

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.

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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 ($\bar{X} \pm \text{SE}$: Weight = 0.252 ± 0.021 g; snout-vent length (SVL) = 7.04 ± 0.11 cm). The second female gave birth to seven offspring ($\bar{X} \pm \text{SE}$: Weight = 0.247 ± 0.039 g; SVL = 6.95 ± 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 $24 \pm 0.5^\circ\text{C}$.

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

not feasible to randomize test temperatures for each individual snake, trials for all individuals were conducted in the following sequence: 20, 10 and 30°C, with 2 days between each set of trials. Snakes were acclimated to test temperatures for 2 h before any attempt was made to initiate death-feigning behaviour.

To induce death feigning, a snake was picked up by hand (using the thumb and forefinger) near the region of the vent and immediately placed in a modified gutter (1.5 m long \times 10.6 cm wide \times 8.5 cm deep) filled with water at the test temperature $\pm 1^\circ\text{C}$. When snakes began to feign death, I recorded the duration of writhing on the surface, total duration of the death feign (time when snakes flipped over on their backs until they turned up-right) and posture of the body when in the immobile state (coiled versus straight). All durations were measured to the nearest 0.1 s with a digital stopwatch. At the onset of death feigning, the observer moved as far away from the snake as possible while still allowing observations to be made (approximately 2 m away from the snake) until the snake righted itself. Moreover, all observations for all trials were made by the same individual (G.W.G.).

Immediately following the feigning behaviour at each temperature, swimming velocities were quantified as a measure of locomotor performance. Swimming velocities were measured in all individuals, regardless of whether or not death feigning was displayed. Velocities were measured in the same gutter described above, which was marked off in 25-cm intervals. Large rocks were positioned on either side of the gutter to give snakes something to swim towards. The time it took snakes to swim 1 m was measured with a stopwatch to the nearest 0.1 s. Snakes were stimulated to swim three successive times to determine maximum velocities (m/s), which were determined as being the fastest of the three runs. Following measurements of swimming velocity (for each individual), the water in the gutter was completely changed to eliminate the potential effects of chemical cues on death feigning and locomotor behaviours in subsequent trials. Snakes were not harmed during this study and showed no apparent signs of ill effects after death feigning and following the experiment. All individuals were used in a subsequent, unrelated study at the conclusion of the experiment.

Statistical Analyses

I used a chi-square procedure for comparing more than two proportions along with the multiple comparison procedure described by Zar (1999) to assess differences in the proportion of individuals feigning death among temperatures. The effects of temperature on initial writhing duration and total death-feigning duration were analysed using repeated measures analyses of variance (ANOVAs) and compared to a Bonferroni-adjusted significance level of $\alpha = 0.0167$ to account for the three temperature treatments. Homogeneity of variances among different temperature treatments was assessed using Bartlett test. Q_{10} values were determined for feigning duration and swimming velocities. Q_{10} is a unitless value that represents the change in the rate of a process as a consequence of a 10°C increase in temperature allowing one to compare

the thermal dependencies of different processes. These values were calculated for each individual and compared using paired t tests. Simple linear regressions were used to determine how snout–vent length (SVL) and swimming performance influence death-feigning duration. When SVL was significantly related to death-feigning duration at a particular temperature, I used a general linear model (GLM) with SVL and swimming performance as predictors of death feigning duration at that temperature. Data were analysed with Kaleidograph version 3.6 (Synergy Software, Reading, Pennsylvania, U.S.A.) and SAS version 9.1 (SAS Institute, Cary, NC, U.S.A.). Unless otherwise noted, reported values are means \pm one standard error.

