

Movement patterns of lacertid lizards: effects of temperature on speed, pauses and gait in *Lacerta vivipara*

R.A. Avery, D.J. Bond

Department of Zoology, The University, Bristol BS8 1UG, UK.

Abstract. *Lacerta vivipara* emerging from their overnight retreat before they had the opportunity to thermoregulate moved with an alternation of locomotor bursts and pauses. Mean speed during bursts of locomotion fell with decreasing temperature from 3.21 snout-vent lengths (SVL) s^{-1} at the activity temperature ($T_{act} \sim 33^{\circ}C$) to 0.15 SVL s^{-1} at $5^{\circ}C$. Between T_{act} and $19^{\circ}C$ the reduction was small ($Q_{10} = 1.12$) and statistically not significant; between $19^{\circ}C$ and $5^{\circ}C$ the change was very much greater ($Q_{10} = 7.7$). The pauses between locomotor bursts increased progressively in duration over the whole range of decreasing temperatures from T_{act} to $5^{\circ}C$, although the change from T_{act} to $23^{\circ}C$ was not significant.

Gait changed progressively from almost simultaneous movement of contralateral diagonal limbs at T_{act} to independent movement of limbs in the sequence LF, RH, RF, LH at $7^{\circ}C$, with increases in the mean duty factor of individual feet from 0.50 to 0.76 and in the proportion of time for which 3 or 4 feet were in simultaneous contact with the ground from 0 to 0.92.

Introduction

Locomotion in many species of quadrupedal lizards frequently consists of short bursts of walking or running interspersed with short pauses. It has recently been shown that in European lacertid lizards at their normal activity temperatures (T_{act} : equivalent to Activity Temperature Range as defined by Pough and Gans, 1982), speeds and pause durations vary consistently according to defined experimental conditions (Avery et al., 1987a) and between species (Avery et al., 1987b).

Lizards are ectotherms, and the majority of species function more or less efficiently over a range of body temperatures (Avery, 1982; Huey, 1982). It has been shown that in some species the rates of different physiological processes may respond to change in body temperature (T_b) in different ways (e.g. Marsh and Bennett, 1985, 1986a; Paladino, 1985; Stevenson et al., 1985; van Berkum et al., 1986). Since previous work on speeds and pause durations in lacertid lizards has related only to lizards at T_{act} , we extended the investigation to include the effects of reduced temperature. It was hoped

that the form of the relationship between pauses and temperature might help to explain their mechanisms and function. It became apparent during the course of the work that gait also changes progressively with a reduction in T_b , and so this was also investigated. The experimental animal was the common lizard *Lacerta vivipara*.

Material and methods

The lizards used in this study were captured in the West of England. Methods of maintenance, video filming, measurement and analysis have been described previously (Avery et al., 1987a).

In order to measure locomotion of lizards at T_{act} under defined conditions, Avery et al. (1987a) devised an arena containing two 150W incubator bulbs about 140 cm apart, and filmed lizards moving spontaneously between them. This technique could not be used to examine spontaneous locomotion of lizards with $T_b < T_{act}$ because under these conditions the animals retreated to their shelters and became inactive. The alternative used here was to film a lizard when it was emerging from its shelter and moving towards a bulb in order to bask. The shelters were pieces of thick cardboard folded in such a way that there were gaps at ground level into which the lizards could creep. Emergence from a shelter usually took place quite soon after the bulb had first been switched on in the morning; any delay tended to be greater at lower air temperatures (T_a).

It was found that the horizontal distance between the bulb and the cardboard shelter was critical in determining behaviour. If the distance was too great, a lizard tended not to emerge at all at low T_a . If it was too small then the animal was exposed to radiant heat or bulb-warmed air or substrate immediately upon, or even before, emergence. Intermediate distances satisfied the requirements that the lizard should need to walk sufficiently far to produce several cycles of locomotor bursts and pauses, and more importantly, not be exposed to warming from the bulb whilst being filmed. Under these conditions it could be assumed that $T_b = T_a$ (see Discussion). In order to reduce heating in the environment other than immediately beneath the bulb, 60W reflector bulbs rather than 150W bulbs were used, and the light was shone through a cardboard tube so that it illuminated a circle of about 15 cm². All experiments were carried out in arenas in which the point immediately beneath the bulb was 28 cm from the opening of the shelter which faced it, but only the middle region of the emergence path—about 15 cm—was within the filmed frame. No measurements were made of the movement of any individual lizard until it had lived within the arena for at least one week, and so was familiar with the surroundings and habituated to walk in a direct line from the shelter to the spot of heat and light. All sequences in which the lizard did not walk in such a straight line (they were rare) were ignored.

