HYDRIC CONDITIONS DURING INCUBATION INFLUENCE LOCOMOTOR PERFORMANCE OF HATCHLING SNAPPING TURTLES

By KIRK MILLER

Department of Biology, Franklin and Marshall College, Lancaster, PA 17604, USA

GARY C. PACKARD AND MARY J. PACKARD

Department of Zoology, Colorado State University, Fort Collins, CO 80523, USA

SUMMARY

Locomotor performance of hatchling snapping turtles (*Chelydra serpentina*) was assessed while turtles were running on land and swimming in water. Hatchlings from eggs incubated on a relatively wet substrate were faster than hatchlings from eggs incubated on a drier medium, both in absolute distance and in body lengths moved per unit time. The superior performance of turtles from the wet substrate was not due to differences in hydration of tissues, because differences in performance persisted after turtles from both groups had been fully hydrated. The superior performance of turtles from the wet substrate may stem from a greater aerobic capacity, because these animals accumulated lactate more slowly during locomotion than did turtles from eggs incubated on the dry substrate. These observations may provide a physiological basis for the improved survival of larger hatchlings of many species of reptiles.

INTRODUCTION

Flexible-shelled eggs of turtles exchange water with the environment of the nest cavity (Cagle, 1950; Legler, 1954; Hendrickson, 1958; Montevecchi & Burger, 1975; M. J. Packard, Packard & Boardman, 1982; G. C. Packard, Paukstis, Boardman & Gutzke, 1985*b*). These water exchanges dramatically affect changes in mass of the eggs over the course of incubation. Eggs incubated on relatively wet substrates gain water and mass during incubation, while those incubated on relatively dry substrates lose water and mass over the course of development (Tracy, Packard & Packard, 1978; G. C. Packard, Taigen, Packard & Boardman, 1980; G. C. Packard, Packard & Boardman, 1981*a*, 1982; G. C. Packard, Packard, Boardman & Ashen, 1981*b*; Morris *et al.* 1983; G. C. Packard *et al.* 1983; G. C. Packard, Packard & Gutzke, 1985*a*).

Water exchanges between eggs and their environment affect the incubation and development of embryonic turtles. Embryos developing in eggs on relatively wet

substrates incubate longer, catabolize their yolk more quickly, have a higher meta-bolic rate, and grow faster than embryos in eggs on relatively dry substrates (G. C. Packard *et al.* 1981*b*, 1985*a*; Morris *et al.* 1983; Gettinger, Paukstis & Gutzke, 1984). As a result, turtles hatching from eggs incubated on relatively wet substrates are larger, but contain a smaller mass of residual yolk, than those hatching from eggs incubated on drier substrates (G. C. Packard *et al.* 1980, 1981*b*, 1982, 1985*a*; Morris *et al.* 1983).

Larger hatchlings have been suggested to have a selective advantage, relative to smaller conspecifics, due to increased competitive ability or improved predator evasion, simply as the result of being larger (G. C. Packard *et al.* 1981*b*; Morris *et al.* 1983). We report here that snapping turtles hatching from eggs incubated on wet substrates exhibit improved locomotor performance well beyond that which might be expected on the basis of their larger size.

MATERIALS AND METHODS

Four newly constructed snapping turtle nests were excavated on 12–14 June, 1984 at the Valentine National Wildlife Refuge, Cherry County, Nebraska. As eggs were removed from the nests they were gently brushed free of adhering sand, numbered to identify their clutch, and packed in moist peat moss in styrofoam containers. The containers were stored in a cool pump house until 15 June, when all eggs were transported by car to Colorado State University. On 16 June eggs were removed from the containers, recleaned, weighed, numbered, and assigned to treatments. This last date was regarded as day 0 of the experiment.

The four clutches of eggs were incubated half-buried in vermiculite substrates in covered containers at 29 °C. Twenty-four eggs from each clutch were incubated on vermiculite with a water potential of −150 kPa (relatively wet), and 24 eggs from each clutch were incubated on a substrate with a water potential of −850 kPa (relatively dry). Substrates with a water potential of −150 kPa were produced by adding 333 g of water to 300 g dry vermiculite, and substrates with a water potential of −850 kPa were produced by adding 54 g of water to 300 g dry vermiculite (Morris *et al.* 1983). Incubation under these conditions influences growth of embryos and the size of hatchlings (Morris *et al.* 1983).

Each egg was weighed using a Sartorius electronic balance on day 2 of incubation and at weekly intervals thereafter until the first egg was pipped on day 52 of incubation. Water was added to substrates twice each week to replace that which had been absorbed by eggs or lost through evaporation (G. C. Packard *et al.* 1981*a*, 1985*a*). Thus, relatively constant water content was maintained in incubation sub-strates for the duration of incubation.

