Title of entry: Alarm calling

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Synonyms: Distress calling, alert calling, mobbing calling, anti-predator calling

Definition: Vocal behaviour emitted in response to a threatening situation

Evolutionary function

From an evolutionary perspective, alarm calling is a puzzling behaviour. The term is used to refer to an acoustically diverse group of animal vocalizations, emitted in response to some threatening event, usually a predator. Alarm calling is widespread amongst social animals, although most data are from primates, rodents and birds. But why should an individual vocalise in the presence of a predator and hereby reveal its location and attract attention? How can such seemingly maladaptive behaviour evolve?

Different non-exclusive hypotheses have been proposed to explain the evolution of this seemingly paradoxical behaviour (Stephan & Zuberbühler, 2016). They differ both in terms of the presumed beneficiary (selfish vs. altruistic alarm calling) and in terms of the targeted recipient (predator vs. conspecifics).

Selfish alarm calling

One group of hypotheses presumes that alarm calling is directly beneficial to the caller, either because it impacts on the predator or because it induces behaviour in other prey that is beneficial to the caller. First, alarm calls can signal detection to a predator, the **perception advertisement hypothesis.** This strategy is particularly effective with predators that hunt by surprise and abandon hunting after detection. The hypothesis can also explain alarm calling by lone individuals and non-social species. Related to this is the **pursuit deterrence hypothesis**, put forward to explain stotting behaviour in ungulates, a visual alarm signal that showcases a prey's superior locomotor capacities and the futility of pursuit.

However, selfish alarm calling is not always aimed at the predator. Under the **prey manipulation hypothesis**, alarm calling functions to trigger escape behaviour in other prey, which creates general pandemonium that distracts the predator and, as a consequence, increases the caller's own survival changes. Under the **cooperative defence hypothesis**, alarm calling is also aimed at other prey, but to trigger predator approaching and chasing ('mobbing'), which increases the likelihood of the caller's own survival.

Altruistic alarm calling

A second group of hypotheses presumes that alarm calling evolved to benefit the caller indirectly by favouring genetic relatives and other valuable group members. Under the **kin selection hypothesis**, alarm calling provides genetic advantages to a caller, which is the case the caller is surrounded by own offspring or other closely related individuals. Following Hamilton's rule, alarm calling can evolve even if it is costly to the signaller, provided it sufficiently benefits genetic relatives. In some species, there is evidence that callers maximise their indirect fitness benefits by taking the audience into account, for instance by alarm calling more in the presence of young and vulnerable offspring than other audiences (e.g. yellow-bellied marmots (Blumstein 2007).

Finally, costly alarm calling may also evolve if it favours a caller's reproductive success by preserving mating opportunities, the **sexual selection hypothesis**. This argument has been made for adult males in polygynous species. For example, in Diana monkeys males produce acoustically highly conspicuous alarm call that carry over long distances, much beyond what is predicted for communication to the predator or other group members, suggesting that male alarm calls operate in male-male competition and female choice. However, this is most likely a secondary evolutionary process, by which already existing alarm calls are subject to the forces of sexual selection to take on an additional function in reproduction.

Information content

Call production

What kind of information is encoded in animal alarm calls? Communication involves at least two partners, a signaller and a recipient, which may experience different processes. First, the **acoustic structure** of alarm calls is determined by the shape of the signaller's vocal tract, which provides recipients with reliable information about the caller's body size, age, sex and identity (Bowling et al., 2017). In addition, psychologically relevant events often have physiological effects, such as changes in heart rate, skin temperature, or hormone levels, which creates further variation in a signaller's vocal tract shape and, consequently, the acoustic quality of alarm calls; Morton's motivational-structural rules (Morton, 1977). Since this process is determined by a caller's prior experience with an event, call production is also under cognitive control.

Call comprehension

Recipients, on the other hand, may either be directly affected by the acoustic structure of alarm calls (Owren & Rendall, 2001), or they have learned about the referential relations between alarm call types and events (Schlenker, Chemla, & Zuberbuhler, 2016). One on-going debate is about the nature of the mental representations, or memories, that mediate between alarm calls and events (Seyfarth et al., 2010). If an alarm call is only given to a narrow set of situations, listeners can directly infer the eliciting event, even in the absence of further cues; to the effect that the call obtains something akin to **lexical meaning**. However, most studies are unable to pin down more specifically what type of information is conveyed, such as the type, behaviour or distance of the predator, and many alarm calls are given to a range of situations that do not share clear similarities – at least from a human perspective (Dezecache & Berthet, 2018). Here, listeners appear to rely on **pragmatics** to identify the event that has caused the call. A number of playback studies have tested this idea and produced evidence that referentially broad alarm calls can obtain relatively specific meaning during a process by which listeners can associate the call to a range of possible events and then choose amongst to most probable one. Also, some species use social knowledge to react to others' alarm calls. For example, vervet monkeys react less strongly to alarm calls given by juveniles, possibly because they give alarm calls to wider range of disturbances than adult monkeys that only call in cases of real danger.

Call sequences: temporal and morophological structure

Alarm calls are often emitted in sequences, raising the possibility that information could be conveyed by resulting **structural** differences, such as due to variation in temporal structure. This is the case for titi monkeys that emit alarm calls more regularly in predator-related than non-predator related sequences. In black-capped chickadees, call rate differences also exist but here they have been linked to size differences of predators. Another relevant example is alarm call sequences in black-and-white Colobus and Guereza monkeys, which produce sequences of few roars when encountering leopards and many roars when encountering crowned eagles, a difference discriminated by listeners.

