

- Saint Girons, H. (1957): Le cycle sexuel chez *Vipera aspis* (L) dans l'ouest de la France. *Bull. Biol. Fr. Belg.* **91**: 284-350.
- Saint Girons, H. (1975): Critères d'âge, structure et dynamique des populations de reptiles. Bourlière, F., Lamotte, M., Eds, Paris, Masson.
- Saint Girons, H., Naulleau, G. (1981): Poids des nouveau-nés et stratégies reproductrices des vipères européennes. *Rev. Ecol.* **35**: 597-615.
- Seigel, R.A., Ford, N.B. (1987): Reproductive ecology. In: *Snakes, Ecology and Evolutionary Biology*. Seigel, R.A., Collins, J.T., Novak, S.S., Eds, New York, Macmillan.
- Shine, R. (1988): Parental care in reptiles. In: *Biology of the Reptilia*, Vol. 16. Gans, C., Huey, R.B., Eds, New York, Alan R. Liss.
- Sinervo, B. (1990): The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution* **44**: 279-294.
- Sibly, R.M., Calow, P. (1986): *Physiological Ecology of Animals*. Blackwell Scientific Publications, Oxford.
- Smith, C.C., Fretwell, S.D. (1974): The optimal balance between size and number of offspring. *Am. Nat.* **108**: 499-506.
- Stearns, S.C. (1992): *The Evolution of Life Histories*. Oxford University Press, New York.

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## Do training and captivity affect maximal metabolic rate of *Varanus gouldii* (Squamata: Varanidae)?

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The metabolic rate of animals is potentially affected by biological conditions such as thermal acclimation, sex, temperature, reproductive state, activity and body mass (Bennett and Dawson, 1976; Gleeson, 1979; Heusner and Jameson, 1981; Garland and Else, 1987; Garland et al., 1987; Tsuji, 1988a, b; Beuchat and Vleck, 1990; Niewiarowski and Waldschmidt, 1992; DeMarco, 1993; Beaupre et al., 1993). Physiological responses to endurance training are well documented in several species of mammals (Hickson et al., 1977; Scheuer and Tipton, 1977; Saltin and Rowell, 1980; Harpur, 1980; Tipton et al., 1979; Dudley et al., 1982). The training response to increased levels of activity is often dramatic, with increases in endurance, maximal metabolic rate ( $VO_{2max}$ ) and tissue oxidative capacities. Conversely, chronic decreases in activity generally have the opposite effect of those induced by increases in activity (Garland et al., 1987). Bennett (1982) indicated that there were few data on the extent to which reptilian aerobic activity performance was influenced by training or the effects of long term captivity where activity levels might be less than would be the situation in their normal habitat. Gleeson (1979)



reported that the maximal aerobic ability of *Sceloporus occidentalis* was unchanged by 6-8 weeks of daily exercise, a similar finding to that reported by Garland et al. (1987) for *Ctenophorus nuchalis*.

In contrast to the lizards studied by Gleeson (1979) and Garland et al. (1987), most goannas are widely-foraging predators with a comparatively high aerobic capacity and as a consequence may respond differently to captivity or sustained bouts of forced activity (training). *Varanus gouldii* remain inactive in their burrows for approximately five months over winter (Pianka, 1994; personal observation) and emerge during late spring. After emerging they remain around their burrows for a few days before they commence to forage widely on a daily basis (Thompson, 1992). If this lack of activity over an extended period resulted in a lowering of their maximal aerobic capacity, then it would have significant ecological consequences (e.g., reducing the extent of foraging, reducing the capacity to catch prey). If maximal metabolic rate altered during the first few weeks after emerging as a result of increased levels of activity then this seasonal variation should be taken into account when measuring  $VO_{2max}$ . Similarly, if prolonged periods of captivity altered maximal metabolic rate (Bennett and John Alder, 1984; Garland et al., 1987) then this would limit the use of laboratory reptiles for measuring maximal aerobic metabolism. This study reports the effects of training and long term captivity on  $VO_{2max}$  during forced activity for *V. gouldii*.