This technique could not be employed for determining the pattern of movement at $T_a = 33^\circ\text{C}$ (equivalent to T_{act}) because the lizards had always emerged before the bulb was switched on and they did not usually seek to bask. Under these circumstances the

behaviour filmed was that of the animal moving from the shelter to the bulb during its spontaneous foraging. For similar reasons it was possible to film only a small number of emergences at $T_a = 27^\circ\text{C}$.

The arenas were maintained in a room in which temperature was normally allowed to fluctuate with changing weather conditions outside, but in which subareas could be heated or cooled. Sequences of emergence at different temperatures were filmed on a random schedule, partly taking advantage of natural daily fluctuations in T_a . This avoided acclimation effects which might have been associated with systematic changes in temperature. The number of individual lizards filmed and measured at each temperature varied from 1 (7 and 27°C) to 3, the total number of sequences filmed at each temperature from 2 (7 and 27°C) to 20 (19°C). For technical reasons the steps by which T_a was incremented are not equal (fig. 1).

All experiments were carried out using adult lizards (mass 2.5–3 g, SVL 49–52 mm, total length 114–131 mm) with complete tails. Speeds are expressed in units SVL s^{-1} to standardise for differences in size and relative differences in the length of the tail between individuals.

Results

Emergence

Lacerta vivipara moving towards a single bulb on their first morning emergence showed the same pattern of locomotion that has been described in lizards moving spontaneously at T_{act} between two bulbs: short bursts of locomotor movement alternated with short pauses (Avery et al., 1987a). This movement pattern can be described by three variables: (a) distance moved during locomotor bursts, (b) duration of locomotor bursts and (c) duration of pauses. Derived variables include burst speed (a/b) and overall speed ($\Sigma a / (\Sigma b + \Sigma c)$).

Both burst speed and overall speed decreased with decreasing temperature. The relationship for burst speed (plotted as means for each temperature on semilogarithmic coordinates) is shown at the top of figure 1. Between T_{act} and 19°C the decrease was only slight ($Q_{10} \sim 1.12$) and not significant (ANOVA, Student-Newman-Keuls test, $P > 0.05$). Between 19°C and 5°C the slope was steeper, $Q_{10} = 7.7$. *Lacerta vivipara* were incapable of sustained locomotion below 5°C .

Pauses, in contrast, increased in duration with decreasing temperature from means of 0.11 s at T_{act} to 2.6 s at 5°C (bottom of figure 1). Mean burst duration increased from 0.27 s at T_{act} to 1.57 s at 5°C ; mean distance moved within each burst from 0.89 SVL at T_{act} to 1.05 SVL at 5°C , but this was not significant ($F = 1.84$, $df = 385$, $0.05 < P < 0.01$).

Gait

When a lizard was emerging at T_{act} it moved with a mean burst speed of 3.21 SVL s^{-1} (fig. 1; this is equivalent to 16 cm s^{-1} for an adult lizard of average dimensions). Mean