Immediately after the first egg in a container was pipped, the eggs within the container were separated from one another with hardware cloth partitions so that hatchlings could be individually identified. On the day of emergence, hatchlings

were cleaned of adhering vermiculite, weighed, and their carapace length was measured with a dial caliper. During the first week after hatching turtles remained on, or buried in, the vermiculite substrate of their artificial nests.

One week after hatching, locomotor performance of turtles from each clutch and water potential was determined while they were running on land or swimming in water. Turtles were stimulated to move as fast as possible by pinching their tails with blunt forceps. Lap times were taken at intermediate points during the exercise, and plots of distance moved as a function of time spent moving were constructed for each individual. Plots of carapace lengths (as an estimate of body length) moved as a function of time were also constructed for each individual to help adjust for differences in size among individuals. In both of these cases, distance was plotted as the dependent variable so that the slope of the plotted points would reflect turtle speed.

Performance in water was determined at 29°C in a trough 88·8 cm in circumference and 5·5 cm wide containing water 4 cm deep. Performance on land was determined on a substrate of wet paper towels at 23°C. Twenty-four hours prior to testing, turtles were isolated in closed paper cups containing vermiculite from their incubation box. Turtles tested on land were allowed 30 min prior to testing for their body temperature to reach 23°C.

Immediately following the first determination of performance, turtles were toe-clipped on one rear toe so they could be individually identified, and placed in water 1 cm deep at 21°C for 1 week. Performance on land or in water was then re-determined as described above. Individuals performed in the same medium and at the same temperature as they had during the first determination of performance.

Speeds of turtles were analysed by repeated measures analysis of variance (Dixon, 1981). The fixed factor in these analyses was the water potential of the substrate during incubation (-150 kPa *vs* -850 kPa). Data were blocked by clutch to account for variation among the four clutches, and different estimates of performance from the same individual were treated as repeated measures.

We also determined the rate of lactate accumulation during sprint performance by turtles on land and in water. One week after hatching, turtles from each clutch (when possible) and water potential were forced to move as fast as possible using methods described above. Each animal was forced to move one of seven preselected distances. Immediately following the completion of the exercise, animals were plunged into liquid nitrogen. Whole-body lactate was subsequently determined on the frozen carcasses (Miller, 1983).

Data for lactate accumulation during locomotion were analysed by analyses of covariance (Nie *et al.* 1975). Substrate water potential was the fixed factor in these analyses, and, in the case of lactate accumulation on land, data were blocked by clutch to increase the power of the statistical test. Increasing distance moved by turtles was associated with a linear increase in lactate concentration (see below), so distance moved was used as a covariate to remove the effects of distance on lactate concentration for the purpose of these analyses.

Table 1. *Mean values for data on eggs and hatchlings of snapping turtles incubated on wet and dry substrates at 29°C*

| | Water potential | | | |
	−150 kPa	−850 kPa	LSD	P
Initial egg mass (g)	12·44	12·03	0·448	0·076
Egg mass on day 51 (g)	11·92	9·05	0·045	<0·001
Days to pipping	58·2	54·4	0·210	<0·001
Days to hatching	59·2	55·3	0·201	<0·001
Number hatching	84	66		
Hatching success	87·5 %	68·8 %		
Hatchling mass (g)	9·12	7·11	0·046	<0·001
Carapace length (cm)	2·75	2·44	0·012	<0·001

The least significant difference (LSD) at alpha = 0·05 is included as a measure of dispersion (Snedecor & Cochran, 1980). Probabilities that pairs of means are different were taken from analysis of variance on initial egg mass, and from analyses of covariance, using initial egg mass as a potential covariate, in all other cases. The covariate was a significant source of variation in the data in all cases, indicating that egg mass on day 0 significantly influenced the variable in question.

<div align="center">RESULTS</div>

Eggs incubated on the wetter substrate (−150 kPa) lost an average of 0·5 g over the course of incubation. In contrast, eggs incubated on the drier substrate (−850 kPa) lost an average of 3·0 g in the same interval (Table 1). Eggs on the wetter substrate also incubated longer and produced larger hatchlings than did clutchmates from eggs on the dry medium (Table 1).

Turtles from both treatments lost mass during the first week after hatching. Animals from −850 kPa lost an average of 0·35 g (4·9 % of hatching body mass) while turtles from −150 kPa lost 0·25 g (2·7 % of hatching body mass) during the week spent in their artificial nests prior to the first determination of locomotor performance. Animals from −850 kPa lost significantly more mass during this week than did animals from −150 kPa, as judged by analysis of covariance with egg mass on day 0 of incubation as a potential covariate to adjust for differences in size among turtles ($F_{1,147} = 7·56$, $P = 0·007$).