Nine *V. gouldii* that had been held in captivity for at least 12 months in a single outdoor cage (3 m by 3 m) were tested on three occasions; immediately before the training program ( $T_1$ , 1 November 1992), at the conclusion of the training program ( $T_2$ , 28 November 1992) and approximately 4 weeks later ( $T_3$ , 31 December 1992). The training program consisted of four exercise sessions per week for a period of four weeks. The goannas were removed from their cages about mid-morning, to allow time for them to thermoregulate and achieve their ecclitic body temperature ( $T_b$ ). They were then held in calico bags in a controlled temperature chamber at  $35^{\circ}\text{C}$  ( $\pm 1^{\circ}\text{C}$ ) until they were exercised on a treadmill. All goannas were run on a treadmill at  $0.8 \text{ km h}^{-1}$  for 10 minutes for the first three training sessions, then for 15 minutes for all of the subsequent sessions. The choice of the training treadmill speed and frequency of exercise was influenced by two factors. Firstly, Garland et al. (1987) reported damage to the joints of some *Ctenophorus nuchalis* during a training program of 30 minutes running on a treadmill, 5 days per week at  $1.0 \text{ km h}^{-1}$ . The training protocols for the goannas sought to avoid such potential damage. The prescribed training program approximated the distance travelled on an average day ( $200 \text{ m day}^{-1}$ ) and the daily frequency of activity, by similar-sized goannas at Karrakatta Cemetery during October and November (Thompson, 1992). Goannas were pinched or prodded to ensure that they ran for the entire training period. The 10 minute duration of the first three training sessions reflected the maximum time that most of the goannas could be encouraged to run during the initial training sessions without displaying a high level of annoyance with the researcher.



The three testing trials ( $T_1$ ,  $T_2$  and  $T_3$ ) had identical protocols, with food being withheld for at least 60 hours prior to testing. All goannas were removed from their outside cage mid-morning after they had time to thermoregulate and increase their  $T_b$  to approximately their preferred temperature. They were then held in a controlled temperature chamber at  $35^\circ\text{C}$  ( $\pm 1^\circ\text{C}$ ) for a minimum period of one hour before testing. Cloacal temperature was occasionally measured to ensure that their  $T_b$  was within  $\pm 1^\circ\text{C}$  of  $35^\circ\text{C}$  at the commencement of the test. The mean  $T_b$  of all nine goannas immediately after the tests were:  $T_1$ ,  $35.9^\circ\text{C}$  ( $\pm s_{\bar{x}} 0.28$ );  $T_2$ ,  $36.4^\circ\text{C}$ , ( $\pm s_{\bar{x}} 0.14$ );  $T_3$ ,  $36.2^\circ\text{C}$ , ( $\pm s_{\bar{x}} 0.19$ ).

The highest  $\text{VO}_{2\text{max}}$  values from the three trials for the nine captive *V. gouldii* (mean mass  $327.7 \text{ g} \pm s_{\bar{x}} 41.8$ ) held in captivity for more than 12 months were compared with the highest  $\text{VO}_{2\text{max}}$  values from two trials on successive days for sixteen fresh-caught *V. gouldii* (mean mass  $443.5 \text{ g} \pm s_{\bar{x}} 37.9$ ), 15 from Karrakatta Cemetery, Perth, and one from north of Geraldton, Western Australia. The fresh-caught goannas were all measured within seven days of being captured during December 1992.

Oxygen consumption rate ( $\text{VO}_2$ ;  $\text{ml h}^{-1}$ ) and carbon dioxide production rate ( $\text{VCO}_2$ ;  $\text{ml h}^{-1}$ ) were measured using a flow-through respirometry system. Each goanna was weighed and placed in a controlled temperature chamber for at least one hour at  $35^\circ\text{C}$  ( $\pm 1.0^\circ\text{C}$ ) prior to being run on a treadmill. A vacuum drew ambient air through a lightweight, transparent acetate mask placed over the goanna's head and approximately half of the neck. A controlled air flow rate (Brooks mass-flow controller) of  $800 \text{ ml min}^{-1}$  was used to maintain an excurrent  $\text{O}_2$  content of air at between 17–20.5%. The temperature of the air in the controlled temperature chamber ( $T_a$ ;  $^\circ\text{C}$ ) was constantly measured with a chromel-alumel thermocouple. Excurrent air was dried in a Drierite column before passing through a  $\text{CO}_2$  analyser (Hereus-Leybold Binos) and one channel of a paramagnetic  $\text{O}_2$  analyser (Servomex 184A). The differential output of the  $\text{O}_2$  analyser (ambient air — excurrent air) and the analog outputs of the  $\text{CO}_2$  analyser and thermocouple meter were connected to a Promax XT microcomputer with Analog Device RT1800 A/D interface board. The computer system monitored ambient temperature and excurrent  $\text{O}_2$  and  $\text{CO}_2$  content, and calculated at STPD,  $\text{VO}_2$  (after Withers, 1977), every 15 seconds for 8 to 12 minutes, and stored to disk for subsequent analysis. The  $\text{O}_2$  analyser was regularly calibrated during the experiments with a known sample of air.

