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Avoidance behaviour of bats and moths: when is it predator defence?

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Most animals live in environments where they risk becoming the prey of other animals. Because predation is such a catastrophic event for the prey, we could reasonably expect that most animals will exhibit behaviours that have an anti-predatory function. Typical examples include spatial and temporal avoidance of areas where, and periods when, predators are active. This kind of avoidance behaviour is illustrated by the vertical migration of zooplankton in lakes with fish (e.g. Gliwicz 1986), reduced feeding activity by rodents on moonlit nights (Clarke 1983), and avoidance of areas with high vegetation, that may harbour predators, by grazing antelopes (Underwood 1982).

We have both worked on avoidance behaviours that we believe may serve an anti-predator function, and that presumably also have evolved in that context. In particular, we have argued that predation risk imposed by raptorial birds during the day is the principal reason why bat foraging activity is usually restricted to the night (Speakman 1990, 1991, 1995, Jones and Rydell 1994, Speakman et al. 2000) and also that nocturnality in bats first evolved for this reason (Rydell and Speakman 1995). Likewise, we have argued that the flight activity and behaviour of certain species of crepuscular moths are also shaped by predation risk, this time imposed by insectivorous birds during the day and bats during the night (Andersson et al. 1998, Rydell 1998, Svensson et al. 1999).

Clearly, why bats are nocturnal and not diurnal is a central question for those of us who want to understand the biology of these animals, and the same can be said about many moths. However, when trying to publish our work, we have both repeatedly encountered the same problems when we argue that the temporal activity patterns in bats and moths indeed seem to be maintained by predation. Hence, this note serves to

highlight some of the methodological difficulties that attend demonstrating that an avoidance behaviour has an anti-predatory function. It is to some extent borne out of frustration, because we think that the arguments most frequently delivered by reviewers have the consequence that it becomes impossible to test the hypothesis. The problem is accentuated in situations where most or all individuals of an animal behave according to a certain norm, from which they seldom or never deviate. Insectivorous bats and many insects are normally strictly nocturnal, and only fly in daylight under exceptional circumstances (Speakman 1991, Svensson et al. 1999). An analogous example is the ghost swift moth *Hepialus humuli*, among which the lekking males display intensively together for no more than 30 min each evening, triggered by the falling light intensity, and otherwise remain inactive (Rydell 1998).

The methodological problems may not apply so much to the (much more studied) situation where the behaviour in question changes on a short-term basis or varies between individuals, so that the variation in behaviour can be related to variation in predation risk. Examples of this situation include the male Tungara frog, which stops calling and dives when a predatory bat comes within striking distance (Ryan 1985), and guppies, where some males are bolder than others and therefore are selected for mating by females (Godin and Dugatkin 1996).

In the case of nocturnality in bats it is usually argued (from the reviewers' side) that predation is unlikely to explain the avoidance behaviour because there are few or no direct observations indicating that predation actually occurs (or at least not enough to indicate that it is important). The same applies to the flight activity of some moths, although for some species the problem is the reverse; predation pressure seems so high that it is hard to imagine that the moths perform any anti-preda-

tor behaviour at all. However, we argue that it may be irrelevant whether predation is observed or not, and it may even be irrelevant if it actually occurs. An anti-predator behaviour could still have evolved in that context and also serve that function at present. What counts is, of course, how the predation risk would have changed if the prey had behaved otherwise, i.e. if not performing the presumed anti-predatory behaviour (see e.g. Lima and Dill 1990). However, this situation can be very hard to observe when animals almost consistently adopt the suspected anti-predatory behaviour. This is certainly the case with bats, which seldom fly in daylight (Speakman 1991). When few individuals fail to behave according to the norm, one may be very unlikely to observe any predation events under natural circumstances.

To illustrate the basic problem, we made use of an analogy previously discussed by Lima and Dill (1990), and made observations of the supposed anti-predatory (avoidance) behaviour of (human) pedestrians in the centres of the cities of Aberdeen and Göteborg. The behaviour in question is walking on sidewalks rather than on the roads. We suspect that humans perform this behaviour because of the risk of predation by motor vehicles if they were to walk in the middle of the road (this analogy may be less applicable to some other cities, e.g. Madras or Naples, where the only practical way to cross a street is to step out right in front of the traffic...).