Both running and swimming turtles moved steadily over the relatively short distances we forced our animals to move in the first test of performance. Thus, plots of distance moved as a function of time spent moving for individuals were sufficiently linear (see Figs 1, 2) for us to characterize the performance of each individual by its speed (the slope). Hatchlings from eggs incubated at −150 kPa moved substantially faster than clutchmates from eggs incubated at −850 kPa (Table 2; Fig. 1). When data were expressed in units of body lengths s^{-1}, turtles from the wet environment were still faster than clutchmates from dry settings (Table 2; Fig. 2).

Turtles from both treatments gained mass while they were in water during the second week after hatching. Animals from −850 kPa gained an average of 0·89 g, while turtles from −150 kPa gained 0·08 g prior to the second determination of locomotor performance. Animals from −850 kPa gained significantly more mass during this week than did animals from −150 kPa, as judged by analysis of covariance

Table 2. *Locomotor performance of hatchling snapping turtles*

| | Water potential of incubation substrates | |
	−150 kPa	−850 kPa
First determination		
swimming speed (cm s^{-1})	3·3 (0·81)	2·0 (0·46)
(lengths s^{-1})	1·15 (0·26)	0·79 (0·18)
running speed (cm s^{-1})	2·0 (0·72)	1·2 (0·67)
(lengths s^{-1})	0·72 (0·27)	0·49 (0·29)
Second determination		
swimming speed (cm s^{-1})	4·0 (0·50)	3·5 (0·62)
(lengths s^{-1})	1·42 (0·19)	1·34 (0·22)
running speed (cm s^{-1})	4·0 (0·75)	3·0 (0·71)
(lengths s^{-1})	1·38 (0·28)	1·15 (0·26)

The standard deviation is included in parentheses beside each mean performance as a measure of dispersion. Sample sizes were 11 and 8 for swimming performance of turtles from wet and dry boxes, respectively, and 9 and 8 for running performance of turtles from wet and dry boxes, respectively.

Turtles from eggs incubated at −150 kPa swam significantly faster, on both absolute (cm s^{-1}) and relative scales (body lengths s^{-1}), than their counterparts from eggs incubated at −850 kPa ($F_{1,11} = 9·58$, $P = 0·010$, for absolute swimming speed; $F_{1,11} = 4·56$, $P = 0·056$, for relative swimming speed). Turtles from eggs incubated at −150 kPa also ran significantly faster, on both absolute and relative scales, than their counterparts from eggs incubated at −850 kPa ($F_{1,9} = 16·07$, $P = 0·003$, for absolute running speed; $F_{1,9} = 8·75$, $P = 0·016$, for relative running speed). In all of these analyses the repeated measure was also a significant source of variation ($F_{1,11} = 79·66$, $P < 0·001$; $F_{1,11} = 82·42$, $P < 0·001$ for absolute and relative swimming speed, respectively; $F_{1,9} = 135·97$, $P < 0·001$; $F_{1,9} = 136·81$, $P < 0·001$ for absolute and relative running speed, respectively): turtles moved substantially faster during the second determination of performance.
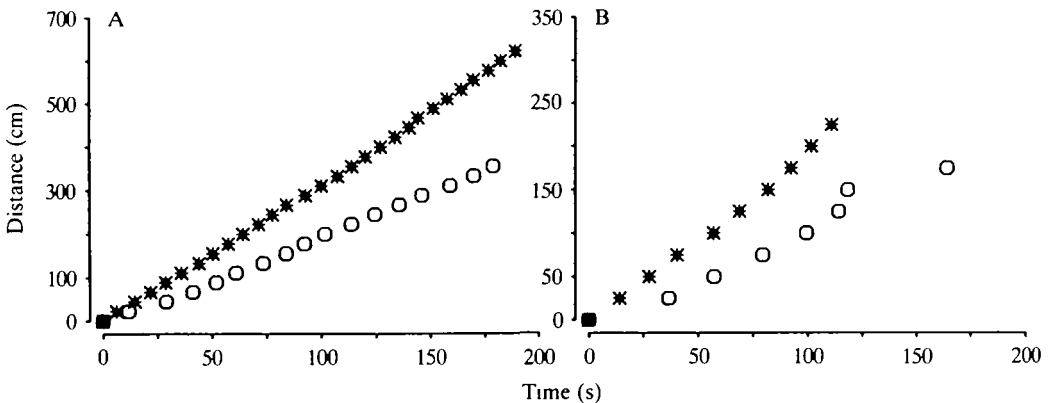

