmoides</i> (largemouth bass)	Visual	<i>Hybognathus nuchalis</i> (silvery minnow)	(ca. 0.5–1) <sup>17</sup>	+ <sup>18</sup> (+)
<i>Morone americana</i> (white perch)	Visual	<i>Fundulus diaphanus</i> (banded killifish)	(ca. 0.5–1)	? <sup>19</sup> (+)
<i>Perca fluviatilis</i> (perch)	Visual	<i>Poecilia vivipara</i> (guppy)	(ca. 0.5–1) <sup>20</sup>	+ <sup>7</sup> (+)
<i>Perca fluviatilis</i> (perch)	Visual	<i>Rutilus rutilus</i> (roach)	(ca. 0.5–1) <sup>20</sup>	+ <sup>16</sup> (+)
<i>Sardinops sagax</i> (South american pilchard)	Visual	<i>Halobates robustus</i> (ocean skater)	(ca. 1) <sup>21</sup>	+ <sup>22</sup> (+)
<i>Stizostedion lucioperca</i> (zander)	Visual	<i>Rutilus rutilus</i> (roach)	(ca. 0.5–1)	– <sup>16</sup> (+)
<b>Amphibians: newts</b>				
<i>Triturus alpestris</i> (Alpine newt)	Visual	<i>D. obtusa</i>	(ca. 0.1) <sup>23</sup>	– <sup>7</sup> (–)
<b>Birds</b>				
<i>Accipiter gentilis</i> (goshawk)	Visual	<i>Columba palumbus</i> (woodpigeon)	(ca. 0.3–1) <sup>24</sup>	+ <sup>25</sup> (+)
<i>Accipiter nisus</i> (sparrowhawk)	Visual	<i>Tringa totanus</i> (redshank)	(ca. 0.3–1)	+ <sup>26</sup> (+)
<i>Falco columbarius</i> (merlin)	Visual	<i>Callidris minutilla</i> (least sandpiper)	(ca. 0.3–1)	? <sup>27</sup> (+)
<i>Falco peregrinus</i> (peregrine falcon)	Visual	<i>Tringa totanus</i> (redshank)	(ca. 0.3–1) <sup>28</sup>	+ <sup>26</sup> (+)
<i>Motacilla</i> spp. (wagtails)	Visual	Scatophagids (Insecta: Diptera)	(ca. 0.5)	+ <sup>29</sup> (+)
<i>Stercorarius parasiticus</i> (Arctic skua)	Visual	Fish-carrying auks	(ca. 1) <sup>30</sup>	– <sup>31</sup> (+)
<b>Mammals</b>				
<i>Panthera leo</i> (lion)	Visual	Ungulates	0.6/1.2 <sup>32</sup>	– <sup>33</sup> (+)

This table lists predator–prey systems in which the relation between predator attack efficiency and the number or density of aggregated prey has been investigated, where attack efficiency is the number of successful attacks divided by the total number of attacks. Confusion is indicated by a decrease in attack efficiency with the number or density of aggregated prey. We do not list predators that apparently show a confusion effect but for which explicit data on the relation between attack efficiency and the number or density of aggregated prey are lacking (Welty 1934; Milinski & Curio 1975; Milinski & Heller 1978; Milinski 1979, 1990; Ohguchi 1981; Schradin 2000; Tosh et al. 2006). The inclusion of such predators would lead to an overestimation of the overall frequency of predator confusion. This frequency is  $p = 0.64 \pm 0.096$  ( $\bar{X} \pm SE$ ,  $N = 25$ ; ambiguous results (?) have been excluded). Sources: (1) Englund & Harms (2001); (2) Nelmes (1974); (3) Neill & Cullen (1974); (4) Paffenhöfer & Stearns (1988); (5) Pritchard (1965); (6) relative prey speed ca. 0.25 (mean *Daphnia* escape speed ca. 0.1 m/s, Brewer et al. 1999; mean odonate larva attack speed ca. 0.4 m/s, Pritchard 1965); (7) this study; (8) counted as “–” in the calculation of  $p$ , Hirvonen & Ranta (1996); (9) Dühr (1955); (10) relative prey speed ca. 0.02 (mean *Daphnia* escape speed ca. 0.1 m/s, Brewer et al. 1999; mean *Chaoborus* attack speed ca. 4.5 m/s, estimation based on *Chaoborus* attacking time given by Pastorok 1981); (11) Jensen & Larsson (2002); (12) Krause & Godin (1995); (13) the presence of confusion is unclear because of a lack of replicates (Krause et al. 1998); (14) mostly *Alburnus alburnus* (bleak) and *Leuciscus leuciscus* (dace); (15) maximum pike attack speed = 4.0 m/s, maximum pike attack acceleration = 120 m/s<sup>2</sup> (Harper & Blake 1990); (16) Turesson & Brönmark (2004); (17) maximum bass attack speed = 1.0 m/s (reviewed by Harper & Blake 1990); (18) Landeau & Terborgh (1986); (19) the presence of confusion is unclear because of inconsistent data (Morgan & Godin 1985); (20) maximum perch attack speed = 1.15 m/s, maximum perch attack acceleration = 24 m/s<sup>2</sup> (reviewed by Harper & Blake 1990); (21) mean ocean skater escape speed = 0.28 m/s (Treherne & Foster 1981); (22) Foster & Treherne (1981), Treherne & Foster (1982); (23) mean *Daphnia* escape speed ca. 0.1 m/s (Brewer et al. 1999); (24) maximum goshawk attack speed = 30 m/s (Alerstam 1987); (25) Kenward (1978); (26) Cresswell (1994); (27) the data provided by Page & Whitacre (1975) do not allow a decision on the presence or absence of confusion in their predator–prey system; (28) maximum peregrine attack speed = 44 m/s, maximum peregrine attack acceleration = 5 m/s<sup>2</sup> (Peter & Kestenholz 1998); (29) Davies (1977); (30) maximum prey escape speed = 24 m/s (*Alca torda*, razorbill: 24 m/s; *Fratercula arctica*, Atlantic puffin: 23 m/s; *Uria aalge*, guillemot: 25 m/s; Meinertzhagen 1955); (31) Caldow & Furness (2001); (32) relative prey speed = 1.2 (maximum prey escape speed = 19 m/s; *Connochaetes taurinus* (wildebeest): 22 m/s; *Equus* spp. (zebras): 19 m/s; *Syncerus caffer* (buffalo): 16 m/s; reviewed by Garland 1983; maximum lion attack speed = 16 m/s; reviewed by Garland 1983); relative prey acceleration = 0.6 (maximum prey escape acceleration = 5.3 m/s<sup>2</sup>; wildebeest: 5.6 m/s<sup>2</sup>; zebra: 5.0 m/s<sup>2</sup>; Elliott et al. 1977; maximum lion attack acceleration = 9.5 m/s<sup>2</sup>; Elliott et al. 1977); (33) Van Orsdol (1984).

\* When possible, we have calculated the relative prey agility as relative prey speed (i.e. mean or maximum prey escape speed divided by mean or maximum predator attack speed, respectively) or relative prey acceleration (i.e. maximum prey escape acceleration divided by maximum predator attack acceleration). When no such data were available, we have estimated relative prey agility. Such estimations are in parentheses.

† The ‘expectations’ are based on the conceptual summary given in the Results. They are correct in 20 cases (80%).