RESULTS

Temperature Effects

There were no differences in size, death-feigning duration or swimming velocity between the two litters at any temperature (Mann–Whitney U tests: $P > 0.25$; Table 1), so all snakes from both litters were combined for subsequent analyses. The proportion of snakes that feigned death increased with increasing temperature (chi-square test: $\chi^2_2 = 23.42$, $P < 0.001$; Fig. 1a) with 10, 17 and 24 of the snakes feigning death at 10°C , 20°C and 30°C , respectively. All but one snake that feigned death at 10°C also feigned death at 20°C and 30°C , and all snakes that feigned death at 20°C also did so at 30°C . Snakes showed no difference in writhing duration at the onset of the death feign ($\bar{X} \pm \text{SE} = 1.1 \pm 0.09$ s; repeated measures ANOVA: $F_{2,23} = 1.51$, $P = 0.49$) or in their posture during the behaviour (chi-square test: $\chi^2_2 = 2.09$, $P = 0.90$) across temperatures. However, total feigning duration differed significantly between temperatures (repeated measures ANOVA: $F_{2,23} = 14.47$, $P < 0.0001$; Fig. 1b): durations at 10°C were significantly shorter than those at 20°C and 30°C (Bonferroni-adjusted: $P < 0.001$). The difference in mean feigning duration between 20°C and 30°C was not statistically significant (Bonferroni-adjusted: $P = 0.027$). Variance in feigning duration at 10°C was significantly less than that at higher temperatures (Bartlett test: $B_2 = 17.42$, $P < 0.001$). Lastly, all measures of swimming velocity significantly increased with temperature following death feigning (repeated measures ANOVA: $F_{2,25} = 11.04$, $P < 0.001$; Fig. 1c).

Table 1. Results of Mann–Whitney U tests comparing death-feigning (DF) durations and swimming speeds at three temperatures, and snout–vent length between two litters of neonate brown snakes, *Storeria dekayi*

	N_1, N_2	U	P
DF duration, 10°C	7, 3	15	0.383
DF duration, 20°C	14, 3	23.5	0.768
DF duration, 30°C	17, 7	74.5	0.349
Speed, 10°C	19, 7	72	0.7777
Speed, 20°C	19, 7	74.5	0.6512
Speed, 30°C	19, 7	74	0.6925
Snout–vent length	19, 7	86	0.2792