Fig. 1. (A) Locomotor performance of hatchling snapping turtles swimming in water. Points are the mean performance of 11 turtles from four clutches reared on a substrate with a water potential of −150 kPa (●) or of eight turtles from the same four clutches reared at −850 kPa (○). (B) Locomotor performance of hatchling snapping turtles running on land. Points are the mean performance of nine turtles from four clutches reared on a substrate with a water potential of −150 kPa (●) or of nine clutchmates reared at −850 kPa (○). These figures are drawn such that the slope of the line describing the data reflects speed.
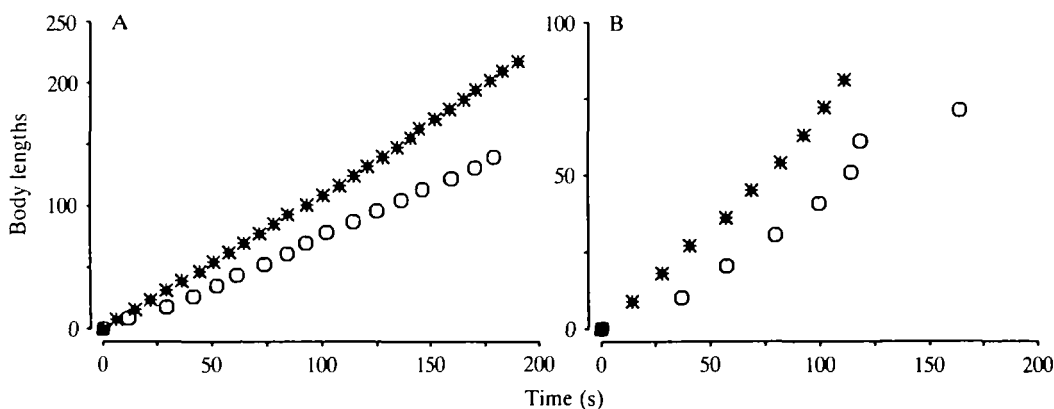
Fig. 2. (A) Relative locomotor performance of hatchling snapping turtles swimming in water. (B) Relative locomotor performance of hatchling snapping turtles running on land. Sample sizes and symbols are the same as in Fig. 1.

with egg mass on day 0 of incubation as a potential covariate to adjust for differences in size among animals ($F_{1,33} = 97.30$, $P < 0.001$).

All turtles were considerably faster during the second test of performance, and turtles from eggs incubated at -150 kPa were still faster, on both absolute and relative scales, than were their counterparts from eggs incubated at -850 kPa (Table 2).

The water potential of the incubation substrate also affected the rate of increase in lactate concentration during sprint performance by turtles, both while they were swimming in water ($F_{1,34} = 8.16$; $P = 0.007$) and running on land ($F_{1,47} = 5.27$; $P = 0.026$). Hatchlings from eggs incubated on the relatively dry substrate accumulated lactate at a greater rate than their counterparts from eggs incubated on the wetter substrate, despite moving at a considerably slower speed (Fig. 3).

Turtles from eggs incubated at -850 kPa also accumulated more lactate than those from eggs incubated at -150 kPa. Turtles from the dry substrate accumulated an average of 1·01 mg lactate while running 132 cm at 1·2 cm s^{-1}, while turtles from the wet substrate accumulated only 0·69 mg running the same distance at 2·0 cm s^{-1}. Further, turtles from the dry substrate accumulated an average of 1·12 mg lactate while swimming 266 cm at 2·0 cm s^{-1}, while those from the wet substrate accumulated 0·34 mg lactate swimming the same distance at 3·3 cm s^{-1}.

DISCUSSION

Eggs incubated on the wet substrate declined 4% in mass over the course of incubation, while those incubated on the dry substrate lost 24% of their initial mass over the same interval. This pattern of response by incubating eggs to substrate water potential has been observed previously for eggs of snapping turtles (G. C. Packard et al. 1980, 1981b; Morris et al. 1983). Changes in the mass of eggs during incubation represent net transfers of water between incubating eggs and their environment. These water exchanges affect the physiology of developing turtles such

that turtles incubating on relatively wet substrates incubate longer and are larger at hatching compared with those incubating on drier substrates (G. C. Packard *et al.* 1980, 1981*b*; Morris *et al.* 1983; Table 1). The mechanism through which water exchanges during incubation affect the physiology of developing turtles is not known (G. C. Packard & M. J. Packard, 1984). However, we have shown here that the impact of embryonic water exchanges on the physiology of developing turtles extends beyond hatching and affects the locomotor performance of young turtles.