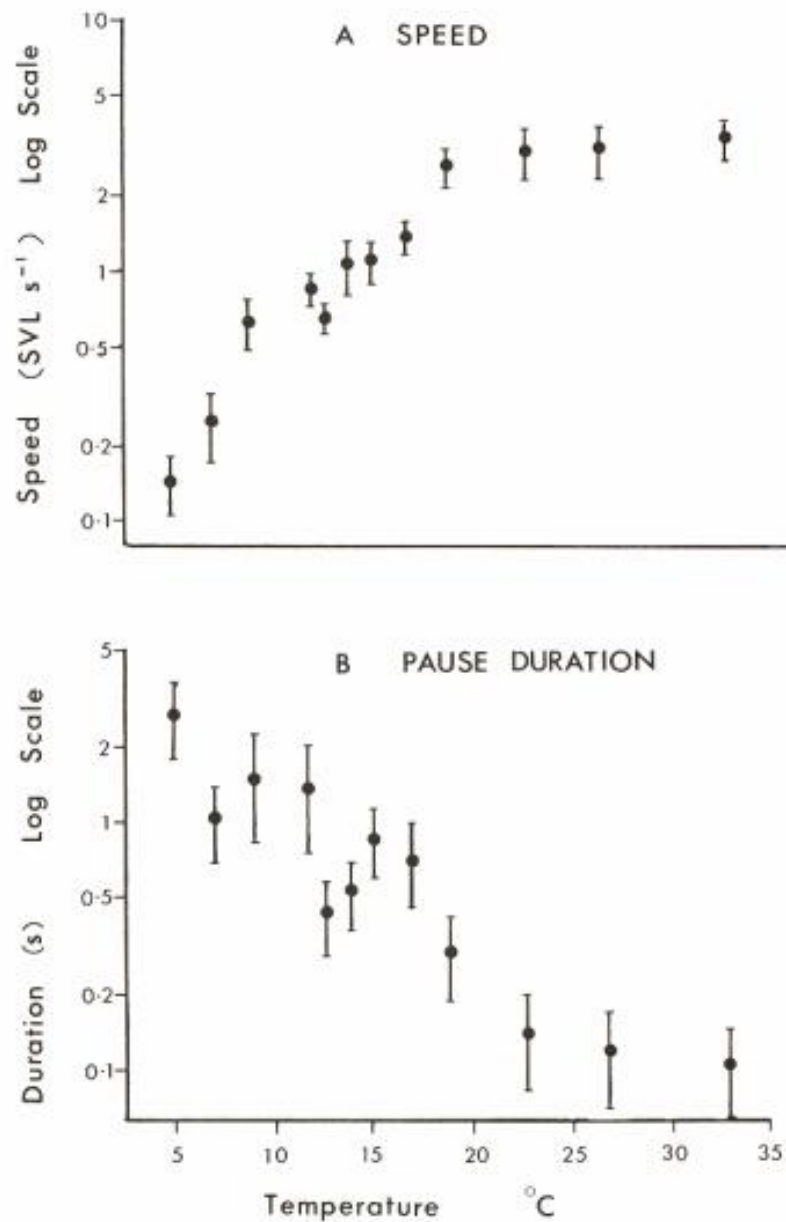


Figure 1. Burst speed and pause duration (logarithmic scales) in relation to body temperature. Vertical bars show ± 2 SD.

stride frequency was 4.9 s^{-1} . Contralateral diagonal limbs were moved simultaneously, and each limb was in movement for almost exactly one half of the entire stride cycle (fig. 2), i.e. the duty factor for each foot was 0.5.

This pattern changed with decreasing temperature. Gaits became progressively less regular. At 7°C (no data were obtained for lizards moving at 5°C) mean stride frequency had fallen to 0.42 s^{-1} and the mean duty factor had increased to 0.76. The synchrony of contralateral diagonal limbs had been lost, the four limbs moving independently in the order (with arbitrary origin) LF, RH, RF, LH (fig. 2). Mean phase difference (relative to fore limbs) changed between T_{act} and 7°C by the following mean amounts (coefficients of variation of 7°C means in brackets): contralateral diagonal pairs - 0 to 0.13 (23%); ipsilateral pairs - 0.50 to 0.71 (9.5%), contralateral opposite

