Effects of endurance training and captivity on activity metabolism of lizards

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GARLAND, THEODORE, JR., PAUL L. ELSE, ANTHONY J. HULBERT, AND PATRICK TAP. *Effects of endurance training and captivity on activity metabolism of lizards.* Am. J. Physiol. 252 (Regulatory Integrative Comp. Physiol. 21): R450–R456, 1987.—Two groups of *Amphibolurus nuchalis*, an Australian agamid lizard, were maintained in captivity for 8 wk. The "trained" group was given submaximal exercise at 1 km/h on a motorized treadmill, 30 min/day, 5 days/wk; the treadmill was inclined 10% for the last 5 wk. The "sedentary" group was not exercised. Endurance capacity did not change significantly in either group, but sprint speed decreased in trained lizards. The sedentary group exhibited significant decreases in maximal O_2 consumption, standard metabolic rate, and heart mass, but an increase in liver mass. Trained lizards exhibited significant decreases in heart and thigh muscle masses, but significant increases in liver mass, hematocrit, liver pyruvate kinase, and heart citrate synthase activities. It is concluded that the adaptive response to endurance training, typical of mammals, does not generally occur in lizards. Moreover, levels of chronic activity that would elicit adaptive responses in mammals may be excessive for lizards and may induce pathological effects in joints and skeletal muscle. The ecological and evolutionary significance of these conclusions is discussed.

aerobic capacity; *Amphibolurus nuchalis* (*tenophorus*); enzyme activities; evolution; exercise; maximum oxygen uptake; physical training; standard metabolic rate

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ADAPTIVE RESPONSES to endurance training are well characterized in several mammalian species (e.g., Refs. 3, 4, 12, 13, 19, 20, 25, 30–34). Results are often dramatic and include increases in endurance, maximal O_2 consumption, and tissue oxidative capacities. Chronic decreases in physical activity generally have effects opposite to those induced by increases in activity.

In contrast with the large body of literature on mammalian responses to endurance training and/or inactivity, there is only one published study concerning such effects in a reptile. Gleeson (18) found that 6–8 wk of training or captivity had no significant effects on running performance or its presumed metabolic correlates in the iguanid lizard *Sceloporus occidentalis*. Gleeson suggested that the lizard was "metabolically inflexible" in regard to training state and perhaps fundamentally "different from mammalian patterns."

Such a conclusion, if warranted, would be of considerable significance. Most metabolic differences between reptiles and mammals, and especially those related to O_2 consumption and its correlates, appear to be of a quantitative rather than a qualitative nature (e.g., Refs. 6, 10, 14, 15, 28, 29). Thus a qualitative difference with regard to metabolic flexibility could have far-reaching physiological and evolutionary implications.

Recent studies of locomotor performance and metabolism in natural populations of lizards have revealed surprisingly large amounts of variation in sprint speed and especially in endurance (Refs. 6, 15–17, T. Garland, unpublished observations). Sprint speed typically varies two- to threefold, and treadmill endurance capacity by as much as an order of magnitude, among apparently healthy animals of similar size. The source of this variation is currently unknown. One possibility is genetic differences among individuals. Although there are as yet no published results concerning the heritability of locomotor performance in any wild vertebrate, ongoing research (bibliography in 17) indicates that speed and stamina may be significantly heritable in both fence lizards and garter snakes.

Another possibility, not mutually exclusive with the former, is that of "natural conditioning" (discussions in Refs. 7, 10, 17, 18, 23). Natural training could occur if differences in activity levels among individuals in the wild are of sufficient magnitude to induce changes in performance and metabolism, similar to those that can be induced experimentally in the laboratory. The potential importance of such natural training for mammals has been considered (review in Ref. 10). If lizards are generally "metabolically inflexible" in response to chronic exercise or inactivity, then differences among individuals taken from natural populations are less likely to be solely of environmental origin. If, on the other hand, lizards (or any other wild animals) are metabolically flexible (as are most if not all mammals), then natural differences in activity patterns might be the basis for a substantial fraction of the total variation seen among individuals taken from a wild population.