Turtles from eggs incubated at −150 kPa moved substantially faster than clutch-mates from eggs incubated at −850 kPa (Table 2; Fig. 1). We fully expected turtles from the wet substrate to move faster than their counterparts from eggs incubated on the dry substrate, because of their larger size. Larger animals typically move faster than smaller members of the same species. However, when speeds were expressed relative to body size (as body lengths s^{-1}), turtles from the wet environment were still faster than clutchmates from dry settings (Table 2; Fig. 2). This finding was not
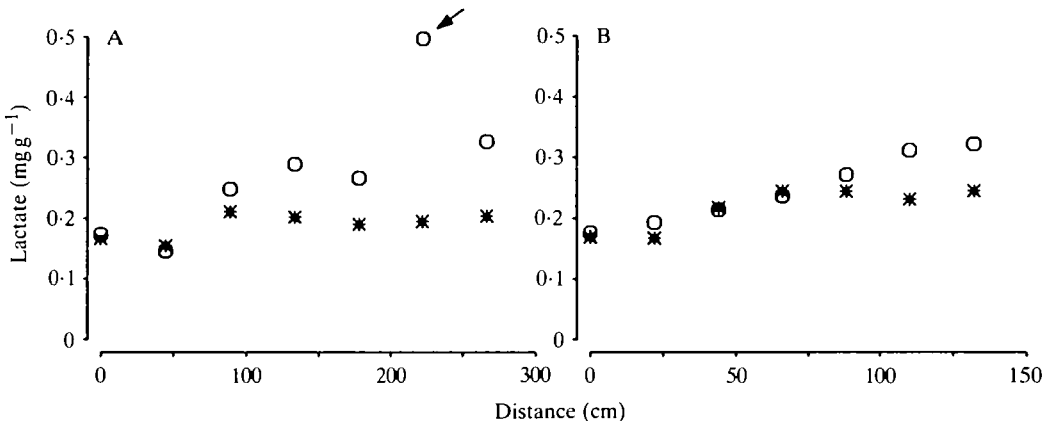

Fig. 3. (A) Lactate accumulation by hatchling snapping turtles swimming in water. Each point is the mean concentration of lactate (mg lactate g^{-1} body mass) accumulated by turtles while swimming the distance indicated on the x-axis at speeds as shown in Fig. 1A. Each point represents the mean whole-body lactate accumulated by four turtles from four different clutches from eggs incubated on a substrate with a water potential of −150 kPa (✳), or of two turtles [except for the outlying point (arrow), which is based on one observation] from two of those clutches from eggs incubated at −850 kPa (○). Hatchlings from eggs incubated at −850 kPa water potential accumulated lactate at a rate of 0·95 μg g^{-1} body mass cm^{-1} swum ($r^2 = 0.62$) while swimming at 2·0 cm s^{-1}, where-as hatchlings from eggs incubated at −150 kPa water potential accumulated lactate at a rate of 0·14 μg g^{-1} body mass cm^{-1} swum ($r^2 = 0.41$) while swimming at 3·3 cm s^{-1}. (B) Lactate accumulation by hatchling snapping turtles running on land. Each point is the mean concentration of lactate (mg lactate g^{-1} body mass) accumulated by turtles while running the distance indicated on the x-axis at speeds as shown in Fig. 1B. Each point represents the mean whole-body lactate accumulated by four turtles from four different clutches from eggs incubated on a substrate with a water potential of −150 kPa (✳), or of four clutchmates from eggs incubated at −850 kPa (○). Hatchlings from eggs incubated at −850 kPa accumulated lactate at a rate of 1·2 μg g^{-1} body mass cm^{-1} run ($r^2 = 0.98$) while running at 1·2 cm s^{-1}, whereas hatchlings from eggs incubated at −150 kPa accumulated lactate at a rate of 0·63 μg g^{-1} body mass cm^{-1} run ($r^2 = 0.72$) while running at 2·0 cm s^{-1}.

anticipated, as larger animals typically move relatively more slowly (fewer body lengths s^{-1}) than smaller ones. This finding is without parallel in the literature on locomotion (see below).

The maximum speed sustained during prolonged bouts of swimming is absolutely faster but relatively slower in larger fish. However, the relative speed of burst locomotion in fish (lasting less than 15 s) is independent of body length (and about 10 lengths s^{-1}) (Bainbridge, 1960; Brett, 1965; Webb, 1975; Wu, 1977; Beamish, 1978). As a rule, the maximum running speed of mammals is absolutely faster but relatively slower in larger animals (Garland, 1983). Among reptiles, sprint speeds of lizards have been reported to increase in proportion to their body mass raised to powers ranging from 0 to 0·34 (Huey & Hertz, 1982; Garland, 1984 and references cited therein, 1985). This means that, at the extremes, absolute lizard speed is independent of lizard length (all lizards run at the same speed), or that relative lizard speed is independent of lizard length (a doubling of lizard length leads to a doubling of lizard speed). It has been proposed on theoretical grounds that the maximum speed of movement is independent of animal size (Thompson, 1942; Hill, 1950), and this has been observed in certain groups of mammals (Alexander, Langman & Jayes, 1977; Garland, 1983). In this case, all animals move at the same absolute speed, so smaller animals move at much faster relative speeds. In no case are larger animals predicted or observed to move at greater relative speeds.