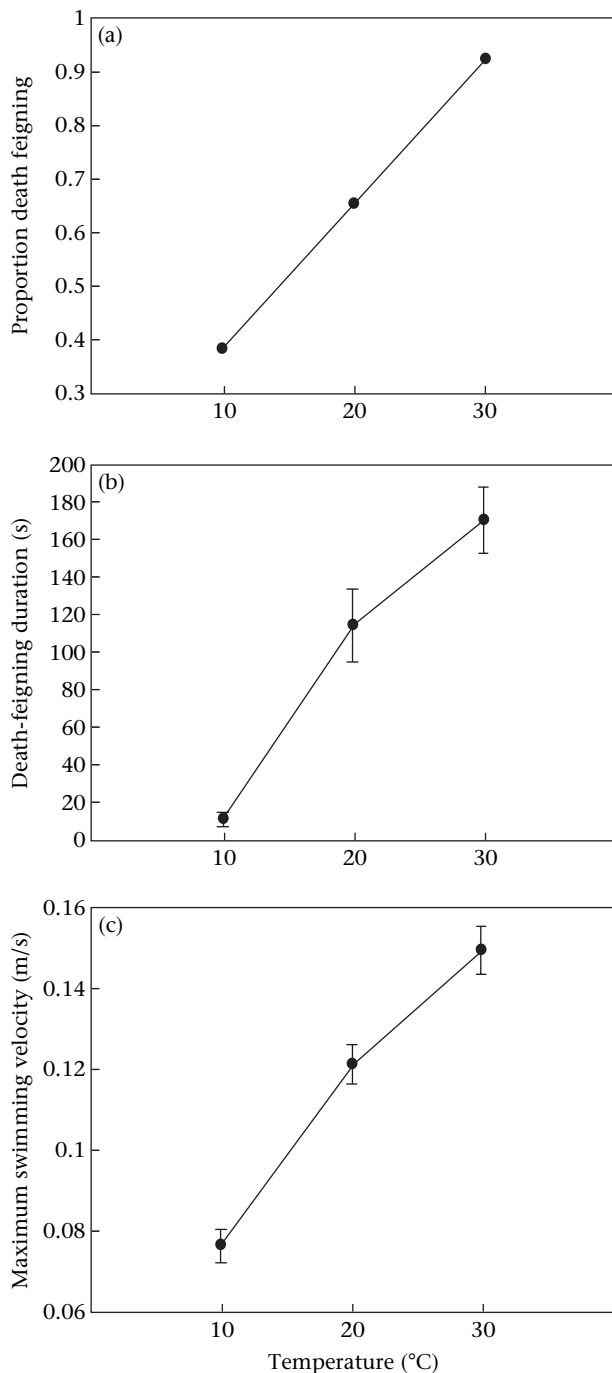


Figure 1. Effects of temperature on (a) the proportion of individuals performing death-feigning behaviours, (b) death-feigning duration and (c) absolute swimming velocity by newborn brown snakes, *Storeria dekayi*, that feigned death in water. Values are means \pm SE.

Q_{10} values for death-feigning durations ($\bar{X} \pm \text{SE} = 2.79 \pm 0.29$) were greater than those for maximal swimming velocities (1.77 ± 0.17) between 10°C and 20°C (paired t test: $t_9 = 2.63$, $P = 0.027$; Fig. 2). However, no statistical difference was detected between Q_{10} values for feigning durations ($\bar{X} \pm \text{SE} = 1.11 \pm 0.07$) and swimming velocities (1.28 ± 0.07) between 20°C and 30°C (paired t test: $t_{16} = -1.47$, $P = 0.162$; Fig. 2).

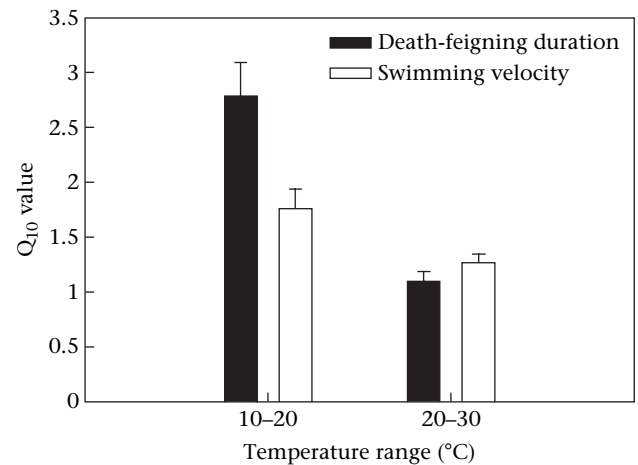


Figure 2. Q_{10} values (means \pm SE) for death-feigning duration and maximum swimming velocity for newborn brown snakes, *Storeria dekayi*.

Effects of Size and Locomotor Performance

Body size (measured as SVL) was not significantly correlated with maximum swimming velocity at 10°C (linear regression: $R^2 = 0.023$, $F_{1,8} = 0.195$, $P = 0.67$) or 20°C ($R^2 = 0.004$, $F_{1,15} = 0.055$, $P = 0.82$), but it was positively correlated with maximum swimming velocity at 30°C, suggesting that larger neonates were faster swimmers ($R^2 = 0.200$, $F_{1,22} = 5.48$, $P = 0.029$). Univariate tests showed that death-feigning duration was not significantly correlated with SVL at 10°C (linear regression: $R^2 = 0.278$, $F_{1,8} = 3.08$, $P = 0.118$) or 20°C ($R^2 = 0.155$, $F_{1,15} = 2.76$, $P = 0.120$), but it was negatively correlated with SVL at 30°C ($R^2 = 0.467$, $F_{1,22} = 19.28$, $P < 0.001$; Fig. 3). Hence, SVL was included as an additional independent variable in a GLM to determine the extent to which variation in death-feigning duration could be explained by SVL and maximum swimming velocity at 30°C. No significant correlations were detected between maximum swimming velocity and death-feigning duration at 10°C (linear