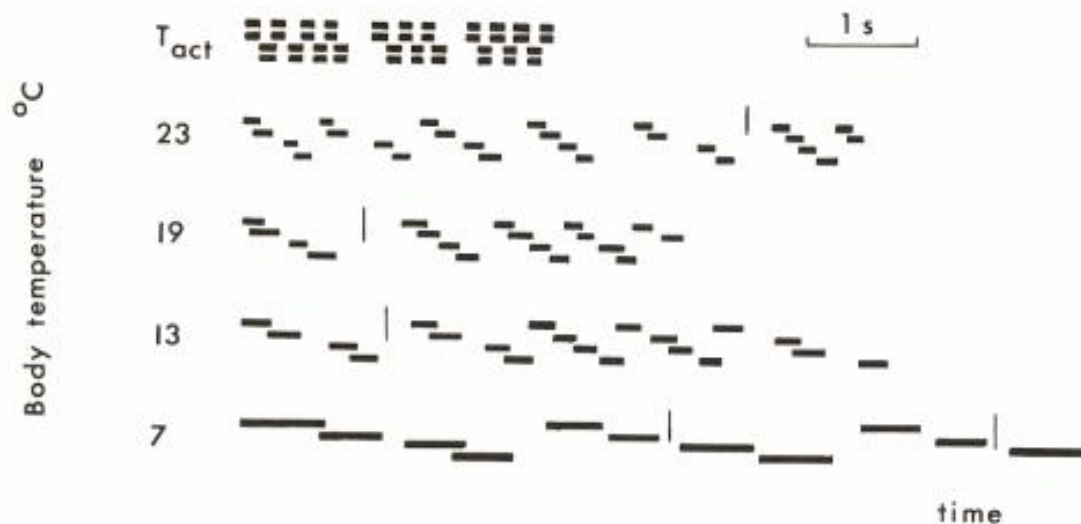


Figure 2. Sample gaits at five body temperatures. Horizontal black bars show the times during which each foot was in forward motion, in the order (from the top) LF, RH, RF, LH. Vertical bars represent long pauses in which the plotted duration is notional in order to fit the figure conveniently on a page.

pairs - 0.5 to 0.45 (18%). A consequence of these changes is that the proportion of time for which 3 or 4 feet were simultaneously placed on the ground changed from 0 at T_{act} to 0.92 at 7°C. All of these calculations are for periods of actual movement, i.e. within locomotor bursts; pauses are not included.

Discussion

Lacerta vivipara usually inhabit environments in which vegetation is fairly dense (Arnold, 1973; Arnold et al., 1978). Because such vegetation creates obstacles to direct movement, speeds and gaits of lizards in the wild are usually very variable. The arenas devised for these experiments represented an attempt to minimise this variability for the purposes of quantitative description. Although the environments of the arenas were in this sense artificial, the emergence behaviour of the lizards within them must have been similar to that in the wild. This is because the first activity of a common lizard on emergence from its overnight retreat is always to bask, using solar radiation to raise T_b (Avery and McArdle, 1975; Hailey, 1982), and the animal must move from the retreat to the basking site. *L. vivipara* occur in cool climates, and so this movement must often take place at low temperatures; Simms (1970) has written in this connection "parts of the trunk, or hind the limbs, are sometimes dragged about grotesquely until the lizard has had the opportunity to bask enough to thaw them out. This is particularly noticeable during periods when there are ground frosts". It is interesting to note that the T_b at which *L. vivipara* become incapable of walking—about 4°C—is lower than the equivalent temperatures recorded for *Dipsosaurus dorsalis* and *Sceloporus occidentalis*, which inhabit warmer climates (Marsh and Bennett, 1985, 1986a); *L. vivipara* is clearly a cold-adapted lizard (see also Spellerberg, 1976).

Confining the measurements to the middle period of each sequence of emergence was a further factor which reduced variability. During the early part of emergence, and especially before the whole body had been exposed, the lizards often paused for exceptionally long periods. When they approached the pool of heat and light cast by the bulb, they often speeded up.

There are no data in the literature with which the results presented here can be directly compared. Much of what has been recorded about lizard movement relates to their maximum speeds (V_{\max}), which have been used as indices of physiological capacity and performance (e.g. Garland, 1985; Marsh and Bennett, 1986a; van Berkum et al., 1986). It appears to be a characteristic feature of the muscle physiology of many species that Q_{10} for V_{\max} is high at low T_{bs} , but low at T_{bs} between 20–25°C and T_{act} (which varies from species to species, but is usually within the range 30–40°C - see Avery, 1982). Such a pattern has been observed in at least eight species (recent references: Crowley, 1985; Marsh and Bennett, 1985). A similar pattern has been recorded for speeds of snakes (Stevenson et al., 1985) and crocodylians (Turner et al., 1985), but it is not characteristic of all ectotherms—it is not observed in the tiger beetle *Cincindela tranquebarica*, for example (Morgan, 1985). The data for *L. vivipara* show that spontaneous voluntary emergence speeds, which are about four times lower than V_{\max} at both T_{act} (Avery et al., 1987a) and when $T_b < T_{act}$ (Avery: unpublished data), also fit this pattern. This is consistent with the current interpretation for the flattening of the curve relating V_{\max} to T_b at higher temperatures—that it is produced by temperature-compensation of enzyme systems over the normal activity temperature range of a species (Marsh and Bennet, 1986a)—since such compensation should presumably operate over the whole range of muscle fibre contraction speeds.

