427. Romero, A. 2004. Adaptation: Behavioural. pp. 3-4, *In*: J. Gunn, Ed. *Encyclopedia of Cave and Karst Science*. New York: Fitzroy Dearborn.

ADAPTATION: BEHAVIOURAL

Of all phenotypic traits, behaviour plays the most immediate role in determining the ability of a group of individuals to survive during colonization of the subterranean (hypogean) environment. Changes in behaviour as a response to environmental change are thus crucial to understanding the phenomenon of adaptation to hypogean environments. In the following overview of current understanding of behavioural adaptations in caves, most of the examples presented come from studies of fish, the taxon on which most behavioural experiments have been performed.

Numerous animals colonize the hypogean environment by developing entirely new behaviours such as echo-location (e.g. bats and the nocturnal oilbird *Steatornis caripensis*), bioluminescence (e.g. the New Zealand glow-worm—actually a fly larva—*Arachnocampa luminosa*), or hibernation (e.g. a carp from China, *Varicorhinus* [*Scaphestes*] *macrolepis*). However, these types of behavioural modifications are the exception, not the rule. Most can be grouped into one of the following categories: feeding, reproduction, social behaviour (including aggregation, responses to alarm substances, and antagonistic behaviour), photoresponses, and circadian rhythms.

Feeding

Many cave animals have enlarged sensory systems that allow them to sense the presence of food. To improve their ability to find food, many cave animals move continuously in their environment; for example the troglomorphic form of the fish *Astyanax fasciatus* swims continuously. In studies, these fish also decrease the angle of their body relative to the bottom of the aquarium in order to increase the area of contact between food on the bottom and areas of their skin where there are larger numbers of chemoreceptors (Schemmel, 1980). Similar adaptations have been reported for the toothless blindcat *Trogloglanis pattersoni*, the Somalian cave fish *Phreatichthys andruzzii*, and the catfish *Trichomycterus itacarambiensis*. Coprophagy (feeding on excrement) is not uncommon in caves, and some animals specifically choose such environments. For example, larvae of the pyralid moth *Aglossa pinguinalis* are found inside caves in densities 700 times greater than at the surface. This is apparently due to the fact that in more exposed excrement they cannot compete with other coprophagous specialists, owing to a lack of parental care and slow growth rates for this species (Piñero & López, 1998).

Reproductive Behaviour

The use of chemicals to attract mates has been reported in a number of cave organisms, ranging from crickets to fish. This behaviour has yet to be studied thoroughly in natural conditions. Aggressive behaviour associated with reproduction has been observed to decrease, probably due to a lack of visual information (Parzefall, 2000) (see below).

Aggregation/Schooling

In general, all hypogean animals show a tendency to reduce organized forms of aggregation, from insects (Christiansen, 1970) to fish (Romero, 2001). Romero (1984, 1985a), for example, observed that individuals of *A. fasciatus* morphologically identical to the epigean populations of the same species actively entered a cave in Costa Rica for both feeding and to escape from predators (the fishing bat *Noctilio leporinus*). However, unlike the typical epigean *A. fasciatus*, the population did not form schools.

Responses to Alarm Substances

Many bony fishes contain an "alarm substance" in their skin that is released into the water when the skin is damaged, for example by biting. It is believed that this substance is sensed by conspecifics (members of the same species) of the individual that has been harmed, and thus they use the information to escape or seek refuge. Although the substance is produced by many hypogean fishes, the response to its release is either highly reduced or lost (Fricke, 1988).

Aggression and Antagonistic Behaviour

Aggression has been reported for many cave fishes, and some amphibia and crustaceans (Parzefall, 2000). Aggression is usually reduced, but antagonistic (confrontational behaviour without fighting) behaviour persists in many species, including amblyopsids (where the rituals decrease in complexity in parallel with the degree of cave adaptation, Bechler, 1983), the Ceguinho catfish *Pimelodella kronei*, and the Cueva del Guácharo blind catfish *Tricomycterus conradi*.

Responses to Light

Many blind, depigmented hypogean animals do show behavioural responses to light. Photoresponses are mediated by the pineal organ and—to a certain extent—by extrapineal organs (Langecker, 1992; see Adaptation: Morphological-Internal). They are termed scotophilia (the tendency to stay in the dark side of an aquarium under experimental conditions) and have been reported for many species of hypogean fishes (Romero, 2001). The behaviour of staying away from light is usually more common among recent invaders of the hypogean environment than among more troglomorphic species (Green & Romero, 1997). Also, the degree of scotophilia (in which the fish moves away from light) increases with development, as it does for epigean forms (Romero, 1985b). Although earlier authors made much of this behaviour as an indication that these species maintain such responses in order to stay in caves, all available evidence suggests that such behaviour is an inherited relic from their epigean ancestors (Romero, 1985b).

Circadian Rhythms

This is a system also known as a "biological clock", which controls a series of physiological and behavioural responses in an organism. The rhythmicity generated by these clocks is usually triggered by light and temperature changes in the environment. Many cave animals show a reduction or total loss in their ability to generate biological rhythms even when exposed to light under experimental conditions (Lamprecht & Weber, 1992). As with the photoresponses mentioned above, circadian cycles are more reduced (or totally absent) in the more troglomorphic species (see also Adaptation: Eyes).

Acoustic Behaviour

Hoch (2000) found that the cave planthopper, *Oliarus polyphemus*, utilizes communication systems similar to those of its epigean ancestor, by communicating using substrate-borne vibrations, and also found that the cave environment seems to be especially suited to low-frequency sound transmissions. No acoustic communication has been demonstrated for hypogean fish, despite the obvious advantage of such behaviour. More research is needed in this area.

In summary, with the exception of a few very specialized types of behaviour, most cave animals tend to reduce or eliminate many of the typical responses of their epigean ancestors. To understand the role played by behaviour during hypogean colonization, ethological studies on hypogean organisms that have yet to achieve a troglomorphic state are probably the most important avenues to explore.

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See also **Colonization**

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Further Reading

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