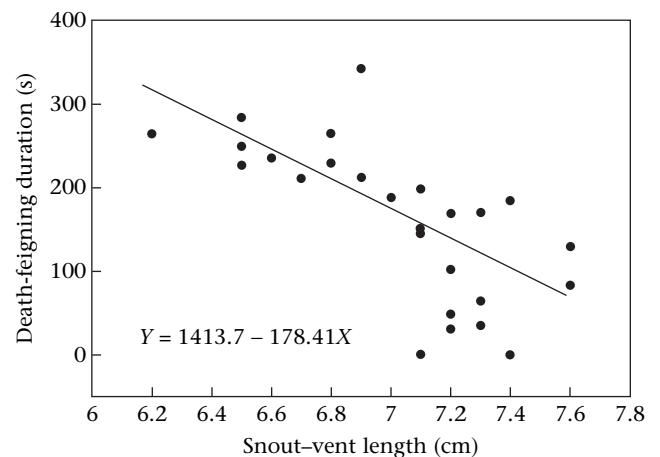


Figure 3. Relationship between body size (measured as snout–vent length) and duration of death feigning by newborn brown snakes, *Storeria dekayi*, at 30°C in water ($R^2 = 0.466$, $P < 0.001$).

regression: $R^2 = 0.001$, $F_{1,8} = 0.01$, $P = 0.925$) or 20°C ($R^2 = 0.008$, $F_{1,15} = 0.12$, $P = 0.732$). Neither SVL (GLM: $R^2 = 0.870$, $F_{11,23} = 1.72$, $P = 0.1316$) nor the interaction between SVL and swimming velocity ($F_{6,23} = 0.75$, $P = 0.6157$) explained a significant amount of variation in death-feigning duration, whereas maximum swimming velocity alone was negatively correlated with death-feigning duration at 30°C ($F_{1,23} = 44.53$, $P = 0.0011$). A stepwise regression analysis revealed that the relationship between maximal swimming velocity and death-feigning duration at 30°C was best described using a quadratic regression model (Fig. 4). Thus, the slowest swimmers tended to feign death longer than the faster swimmers, with the relationship between swimming and feigning levelling off for the fastest swimmers.

DISCUSSION

The majority of past studies on antipredator behaviours of ectothermic animals have shown that warmer animals tend to flee from a potential predator, whereas colder ones tend to show more stationary defensive behaviours to thwart a predator, such as remaining motionless, hissing, or biting (e.g. Hertz et al. 1982; Arnold & Bennett 1984; Schieffelin & de Queiroz 1991). Consequently, death feigning, being defined as a static behaviour (Mori & Burghardt 2004), should also be performed more often at cooler temperatures when the probability of survival by active escape is reduced. In contrast to predictions, neonate *S. dekayi* in the present study were more likely to feign death and to feign death longer at higher temperatures. However, since all individuals were tested at all three temperatures in the same order (20, 10, 30°C), differences resulting from habituation and sensitization cannot be discounted. Previous studies have shown that neonates of some snake species show a modification of antipredator behaviours following habituation to a stimulus (Herzog et al. 1989) and during ontogeny (Herzog et al. 1992). Although it is possible that the snakes in the present study

became habituated to handling over the course of the experiment, this probably had little impact on the results for two reasons. First, group treatment (i.e. temperature) trials were separated by 2 days, making it less likely that snakes would become habituated (Herzog et al. 1989) while mitigating ontogenetic changes in defensive responses (Herzog et al. 1992). Second, differences between treatment groups closely resembled patterns of thermal dependencies for most other performance measures in ectothermic animals (e.g. Hertz et al. 1982; Stevenson et al. 1985; Hailey & Davies 1986; Bennett 1990; Scribner & Weatherhead 1995; Finkler & Claussen 1999; Pinch & Claussen 2003; Elnitsky & Claussen 2006), making it extremely probable that differences between treatment groups resulted from changes in temperature.