Goannas were first placed on a stationary treadmill with their mask attached. The treadmill was then started and the belt speed increased to the maximum rate that each goanna could sustain for the duration of the experiment. Goannas were encouraged to run by being touched or prodded at the base of the tail or hind-limbs.

The highest rate of  $\text{VO}_2$  measured from four consecutive values (15 seconds apart) was used as the measure of  $\text{VO}_{2\text{max}}$ . However,  $\text{VO}_2$  values immediately post release on the treadmill were excluded and only scores after 30 seconds of running on the treadmill were included, as it was apparent that some goannas held their breath while being handled and their measured  $\text{VO}_2$  value immediately after re-commencing to breath was occasionally



higher than their  $VO_{2\max}$  values. Most often,  $VO_{2\max}$  would be achieved within five minutes of the goanna commencing to run on the treadmill.

The mean  $VO_{2\max}$  values for  $T_1$ ,  $T_2$  and  $T_3$  tests were  $1.24 \text{ ml g}^{-1} \text{ h}^{-1}$  ( $\pm s_{\bar{x}} 0.10$ , mean mass  $333.3 \text{ g} \pm s_{\bar{x}} 51.3$ ,  $n = 9$ ),  $1.03 \text{ ml g}^{-1} \text{ h}^{-1}$  ( $\pm s_{\bar{x}} 0.093$ , mean mass  $320.9 \text{ g} \pm s_{\bar{x}} 41.1$ ,  $n = 9$ ) and  $1.07 \text{ ml g}^{-1} \text{ h}^{-1}$  ( $\pm s_{\bar{x}} 0.109$ , mean mass  $337.4 \pm s_{\bar{x}} 40.6$ ,  $n = 9$ ), respectively. A repeated-measures ANOVA showed no significant difference between the three trials ( $F_{2,16} = 1.26$ ,  $P = 0.311$ ). It was therefore presumed that there was no training affect for the captive individuals and so the  $VO_{2\max}$  values of these captive goannas could be pooled and compared with fresh-caught specimens.

There was no significant difference between the mean  $VO_{2\max}$  of the captive ( $1.392 \pm s_{\bar{x}} 0.091 \text{ ml g}^{-1} \text{ h}^{-1}$ ,  $n = 9$ ) and fresh caught ( $1.074 \pm s_{\bar{x}} 0.106 \text{ ml g}^{-1} \text{ h}^{-1}$ ,  $n = 16$ ) *V. gouldii* (ANCOVA,  $F_{1,22} = 2.47$ ,  $P = 0.130$ ).

Maximal metabolism of *V. gouldii* appears to be inflexible to the effects of training, a finding that is similar to that reported for some other squamates (Gleeson, 1979; Garland et al., 1987), although, captivity has been shown to reduce  $VO_{2\max}$  values for *Ctenophorus nuchalis* (Garland et al., 1987) and *Tupinambis nigropunctatus* (Bennett and John Alder, 1984) but not for *V. gouldii*. However, the extent or duration of activity during the period of captivity is largely an uncontrollable factor and may play an important, but unknown role in determining  $VO_{2\max}$  values. The lack of a training affect in this study on the maximal metabolic rate for *V. gouldii* supports the speculation of Garland et al. (1987: 455) that "the generally lower activity levels of lizards have made it evolutionally infeasible to incorporate 'natural training' as a typical and beneficial part of the life cycle".