Turtles hatching from eggs incubated at −850 kPa were probably dehydrated compared with those incubated at −150 kPa (Morris et al. 1983). Furthermore, animals from eggs incubated at −850 kPa lost more mass during the first week after hatching, which they spent in their artificial nests, and gained more mass during the second week after hatching, which they spent in water, compared with turtles from eggs incubated at −150 kPa. These observations suggest that turtles from eggs incubated on the dry substrate were slightly dehydrated during the first test of locomotor performance, compared with those from eggs incubated on the wet substrate, and this may explain some of the difference in performance between the two groups (Claussen, 1974; Beuchat, Pough & Stewart, 1984; Feder & Londos, 1984; Crowley, 1985; Stefanski, Gatten & Pough, 1985). All of our animals improved their performance during the second test, and turtles from eggs incubated on the dry substrate improved their performance more than those from eggs incubated on the wet substrate (Table 2). This suggests that dehydration was indeed a factor affecting the performance of both groups, and the magnitude of the difference in performance between the groups. Alternatively, the improved performance of animals in both groups during the second test of their locomotor performance may reflect an ontogenetic change in their ability due to the greater age of turtles during the second test of performance (Pough, 1978; Taigen & Pough, 1981).

Although all turtles were considerably faster during the second test of performance, turtles from eggs incubated at −150 kPa were still faster, on both absolute and relative scales, than their counterparts from eggs incubated at −850 kPa (Table 2). Whereas some of the difference in initial performance between turtles from eggs incubated on substrates differing in water potential may have been due to differences

in hydration of animals, not all of the difference between groups can be explained on this basis.

To examine the metabolic basis for the superior locomotor performance by turtles from eggs incubated at $-150\,\text{kPa}$, we determined the rate of lactate accumulation during sprint performance by turtles. Lactate accumulation is a measure of the extent of anaerobic metabolism during locomotion by reptiles (Bennett, 1982). The rate of lactate production during a sprint gives an estimate of the energy cost of locomotion (Miller, 1983). Differences in the rate of lactate accumulation among groups reared at different substrate water potentials presumably reflect different degrees of reliance on anaerobic metabolism in support of locomotion. Turtles from eggs incubated at $-850\,\text{kPa}$ may be more reliant on lactate production to supply energy for locomotion because of lower relative tissue hydration (see above). However, differences in tissue hydration of turtles from eggs incubated at the two water potentials were probably too small to affect cellular metabolism (Hillman, 1978; Clegg, 1981, 1984). Alternatively, lower rates of locomotion and increased reliance on anaerobic metabolism of turtles from eggs incubated on the drier substrate may be due to a greater percentage of body mass due to the mass of residual yolk in these hatchlings (Morris *et al.* 1983). The mass of residual yolk represents body mass that does not contribute to the generation of force during movement. The body mass of hatchling snapping turtles from eggs reared at $-850\,\text{kPa}$ includes about 18 % yolk, while that of hatchlings from eggs reared at $-150\,\text{kPa}$ includes only 4 % residual yolk (Morris *et al.* 1983). However, most of the residual yolk is metabolized by the end of the second week after hatching in snapping turtles (Wilhoft, 1985), and so, at least during the second test of performance, most of our animals should have had little residual yolk left to carry. The improved locomotor performance of turtles from eggs experiencing favourable water exchanges may, however, reflect ontogenetic changes in endurance and metabolism (Pough, 1978; Taigen & Pough, 1981), expressed as a result of longer incubation times (Morris *et al.* 1983). Hatchling snapping turtles from eggs incubated on a wet substrate may be developmentally more mature compared with those from eggs incubated on a dry substrate.

Increased speed on land and reduced reliance on anaerobic metabolism to provide energy for locomotion should allow hatchling snapping turtles from nests constructed in relatively wet substrates to move the distance from nest to water more quickly than turtles from nests in drier settings. Further, once hatchlings from relatively wet nests reach water, their faster swimming speeds and lower reliance on anaerobic processes to provide energy for swimming locomotion may allow them to evade predators more successfully and to take a greater variety of food items than turtles from nests constructed in drier substrates. Thus, the adaptive value of experiencing favourable water exchange during incubation may be expressed as an improved locomotor performance resulting from physiological advantages exceeding those expected on the basis of larger size alone. This may be the basis for the improved competitive ability and increased survival of larger hatchlings of reptiles (Froese & Burghardt, 1974; Ferguson & Bohlen, 1978; Fox, 1978; Swingland & Coe, 1979; Ferguson, Brown & DeMarco, 1982; Ferguson & Fox, 1984).

REFERENCES

ALEXANDER, R. McN., LANGMAN, V. A. & JAYES, A. S. (1977). Fast locomotion of some African ungulates. *J. Zool., Lond.* **183**, 291–300.

BAINBRIDGE, R. (1960). Speed and stamina in three fish. *J. exp. Biol.* **37**, 129–153.