Second, alarm call sequences sometimes consist of different call types, which results in sequences that qualify as ordered **permutations** or unordered **combinations** (Zuberbühler, in press). An example of call combinations is titi monkeys combining A and B alarm calls into sequences, whereby the proportion of B-call combinations reliably encodes predator type and location.

An example of a permutation is male Campbell's monkeys combining 'krak' alarms (typically given to leopards) and 'hok' alarms (typically given to eagles) with an acoustically invariable vocal unit ('oo') in cases of non-imminent danger. Recipients discriminate krak from krak-oo alarms, suggesting that –oo performs a semantic operation. The system thus resembles a common operation in human language, **affixation,** whereby an utterance with lexical meaning is combined with a meaningless affix, to generate a derived meaning.

Another example of a permutation is male Campbell's monkey 'boom' calls, produced prior to subsequent krak-oos, whenever the disturbance is non-predatory (e.g. falling tree). In playback experiments, Diana monkeys discriminated alarm sequences with and without preceding booms, suggesting that the booms altered the meaning of the sequence.

Permutations have also been found in putty-nosed monkeys. Here, males produce series of pyows to terrestrial disturbances and series of hacks to crowned eagles. In addition, males sometimes add brief combinations of several pyows, followed by several hacks. The pyow-hack transition appears to carry its own meaning, unrelated to the meaning of the constituent parts, by announcing forthcoming group movement. The pyow-hack transition hence resembles an **idiomatic** expression, i.e., the meaning of the call combination cannot be derived from the meaning of its parts, similar to English expressions such as "raining cats and dogs", i.e., raining heavily.

Compositionality

An important discussion is whether any animal call sequence qualifies as truly **compositional** (Townsend, Engesser, Stoll, Zuberbuhler, & Bickel, 2018). Compositionality is a defining feature of human language whereby the meaning of an expression is determined by the meaning of its parts and the rule that combines them. Some of the best current examples of animal compositionality come from studies on bird alarm calls. For instance, Japanese tits possess “alert” calls that warn conspecifics about the presence of predators and “recruitment” calls that attract conspecifics in non-dangerous situations, for example to food. When mobbing a predator, however, tits combine the two calls to “alert-recruitment” sequences, which engages nearby conspecifics into cooperative anti-predator behaviour. Interestingly, reversed sequences do not elicit mobbing behaviour, suggesting that the system is both permutational and compositional (Zuberbühler, in press).

Ontogeny and learning

Comprehension

How do animals acquire their alarm calls? Most ontogenetic studies of alarm calls have focussed on recipients, i.e., how animal learn to comprehend the meaning of alarm calls. In many species, infants appear to be born with partly innate knowledge of alarm calls. For example, new-born ground squirrels react to conspecific alarm calls by freezing or increasing vigilance. Similarly, cross-fostered dunnocks cease to beg for food when hearing conspecific, but not foster parent alarm calls. Nevertheless, their response is weaker compared to normally raised chicks, suggesting that learning plays a moderating role (Hollen & Radford, 2009). In many species, however, alarm call comprehension is subject to social learning. Social learning is highly adaptive, especially in acquiring anti-predator behaviour, as it protects infants from committing fatal errors. For example, infant meerkats that have stayed close to adults are more likely to respond appropriately to alarm calls than other infants.

Production

Research on the ontogeny of alarm call production is more limited. Generally, learning appears to have only minor effects on the acoustic structure of alarm calls. For example, in species such as yellow-bellied marmots, great gerbils and meerkats, juvenile and adult alarm calls are nearly identical. Partly, this may be because the acoustic structure of animal alarm calls itself has been under strong selection pressure. For example, bird raptor alarms are often difficult to localise (presumably to prevent detection), whereas monkey leopard alarms are highly conspicuous (presumably to promote dissuasion). A notable exception is the **fork-tailed drongo** that, in addition to its own species-specific alarm calls, is able to mimic other species' alarm calls, although this ability functions in deceptive foraging.

Usage

Call use, finally, appears to be more plastic, but again relatively little work has been carried out. As a basic principle, infants must learn to recognise the dangerous species, which can either happen through a process of elimination or addition. For example, young vervet monkeys begin by giving alarm calls to a broad range of stimuli, including non-predatory species (e.g. flying pigeons), albeit in a non-random manner: eagle alarms are produced to flying animals, leopard alarms to terrestrial species, and snake alarms to snake-like objects. This has also been demonstrated in monkeys experimentally exposed to unfamiliar threat. For example, green monkeys exposed to a drone will produce alarm calls that resemble vervet monkey eagle alarms. The inverse process has been described in infant chimpanzees that do not appear to have any pre-existing knowledge of alarm call use, but learn by observing others interacting with unfamiliar threats.

Conclusion

Alarm calling is of importance to various scientific disciplines, including evolutionary theory, behavioural ecology, animal cognition, comparative linguistics and philosophy of mind. They are relatively uncomplicated to work with and easily recognisable, due to their context-specificity and unique acoustic structure. They have been essential in addressing a range of basic questions, such as the evolution of altruism, the behavioural ecology of predator-prey relations, and the evolution of animal cognition. Detailed behavioural analyses, based on naturalistic observations and experiments across a wide range of species have produced much progress and provided a window into the animal mind and some of the basic forces that drive evolution.

Cross-References (related chapters selected from the table of contents)

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