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Feign versus flight: influences of temperature, body size and locomotor abilities on death feigning in neonate snakes

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Death feigning is a potentially important behaviour used by a wide variety of animals to increase the probability of escape from a would-be predator. Few data are available on the influence of various factors on death feigning in vertebrates, especially ectotherms, because of difficulties in consistently stimulating the behaviour under controlled conditions. I examined the effects of temperature, body size and locomotor performance on death feigning in neonate brown snakes, *Storeria dekayi*, in the laboratory. Brown snakes consistently feigned death in water, and contrary to predictions, were more likely to feign death and to feign death longer as temperature increased. Q_{10} values for death-feigning durations (mean = 2.79) were greater than those for maximal swimming velocities (mean = 1.77) between 10°C and 20°C. However, no statistical difference was detected between Q_{10} values for feigning durations (mean = 1.11) and swimming velocities (mean = 1.28) between 20°C and 30°C. At 30°C, swimming velocity was negatively correlated with death-feigning duration. Moreover, body size was negatively related to death-feigning duration at 30°C. These results suggest that temperature probably plays a large role in the decision by ectotherms to death feign, and that an animal's locomotor abilities and body size potentially influence the likelihood and duration of death feigning at optimal temperatures. However, physiological constraints greatly reduce the use of death-feigning behaviours at suboptimal temperatures, regardless of locomotor abilities and body size. Therefore, other stationary defensive behaviours are probably more important at suboptimal temperatures.

Keywords: brown snake; death feigning; letisimulation; *Storeria dekayi*; swimming; thanatosis; thermal; tonic immobility

Death feigning (i.e. thanatosis, tonic immobility, letisimulation) completely reduces an animal's responsiveness to external stimuli and is a secondary defence initiated following an encounter with a predator (Gallup 1974). The use of death feigning as a defensive response has been reported in a variety of ectothermic animals, including mites (e.g. Ebermann 1991), insects (e.g. Miyatake 2001a; Honma et al. 2006), fish (e.g. Tobler 2005), amphibians (e.g. Williams et al. 2000; Gomes et al. 2002) and reptiles (e.g. Gehlbach 1970; Greene 1988). Thanatosis probably disrupts typical predatory behaviours or minimizes stimulation for further attack, thereby increasing the probability of escape and reducing further injuries (Gallup et al. 1971). Studies have demonstrated that thanatosis by some animals is adaptive in that it increases the probability of survival when predators attack (Sargent & Eberhardt 1975; Miyatake et al. 2004; Honma et al. 2006).

Despite the potential importance of this behaviour for survival, studies examining the influence of intrinsic and extrinsic factors on death feigning in animals are scarce. Death feigning is much better understood in insects (e.g. beetles) than in vertebrates (e.g. Miyatake et al. 2004; Honma et al. 2006). In insects, duration of death feigning is heritable (Prohammer & Wade 1981; Miyatake et al. 2004) and is affected by light cycles (Miyatake 2001a), starvation (Miyatake 2001b) and body size (Hozumi & Miyatake 2005). The influence of these various factors on death feigning in vertebrates is much less understood, probably because of the difficulties in consistently stimulating the behaviour under controlled conditions.

For ectothermic vertebrates, many behavioural strategies are affected by temperature, which dictates the underlying

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physiological and biochemical mechanisms governing performance (Hertz et al. 1982; Bennett 1990). Ectotherms often display fight rather than flight defensive behaviours when environmental conditions do not permit optimal locomotor performance (e.g. Hertz et al. 1982; Keogh & DeSerto 1994; Mori & Burghardt 2001). For example, many reptiles are less likely to flee a potential predator and more likely to show more static antipredator behaviours, such as striking and tail vibration, at cooler temperatures where locomotor abilities are reduced (Mori & Burghardt 2004). Death-feigning behaviours may also be temperature dependent and used in a similar fashion. However, no study has examined the thermal capacities of death feigning in ectothermic vertebrates, especially in relation to locomotor performance.

Antipredator behaviours also vary with body size for many ectotherms (Lima & Dill 1990; Alexander & Covich 1991). Smaller animals are typically more vulnerable to predation because they are potential prey to a larger variety of predators (small and large) and because their locomotor abilities are reduced relative to those of adults. If death feigning, as a behaviour for surviving a predatory attack, is at least somewhat effective as an alternative to flight, then intraspecific variation in its duration should show a close negative relationship with body size and intraspecific variation in locomotor performance. No study has investigated the influence of body size or locomotor performance on death feigning in ectothermic vertebrates.