BEAMISH, F. W. H. (1978). Swimming capacity. In *Fish Physiology*, vol. 7 (ed. W. S. Hoar & D. J. Randall), pp. 101–187. New York: Academic Press.

BENNETT, A. F. (1982). The energetics of reptilian activity. In *Biology of the Reptilia*, vol. 13 (ed. C. Gans & F. H. Pough), pp. 155–199. New York: Academic Press.

BEUCHAT, C. A., POUGH, F. H. & STEWART, M. M. (1984). Response to simultaneous dehydration and thermal stress in three species of Puerto Rican frogs. *J. comp. Physiol.* **154**, 579–585.

BRETT, J. R. (1965). The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). *J. Fish. Res. Bd Can.* **22**, 1491–1501.

CAGLE, F. R. (1950). The life history of the slider turtle, *Pseudemys scripta troostii* (Holbrook). *Ecol. Monogr.* **20**, 31–54.

CLAUSSEN, D. L. (1974). Water balance and jumping ability in anuran amphibians. *Am. Zool.* **14**, 1257.

CLEGG, J. S. (1981). Metabolic consequences of the extent and disposition of the aqueous intracellular environment. *J. exp. Zool.* **215**, 303–313.

CLEGG, J. S. (1984). Properties and metabolism of the aqueous cytoplasm and its boundaries. *Am. J. Physiol.* **246**, R133–R151.

CROWLEY, S. R. (1985). Insensitivity to desiccation of sprint running performance in the lizard, *Sceloporus undulatus*. *J. Herpetol.* **19**, 171–174.

DIXON, W. J. (1981). *BMDP Statistical Software*. Berkeley: University of California Press.

FEDER, M. E. & LONDOS, P. L. (1984). Hydric constraints upon foraging in a terrestrial salamander *Desmognathus ochrophaeus* (Amphibia: Plethodontidae). *Oecologia* **64**, 413–418.

FERGUSON, G. W. & BOHLEN, C. H. (1978). Demographic analysis: a tool for the study of natural selection of behavioral traits. In *Behavior and Neurology of Lizards* (ed. N. Greenberg & P. D. MacLean), pp. 227–243. Rockville, MD: US Department of Health, Education and Welfare, NIMH.

FERGUSON, G. W., BROWN, K. L. & DEMARCO, V. G. (1982). Selective basis for the evolution of variable egg and hatchling size in some iguanid lizards. *Herpetologica* **38**, 178–188.

FERGUSON, G. W. & FOX, S. F. (1984). Annual variation of survival advantage of large juvenile side-blotched lizards, *Uta stansburiana*: its causes and evolutionary significance. *Evolution* **38**, 342–349.

FOX, S. F. (1978). Natural selection on behavioral phenotypes of the lizard *Uta stansburiana*. *Ecology* **59**, 834–847.

FROESE, A. D. & BURGHARDT, G. M. (1974). Food competition in captive juvenile snapping turtles, *Chelydra serpentina*. *Anim. Behav.* **22**, 735–740.

GARLAND, T., JR (1983). The relation between maximal running speed and body mass in terrestrial mammals. *J. Zool., Lond.* **199**, 157–170.

GARLAND, T., JR (1984). Physiological correlates of locomotory performance in a lizard: an allometric approach. *Am. J. Physiol.* **247**, R806–R815.

GARLAND, T., JR (1985). Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. *J. Zool., Lond.* **207**, 425–439.

GETTINGER, R. D., PAUKSTIS, G. L. & GUTZKE, W. H. N. (1984). Influence of hydric environment on oxygen consumption by embryonic turtles *Chelydra serpentina* and *Trionyx spiniferus*. *Physiol. Zool.* **57**, 468–473.

HENDRICKSON, J. R. (1958). The green sea turtle, *Chelonia mydas* (Linn.) in Malaya and Sarawak. *J. Zool., Lond.* **130**, 455–535.

HILL, A. V. (1950). The dimensions of animals and their muscular dynamics. *Scient. Prog., Oxford* **38**, 209–230.

HILLMAN, S. S. (1978). The roles of oxygen delivery and electrolyte levels in the dehydrational death of *Xenopus laevis*. *J. comp. Physiol.* **128**, 169–175.

HUEY, R. B. & HERTZ, P. E. (1982). Effects of body size and slope on sprint speed of a lizard (*Stellio (Agama) stellio*). *J. exp. Biol.* **97**, 401–409.

LEGLER, J. M. (1954). Nesting habits of the western painted turtle, *Chrysemys picta bellii* (Gray). *Herpetologica* **10**, 137–144.

MILLER, K. (1983). The role of lactate production in the metabolic support of locomotion by clawed frogs *Xenopus laevis*. *Physiol. Zool.* **56**, 580–584.