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## References

- Beuchat, C.A., Vleck, D. (1990): Metabolic consequences of viviparity in a lizard, *Sceloporus jarrovi*. *Physiol. Zool.* **63**: 555-570.
- Beaupre, S.T., Dunham, A.E., Overall, K.L. (1993): Metabolism of a desert lizard: The effects of mass, sex, population of origin, temperature, time of day, and feeding on oxygen consumption of *Sceloporus merriami*. *Physiol. Zool.* **66**: 128-147.
- Bennett, A.F. (1982): The energetics of reptilian activity. In: *Biology of the Reptilia*, Vol. 13, p. 155-199. Gans, C., Pough, F.H., Eds, London, Academic Press.
- Bennett, A.F., Dawson, W.R. (1976): Metabolism. In: *Biology of the Reptilia*, Vol. 5, p. 127-133. Gans, C., Dawson, W.R., Eds, London, Academic Press.
- Bennett, A.F., John-Alder, H.B. (1984): The effects of body temperature on the locomotory energetics of lizards. *J. Comp. Physiol. B.* **155**: 21-27.
- DeMarco, V. (1993): Metabolic rates for female viviparous lizards (*Sceloporus jarrovi*) throughout the reproductive cycle: Do pregnant lizards adhere to standard allometry? *Physiol. Zool.* **66**: 166-180.



- Dudley, G.A., Abraham, W.M., Terjung, R.L. (1982): Influence of exercise intensity and duration on biochemical adaptations in skeletal muscle. *J. Appl. Physiol.* **53**: 844-850.
- Garland, T. (1984): Physiological correlates of locomotory performance in a lizard: an allometric approach. *Am. J. Physiol.* **247**: R806-R815.
- Garland, T., Else, P.E. (1987): Seasonal, sexual, and individual variation in endurance and activity metabolism in lizards. *Am. J. Physiol.* **252**: R439-R449.
- Garland, T., Else, P., Hulbert, A.J., Tap, P. (1987): Effects of endurance training and captivity on activity metabolism of lizards. *Am. J. Physiol.* **252**: R450-R456.
- Gleeson, T.T. (1979): The effects of training and captivity on the metabolic capacity of the lizard *Sceloporus occidentalis*. *J. Comp. Physiol.* **129**: 123-128.
- Harpur, R.P. (1980): The rat as a model for physical fitness studies. *Comp. Biochem. Physiol.* **66**: 553-574.
- Heusner, A.A., Jameson, E.W. (1981): Seasonal changes in oxygen consumption and body composition of *Sceloporus occidentalis*. *Comp. Biochem. Physiol.* **69A**: 363-372.
- Hickson, R.C., Bomze, H.A., Holloszy, J.A. (1977): Linear increase in aerobic power induced by a strenuous program of endurance exercise. *J. Appl. Physiol.* **42**: 372-376.
- Niewiarowski, P.H., Waldschmidt, S.R. (1992): Variation in metabolic rates of a lizard: use of SMR in ecological contexts. *Funct. Ecol.* **6**: 15-22.
- Pianka, E.R. (1994): Comparative ecology of *Varanus* in the Great Victoria Desert. *Aust. J. Ecology* **19**: 395-408.
- Saltin, B., Rowell, L.B. (1980): Functional adaptations to physical activity and inactivity. *Federation Proc.* **39**: 1506-1513.
- Scheuer, J., Tipton, C.M. (1977): Cardiovascular adaptations to physical training. *Annu. Review Physiol.* **39**: 221-251.
- Thompson, G. (1992): Daily distance travelled and foraging areas of *Varanus gouldii* (Reptilia: Varanidae) in an urban environment. *Wildl. Res.* **19**: 743-753.
- Tipton, C.M., Matthes, R.D., Vailas, A.C., Schnoe-Belen, C.L. (1979): The response of the *Galago senegalensis* to physical training. *Comp. Biochem. Physiol. A.* **63**: 29-36.
- Tsuji, J.S. (1988a): Seasonal profiles of standard metabolic rate of lizards (*Sceloporus occidentalis*) in relation to latitude. *Physiol. Zool.* **61**: 230-240.
- Tsuji, J.S. (1988b): Thermal acclimation of metabolism in *Sceloporus* lizards from different latitudes. *Physiol. Zool.* **61**: 241-253.
- Withers, P.C. (1977): Measurement of  $\dot{V}O_2$ ,  $\dot{V}CO_2$  and evaporative waste loss with a flow-through mask. *J. Appl. Physiol.* **42**: 120-123.

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