Previous reports on death feigning by ectothermic vertebrates at different temperatures have produced inconsistent conclusions. Gomes et al. (2002) noted higher frequencies of death feigning by a hylid frog (*Scinax hiemalis*) at lower temperatures when a snake (*Liophis poecilogyrus*) that regularly feeds on amphibians was placed in close proximity to the frog. Mutoh (1983) induced death-feigning behaviours in the snake *Rhabdophis tigrinus* at $16\text{--}30^\circ\text{C}$ (by placing a foot on the snake until it feigned death) and found fewer instances of thanatosis at higher temperatures, thereby suggesting that death feigning is a behavioural strategy to be used when environmental factors constrain successful active escape.

Gomes et al. (2004) noted the reverse pattern following an experiment in which feigning behaviours in the lizard *Eurolophosaurus divaricatus* were initiated by grasping the animal by the neck and holding firmly until the onset of death feigning at 20°C , 30°C and 40°C . They found that it took longer to initiate thanatosis at 20°C , whereas less handling time was required to instigate the behaviour at higher temperatures. The results from Gomes et al. (2004) suggest that death feigning by *E. divaricatus* may not be related to the likelihood of active escape, but instead, is simply limited by the thermal influences on the underlying physiological processes driving antipredator behaviours.

The reason for the disparity among findings of this study and those of the aforementioned studies is unclear. Earlier reports suggesting that thanatosis occurs more often at lower temperatures differ in how the behaviour was elicited, which may or may not be a good representation of a predation attempt for the prey species being investigated. Gomes et al. (2002) examined thanatosis at the approach of a predator, a different part of the predation event (i.e. precapture), whereas the results from Mutoh (1983) were determined later in the predation event (i.e. postcapture). Similarly, the present findings, along with those of Gomes et al. (2004), were made following handling (postcapture) under more controlled conditions, making comparisons to previous studies somewhat problematic. If physically picking up and handling an animal is a better simulation of an actual predation attempt, then the current findings better represent the influence of temperature on death-feigning behaviours in ectothermic vertebrates when active escape is not a viable option. The present results also suggest that

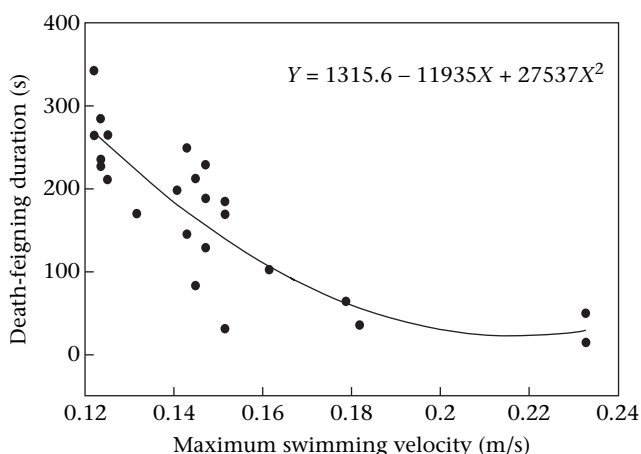


Figure 4. Relationship between maximal swimming velocity and duration of death feigning at 30°C in newborn brown snakes, *Storeia dekayi*, using a second-order term in the regression model ($R^2 = 0.724$, $F_{2,21} = 27.54$, $P < 0.0001$).

death feigning is an energetically demanding task that, like many other performance capabilities by ectothermic animals, is reduced at lower temperatures. However, no data currently exist on the energetic costs of death feigning to explicitly test this hypothesis.

Not surprisingly, swimming velocities attained by neonates during this study were also reduced at lower temperatures. Thus, the relationship between death-feigning duration and swimming velocity must be assessed at the same experimental temperature to examine the hypothesis that these variables are negatively related. Although no significant correlations were detected at 10°C or 20°C, the predicted negative relationship was observed between death-feigning duration and swimming velocity at 30°C (Fig. 4), with a lower limit on death-feigning duration for the fastest individuals. This result suggests that faster newborn brown snakes rely more on active escape than do slower individuals, which, because of reduced locomotor abilities, must invest more energy in death-feigning behaviours to increase the likelihood of surviving a predatory attack. This trade-off in behavioural strategies may only be apparent when environmental conditions allow the performance of both behaviours to be maximized (i.e. at optimal temperatures). It is also likely that death-feigning performance decreases very rapidly at temperatures above the optimal temperature range (at which an animal can perform at 95% of its maximum capacity or better) up to the critical thermal maximum (Bennett 1990). Difficulties in motivating some snakes to achieve maximal swimming velocities and the higher instances of other static defensive behaviours (e.g. striking) at the two lower experimental temperatures probably explain the lack of significance between duration and velocity at lower experimental temperatures.