Thankfully, during the observations, neither of us saw a motor vehicle knock down and kill, or even maim a person, and hence, we found no direct indication that predation is important or even that it occurs in these cities. Should we then conclude that the hypothesis is falsified and that walking on sidewalks has nothing to do with the presence of cars on the road? Obviously not. Instead, we can reasonably infer an anti-predatory function of this behaviour because: a) the prey spatially segregate themselves from the predators (temporal segregation would be an equivalent criterion), and b) although we have not observed cars killing people in any of the two cities, we know from data collected elsewhere that they are perfectly capable of doing this.

To substantiate our argument further we can envisage two experimental tests. First, we could wander the two cities pushing people out onto the streets to see if they got run over (predated). Second, we could exclude the cars (predators) from an area to see if the people (prey) changed their behaviour (in fact in pedestrianized areas this is exactly what happens – but see below). The first option is ethically unacceptable both for humans and other animals, because the experiment will inevitably result in deaths of some participants. It may also be of questionable scientific value, particularly if we already know the result from observations elsewhere. The second alternative is also ethically question-

able in most cases, since “removing” predators usually means that they would have to be killed.

In any case, assume that the removal experiment was nevertheless performed, and, as seems likely, that the prey did not change their behaviour in any noticeable way. Should we then conclude that the hypothesis was disproved, and that the suspected avoidance behaviour does not in fact serve an anti-predatory function? Probably not, because we could never be sure that the prey were aware of our experiment. They may not have realised that the predators had been removed, and may therefore have behaved as if they could still be around. The prey may perhaps also have been evolutionarily adapted to the expected predation risk levels, and may therefore have maintained the original avoidance behaviour for a long time following the experiment. Hence removal experiments are probably meaningless, unless adequate information about the removal is also transmitted to the prey. Clearly, the prey’s decisions on how to behave must be based on the *perceived* risk (Lima and Dill 1990). The *real* risk is probably unknown to the prey in most situations (although it may of course be known to the experimenter). In fact pedestrians in Aberdeen and Göteborg still stick to the sidewalks in the early morning, when few cars are around, probably because they still perceive a “predation risk”. In the pedestrianized areas, signs provide unambiguous information that there are no longer any predators (cars) around, and, consequently, humans walking in such areas tend to abandon their avoidance behaviour and spread out over the street. To provide such information to a population of wild animals may be nearly impossible, and even if it could be done, a critic would probably claim that the test is no longer valid, because more than just the presence/absence of predators had been altered! So, after all, the two experiments we envisaged may be a waste of effort. They do not provide meaningful ways of testing if the avoidance behaviours have an anti-predatory function.

The only alternative would be to make continuous observations of prey until some of them ventured into the area occupied by the predator and were predated. In theory, if you could show that susceptibility to predation for those individuals abandoning the suspected anti-predatory behaviour significantly exceeded that for those maintaining avoidance, this might demonstrate its anti-predatory function. The time to do this for bats, and probably many other animals, however, would be prohibitively if not impossibly long, although it could perhaps be minimised if the potential benefit of the risk taking could be increased. However, there is another problem. It could always be claimed that the individual that did not perform the supposed anti-predatory behaviour suffered from some illness that affected the behaviour and thus the ability to avoid predation. For example, if a drunk staggered into the street and got knocked down by a car, one could argue

that the failure to keep to the sidewalk was also linked to the inability to avoid the car. The general principle could be applied to any case. If an animal is deranged enough to vary from the routine norm, then whatever caused the deviation must also have affected the ability to avoid predation.

Even if we could show that the animals which abandoned the behaviour of interest did not differ in any way from those that do perform the behaviour, there is yet another argument that can be raised against such observations (or experiments where animals are forced to abandon their anti-predation responses). This objection is based on the fact that several predators are known to preferentially select unusual targets (although other predators may avoid such targets). If a single individual was to fail to perform the supposed anti-predator behaviour, it might experience an increased risk of predation, relative to those that exhibit it, only because it would present an unusual target for predators. Showing that these individuals are disproportionately predated does not necessarily prove that if all the prey were to abandon performance of the supposed anti-predator behaviour, they would all experience elevated predation risk. In this situation they would no longer be unusual targets.

How then are we to establish if an avoidance behaviour has an anti-predatory function? The bottom line is that each direct observation or experimental test that we can envisage is open to criticism. Given that this is the case, could we use the above two criteria (a and b above) that we used to infer that staying on the sidewalk is an anti-predator behaviour, to infer that an animal avoidance behaviour has the same function? We would argue that at the very least these criteria demonstrate that an avoidance behaviour has anti-predatory consequences, even if its primary function is not anti-predatory and if it evolved in another context. By this we suggest that they do represent sufficient criteria, but we welcome suggestions on this issue.

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