Observations of thanatosis in snakes have been made on several species representing three families (Leptotyphlopidae, Colubridae and Elapidae; e.g. Gehlbach 1970; Carpenter & Ferguson 1977). In addition to becoming immobile during death feigning, snakes typically show secondary behaviours (i.e. coiling, protruding the tongue and releasing musk and faeces) to thwart a predation attempt (Greene 1988). Other than limited observations of death feigning by a single individual or a few individuals (e.g. Liner 1977; Doody et al. 1996; Rugiero 1999), very little is understood about the factors influencing variation in this seemingly important antipredator behaviour displayed by many snakes. Burghardt & Greene (1988) found that duration of death feigning by the western hognose snake, *Heterodon nasicus*, is influenced by the direction of a predator's eyes. However, experiments assessing the effects of temperature, body size and locomotor performance on death feigning in snakes are lacking.

The purpose of the present study was to examine intraspecific variation in death-feigning behaviours in neonate brown snakes, *Storeria dekayi*, a habitat generalist (Ernst & Ernst 2003) in which death feigning has been previously reported in adults (Liner 1977; Hayes 1987), and to test the following three hypotheses regarding the influence of extrinsic and intrinsic factors on death feigning: (1) snakes will be more likely to feign death and to feign death longer at cooler temperatures because of a temperature-induced reduction in locomotor velocities, (2) smaller neonates will display death feigning longer than larger ones because they attain slower absolute velocities and are more at risk of predation and (3) individual variation in death feigning will be negatively correlated with variation in maximum locomotor velocities.

METHODS

Study Animals

I conducted experiments on neonate brown snakes born in the laboratory to two gravid females that were collected under woody cover objects within an open loblolly pine, *Pinus taeda*, stand in Franklin County, Tennessee, U.S.A. One female gave birth to 19 offspring ($\overline{X} \pm$ SE: Weight $= 0.252 \pm 0.021$ g; snout–vent length (SVL) $= 7.04 \pm 0.11$ cm). The second female gave birth to seven offspring ($\overline{X} \pm$ SE: Weight $= 0.247 \pm 0.039$ g; SVL $= 6.95 \pm 0.15$ cm). Owing to their small size, it was not possible to accurately determine the sex of the offspring. All neonates ($N = 26$) were housed individually in 900-ml plastic containers; snakes received water and small red wiggler worms, *Eisenia foetida*, ad libitum and were maintained on a 12:12 h light:dark cycle at 24 ± 0.5°C.

Neonate *S. dekayi* show thanatosis after being handled and placed in water (personal observation). The aquatic death feigning observed in this species is very similar to that observed by Munyer (1967) in eastern hognose snakes, *Heterodon platirhinos*. The finding that neonate *S. dekayi* consistently display death-feigning behaviour in water allowed for a unique opportunity to explore the influence of various factors on an innate behaviour that, at least in snakes, usually decays rapidly in captivity.

When placed in water following handling, a neonate *S. dekayi* begins to swim or immediately turns on its dorsum, writhes for a few seconds, and then becomes immobile while floating upside-down on the water surface. The head of the snake typically remains on the surface, with the mouth slightly open, and the snake continues to breathe throughout the duration of the display. Posture during the display varies, with some snakes being slightly coiled (C-shaped) and others maintaining a relatively elongated posture. When the snake is slightly coiled during feigning behaviour, it resembles a dead, bloated snake as described by Munyer (1967). However, when a snake feigns death using the elongated posture, it closely resembles a small, woody stem floating on the water surface, which could allow it to evade both terrestrial and aquatic predators. The body is held stiff following the initiation of the death feign so that when slightly touched, the snake's body maintains its position, similar to an elongated inanimate object. Brown snakes perform death feigning for a few seconds up to several minutes, then suddenly turn upright and immediately attempt to swim away. Notably, neonates have not been observed to feign death when placed on a terrestrial substrate, but instead attempt to flee or coil up and perform striking behaviours.

Experimental Treatments

Various aspects of the death-feigning behaviour were assessed at 10, 20 and 30°C beginning 5 days after birth. Attempts were made to elicit the behaviour in all 26 individuals at all three temperatures in a repeated measures design. All trials were conducted in an environmental chamber and the order of individuals tested was randomized within each test temperature. Because it was