Body temperatures of the lizards were not directly measured during these experiments; such measurements would have involved handling or impairing the animals by implanting thermistors or thermocouples. Movement would then have been under stressed, not spontaneous voluntary, conditions. There is ample evidence that in laboratory arenas such as those used here, T_{act} of *L. vivipara* varies within the range 28–36°C with a mode of 33°C (Avery, 1985). Even if body temperatures were biased towards one or other end of this range, the conclusions would not be affected—redrawing figure 1 with $T_{act} = 28$ or 36°C would not alter the general shapes of the curves relating burst speed or pause duration to temperature. There is also abundant evidence for the implicit assumption that $T_b = T_a$ before a lizard has basked, since observations made by capturing animals and simultaneously measuring T_b with a mercury thermometer or thermistor inserted into the cloaca (Avery, 1971 and unpublished data) and using a pyroelectric vidicon infrared camera to determine T_b non-invasively (Avery and D'Eath, 1986), all support it.

The gait of *L. vivipara* at T_{act} is of a kind which is widespread amongst quadrupedal lizards (Sukhanov, 1974). When *L. viridis* are travelling at 42 cm s⁻¹ (equivalent to about 4 SVL s⁻¹), for example, they move in this way. The duty factor of each foot under these circumstances is 0.54 (Daan and Belterman, 1968). The change in gait

with decreasing temperature has not previously been described. At intermediate temperatures (20, 16°C) the gait of *L. vivipara* is similar to the gait of a urodele at unspecified, but presumably normal laboratory temperature; duty factors of the fore and hind feet are 0.74 and 0.71 respectively and the phase difference for ipsilateral pairs is 0.64 (Daan and Belterman, 1968). The corresponding values for *L. vivipara* at 20°C are 0.75, 0.76 and 0.68 respectively.

Decreasing temperature increases the contraction times and decreases the power output of reptilian voluntary muscle fibres (Marsh and Bennett, 1985, 1986b). This is undoubtedly the primary reason why stride frequency decreases (fig. 2). Whether the progressive change in gait with decreasing temperature is a consequence of decreasing stability at the consequent slower speeds (see Jayes and Alexander, 1980) or whether it is mainly a consequence of loss of efficiency of muscles, and perhaps also neuromuscular coordination, is a complex question. A great deal of further work will be needed in order to answer it. The same may be said of the increase in pause duration (fig. 1). This is probably related to changes in central or spinal pattern-generating mechanisms, but too little is known of these processes to enable one even to speculate about possible mechanisms. Empirically the pauses are important because they reduce overall speed, and must increase the vulnerability of the lizards to potential predators (see also Christian and Tracy, 1981).

References

- Arnold, E.N. (1973): Relationships of the Palaearctic lizards assigned to the genera *Lacerta*, *Algyroides* and *Psammotromus* (Reptilia: Lacertidae). *Bull. Br. Mus. Hist., Zool.* **25**: 291-366.
- Arnold, E.N., Burton, J.A., Ovenden, D.W. (1978): A field guide to the Reptiles and Amphibians of Europe. London, Collins.
- Avery, R.A. (1971): Estimates of food consumption by the lizard *Lacerta vivipara*. *J. Anim. Ecol.* **40**: 351-365.
- Avery, R.A. (1982): Field studies of body temperatures and thermoregulation. In: *Biology of the Reptilia 12. Physiology C, Physiological Ecology*. p. 91-166. Gans, C., Pough, F.H., Eds., London, Academic Press.
- Avery, R.A. (1985): Thermoregulatory behaviour of Reptiles in the field and in captivity. In: *Reptiles: breeding, behaviour and veterinary aspects* p. 45-60. Townson, S., Lawrence, K., Eds., London, British Herpetological Society.
- Avery, R.A., D'Eath, F.M. (1986): Thermography, thermoregulation and animal behaviour. In: *Recent developments in medical and physiological imaging* p. 71-75. Clark, R.P., Goff, M.R., Eds., London, *Journal of Medical Engineering and Technology Supplement*, Taylor and Francis.
- Avery, R.A., McArdle, B.K. (1975): The morning emergence of the common lizard *Lacerta vivipara* Jacquin. *Br. J. Herpetol.* **5**: 363-368.
- Avery, R.A., Mueller, C.F., Smith, J.A., Bond, D.J. (1987a): The movement patterns of lacertid lizards: speed, gait and pauses in *Lacerta vivipara*. *J. Zool., Lond.* **211**: 47-63.
- Avery, R.A., Mueller, C.F., Jones, S.M., Smith, J.A., Bond, D.J. (1987b): Speeds and movement patterns of European lacertid lizards: a comparative study. *J. Herpetol.* **21**: 322-327.
- Berkum, F.H. van, Huey, R.B., Adams, B.A. (1986): Physiological consequences of thermoregulation in a tropical lizard (*Amieva festiva*). *Physiol. Zool.* **59**: 464-472.
- Christian, K.A., Tracy, C.R. (1981): The effect of thermal environment on the ability of hatchling Galapagos land iguanas to avoid predators during dispersal. *Oecologia* **49**: 218-223.