MONTEVECCHI, W. A. & BURGER, J. (1975). Aspects of the reproductive biology of the northern diamondback terrapin *Malaclemys terrapin terrapin*. *Am. Midl. Nat.* **94**, 166–178.

MORRIS, K. A., PACKARD, G. C., BOARDMAN, T. J., PAUKSTIS, G. L. & PACKARD, M. J. (1983). Effect of the hydric environment on growth of embryonic snapping turtles (*Chelydra serpentina*). *Herpetologica* **39**, 272–285.

NIE, N. H., HULL, C. H., JENKINS, J. G., STEINBRENNER, K. & BENT, D. H. (1975). *Statistical Package for the Social Sciences*, 2nd ed. New York: McGraw-Hill.

PACKARD, G. C. & PACKARD, M. J. (1984). Coupling of physiology of embryonic turtles to the hydric environment. In *Respiration and Metabolism of Embryonic Vertebrates* (ed. R. S. Seymour), pp. 99–119. Dordrecht, The Netherlands: W. Junk.

PACKARD, G. C., PACKARD, M. J. & BOARDMAN, T. J. (1981a). Patterns and possible significance of water exchange by flexible-shelled eggs of painted turtles (*Chrysemys picta*). *Physiol. Zool.* **54**, 165–178.

PACKARD, G. C., PACKARD, M. J. & BOARDMAN, T. J. (1982). An experimental analysis of the water relations of eggs of Blanding's turtles (*Emydoidea blandingii*). *J. Linn. Soc. (Zool.)* **75**, 23–34.

PACKARD, G. C., PACKARD, M. J., BOARDMAN, T. J. & ASHEN, M. D. (1981b). Possible adaptive value of water exchanges in flexible-shelled eggs of turtles. *Science* **213**, 471–473.

PACKARD, G. C., PACKARD, M. J., BOARDMAN, T. J., MORRIS, K. A. & SHUMAN, R. D. (1983). Influence of water exchanges by flexible-shelled eggs of painted turtles *Chrysemys picta* on metabolism and growth of embryos. *Physiol. Zool.* **56**, 217–230.

PACKARD, G. C., PACKARD, M. J. & GUTZKE, W. H. N. (1985a). Influence of hydration of the environment on eggs and embryos of the terrestrial turtle *Terrapene ornata*. *Physiol. Zool.* **58**, 564–575.

PACKARD, G. C., PAUKSTIS, G. L., BOARDMAN, T. J. & GUTZKE, W. H. N. (1985b). Daily and seasonal variation in hydric conditions and temperature inside nests of common snapping turtles (*Chelydra serpentina*). *Can. J. Zool.* **63**, 2422–2429.

PACKARD, G. C., TAIGEN, T. L., PACKARD, M. J. & BOARDMAN, T. J. (1980). Water relations of pliable-shelled eggs of common snapping turtles (*Chelydra serpentina*). *Can. J. Zool.* **58**, 1404–1411.

PACKARD, M. J., PACKARD, G. C. & BOARDMAN, T. J. (1982). Structure of eggshells and water relations of reptilian eggs. *Herpetologica* **38**, 136–155.

POUGH, F. H. (1978). Ontogenetic changes in endurance in water snakes (*Natrix sipedon*): physiological correlates and ecological consequences. *Copeia* **1978**, 69–75.

SNEDECOR, G. W. & COCHRAN, W. G. (1980). *Statistical Methods*, 7th ed. Ames, Iowa: Iowa State University Press.

STEFANSKI, M., GATTEN, R. E. & POUGH, F. H. (1985). The effect of dehydration on energy metabolism of a terrestrial salamander. *Am. Zool.* **25**, 137A.

SWINGLAND, I. R. & COE, M. J. (1979). The natural regulation of giant tortoise populations on Aldabra Atoll: recruitment. *Phil. Trans. R. Soc. Ser. B* **286**, 177–188.

TAIGEN, T. L. & POUGH, F. H. (1981). Activity metabolism of the toad (*Bufo americanus*): ecological consequences of ontogenetic change. *J. comp. Physiol.* **144**, 247–252.

THOMPSON, D'A. W. (1942). *On Growth and Form*, 2nd ed. Cambridge: Cambridge University Press.

TRACY, C. R., PACKARD, G. C. & PACKARD, M. J. (1978). Water relations of chelonian eggs. *Physiol. Zool.* **51**, 378–387.

WEBB, P. W. (1975). Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd Can.* **190**, 159 pp.

WILHOFT, D. C. (1985). Egg and hatchling components of the snapping turtle (*Chelydra serpentina*). *Am. Zool.* **25**, 27A.

WU, T. Y. (1977). Introduction to the scaling of aquatic animal locomotion. In *Scale Effects in Animal Locomotion* (ed. T. J. Pedley), pp. 203–232. London: Academic Press.