According to Q_{10} values, death-feigning duration and maximal swimming velocity show different thermal dependencies. Time spent feigning death at 10°C was approximately 2.7 times less than that observed at 20°C, whereas swimming speeds at 10°C were on average 1.7 times slower than those recorded at 20°C (Fig. 2). These traits responded similarly to a 10-degree change in temperature between 20°C and 30°C. This result suggests that the total energy demands of the death-feigning display (i.e. turning to expose the venter, maintaining a rigid posture), at least in water, are greater than those of rapid locomotion. This finding should not be too surprising if one considers the difference in time spent performing these two behaviours. At 30°C, brown snakes feigned death for an average of 169.9 s (range 31–342 s), whereas they spent considerably less time swimming (range 6–14 s) depending on the speed and distance covered. The differing responses of thanatosis and swimming performance to temperature changes probably play a large role in the decision to flee or feign death when a predator is encountered. If thanatosis is more energetically expensive than active escape and if active escape is possible, then individuals should decide to flee more often than feign at lower temperatures. This hypothesis is supported by results from this study showing that a smaller proportion of newborn brown snakes feigned death at lower temperatures than at higher temperatures. Other more static

defensive behaviours (i.e. remaining motionless, hissing, striking) should also be performed more often than death feigning at lower temperatures if they require less energy and are successful in thwarting the predator.

This study also examined the hypothesis that smaller snakes would feign death longer than larger ones. This prediction was based on the fact that larger snakes are absolutely faster than smaller snakes (Heckrotte 1967; Hailley & Davies 1986) and, presumably, slower snakes should perform thanatosis longer because they are less likely to successfully flee a potential predator. Despite the small range of body sizes of neonates used in this study, smaller neonates did feign death significantly longer than larger ones, although only at the highest experimental temperature (Fig. 3). Hozumi & Miyatake (2005) found a positive relationship between body weight and duration of death feigning by the adzuki bean beetle, *Callosobruchus chinensis*, at 25°C, possibly because of physiological limitations associated with smaller body sizes or because larger beetles can be seen more easily by larger predators (e.g. birds). The negative relationship observed in this study between neonate size and death feigning is probably a result of the size-induced reduction in maximal swimming velocity of smaller snakes. However, future studies are needed using a larger range of body sizes to examine body size effects on death feigning in vertebrates.

In conclusion, death feigning is a complex behaviour used by many animals, especially snakes, as a last line of behavioural defence to increase the probability of escape after being cornered or captured by a predator. Moreover, this behaviour is likely to vary dramatically among species in terms of (1) the magnitude of predatory behaviours needed to stimulate death feigning (i.e. predator foraging mode), (2) the predisposition of a species to feign death than displaying other behaviours and (3) secondary behaviours (e.g. releasing musk or faeces) performed while death feigning. Results from the current study suggest that the likelihood and duration of death feigning is dependent upon the probability of escape, which is affected by temperature, body size and locomotor abilities. If fleeing is an option, then temperature probably greatly influences the decision to feign death or attempt escape. At higher, optimal temperatures, the decision by newborn brown snakes to feign death or actively escape probably depends more heavily on locomotor abilities, where faster individuals are more likely to attempt active escape and slower individuals are more likely to feign death. At lower, suboptimal temperatures, the death-feigning display of brown snakes appears to be limited primarily by physiological constraints, resulting in fewer and shorter bouts of thanatosis and higher instances of fleeing and other stationary antipredator behaviours. Correlational evidence is consistent with this hypothesis, but additional data are needed to completely understand the use of death feigning in ectotherms.

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