- Crowley, S.R. (1985): Thermal sensitivity of sprint-running in the lizard *Sceloporus undulatus*: support for a conservative view of thermal physiology. *Oecologia* **66**: 219-225.
- Daan, S., Belterman, T. (1968): Lateral bending in locomotion of some lower tetrapods. I. Proc. K. Ned. Akad. Wet. (C) **71**: 245-258.
- Garland, T. (1985): Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. *J. Zool., Lond.* **207**: 425-439.
- Hailey, A. (1982): Choice of substrate and heating rate in *Lacerta vivipara*. *Br. J. Herpetol.* **6**: 207-213.
- Huey, R.B. (1982): Temperature, physiology and the ecology of Reptiles. In: *Biology of the Reptilia* 12. Physiology C, Physiological Ecology p. 25-91. Gans, G., Pough, F.H., Eds., London, Academic Press.
- Jayes, A.S., Alexander, R. McN. (1980): The gaits of chelonians: walking techniques for very low speeds. *J. Zool., Lond.* **191**: 353-378.
- Marsh, R.L., Bennett, A.F. (1985): Thermal dependence of isotonic contractile properties of skeletal muscle and sprint performance of the lizard *Dipsosaurus dorsalis*. *J. Comp. Physiol. B*: **115**: 541-551.
- Marsh, R.L., Bennett, A.F. (1986a): Thermal dependence of contractile properties of skeletal muscle from the lizard *Sceloporus occidentalis* with comments on methods for fitting and comparing force-velocity curves. *J. Exp. Biol.* **126**: 63-77.
- Marsh, R.L., Bennett, A.F. (1986b): Thermal performance of sprint performance of the lizard *Sceloporus occidentalis*. *J. Exp. Biol.* **126**: 79-87.
- Morgan, K.R. (1985): Body temperature regulation and terrestrial activity in the ectothermic beetle *Cincindela tranquebarica*. *Physiol. Zool.* **58**: 29-37.
- Paladino, F.V. (1985): Temperature effects on locomotion and activity bioenergetics of amphibians, reptiles and birds. *Amer. Zool.* **25**: 665-972.
- Pough, F.H., Gans, C. (1982): The vocabulary of reptilian thermoregulation. In: *Biology of the Reptilia* 12. Physiology C, Physiological Ecology. p. 17-23. Gans, C., Pough, F.H., Eds., London, Academic Press.
- Simms, C. (1970): *Lives of British Lizards*. Norwich, Goose & Son.
- Spellerberg, I.F. (1976): Adaptations of Reptiles to cold. In: *Morphology and Biology of Reptiles* p. 261-285. Bellairs, A.d'A., Cox, C.B., Eds., London, Academic Press.
- Stevenson, R.D., Peterson, C.R., Tsuji, J.S. (1985): The thermal dependence of locomotion, tongue flicking, digestion, and oxygen consumption in the wandering garter snake. *Physiol. Zool.* **58**: 46-57.
- Sukhanov, V.B. (1974): General system of symmetrical locomotion of terrestrial vertebrates and some features of movement of lower tetrapods. New Delhi, Amerind Publishing Co Pvt Ltd. (translation from Russian).
- Turner, J.S., Tracy, C.R., Weigler, B., Baynes, T. (1985): Burst swimming of alligators and the effect of temperature. *J. Herpetol.* **19**: 450-458.

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