This study was designed to determine whether chronic strenuous activity or inactivity could induce changes in performance and metabolism in a lizard, similar to those seen typically in mammals. We studied the Australian agamid lizard, *Amphibolurus nuchalis*, because it is well known both ecologically and physiologically (9, 16, 17, 22, and bibliography therein) and because it runs well on

a motorized treadmill. Our training regimen was designed to be comparable to regimens that typically induce large effects in laboratory rats and other mammals and was considerably more strenuous than that employed by Gleeson (18). In the companion paper (17) we describe natural patterns of variation in *A. nuchalis* and use those results as a comparative base for interpreting results of the present experiments.

MATERIALS AND METHODS

Animal collection and maintenance. The *Amphibolurus nuchalis* used in this study were a subset of the adults collected during January, near the University of New South Wales's Arid Zone Research Station, Australia, as described in the companion papers (16, 17). A total of 18 randomly selected adults was used: 8 males were assigned to the "sedentary" group (initial body mass: means ± SE, range = 31.0 ± 3.25 g, 17.0–41.2 g); 8 males and 2 females were assigned to the "trained" group (32.7 ± 2.74 g, 16.3–43.7 g).

Logistical constraints precluded housing each individual separately, so each group was housed in its own cage, having floor areas of 1 m^2. Photoperiod, thermal regimen, water, and food were as described previously (17).

The sedentary group was not handled for 8 wk. The trained group was subject to a training regimen of 30 min of treadmill running, 5 days/wk. The first 3 wk were at 1 km/h, the last 5 wk were at 1 km/h on a 10% incline. Individuals were never run more than 3 days consecutively. Notes regarding individual performance were recorded for each run. Some individuals would not run for 30 min on some days; if this occurred the total time run (<30 min) was recorded.

There were no obvious signs of social interactions that might have induced stress. Food was provided in excess daily, and water was always available. Patterns of weight change were similar in the two groups [sedentary group, range = −3.2 to +31.4% (mean ± SE) = +11.5 ± 4.86%; trained group, −9.0 to +28.1%, +3.4 mean 4.32%]. Overall, six individuals gained weight, four maintained weight, and eight lost weight.

Characters measured. We measured the same characters as in the companion papers (protocols in Refs. 16, 17): maximal running (sprint) speed, endurance at 1 km/h, maximal O_2 consumption ($\dot{V}O_{2 max}$), standard metabolic rate (SMR), liver, heart, and thigh muscle masses, hematocrit, hemoglobin, citrate synthase, and pyruvate kinase activities in all three tissues, and lactate dehydrogenase activity (in the direction of lactate oxidation) in heart only. All characters were measured at 40°C, the approximate mean body temperature of *A. nuchalis* when active in the field (Ref. 9, other Refs. in 15, 17).

Statistical analyses. Natural patterns of variation in the characters measured are described in the companion papers (16, 17). In field-fresh animals, all of the characters measured scale allometrically with body mass, except heart citrate synthase activity. In addition, standard metabolic rate and heart citrate synthase activity differed between males and females, and endurance, $\dot{V}O_{2 max}$, heart lactate dehydrogenase, thigh citrate synthase, and thigh pyruvate kinase activities were elevated in March-

collected animals (representing field-fresh animals at the end of this study), compared with January animals (representing animals at the beginning of the present study). These natural variations were taken into account in statistical analyses as explained below. All characters were log$_{10}$ transformed before analysis. Computations were performed using Statistical Package for the Social Sciences version 1.0 on the U.C., Irvine, Honeywell CP6 computer, or SPSS-PC+. Statistical significance was judged at $P < 0.05$ in all cases.

Organismal characters (speed, endurance, $\dot{V}O_2$), measured before and after 8 wk, were compared using repeated-measures analysis of variance. Because the organismal characters scaled allometrically with body mass in field-fresh lizards, we corrected for body mass differences among individuals by dividing values by the appropriate allometric exponent from Tables 1 or 3 in the companion paper (17). Using standard metabolic rate as an example, we calculated log$_{10}$ [(ml O_2/h)/(body mass)$^{0.830}$] and performed statistical analyses on these mass-corrected and log-transformed values (cf., Ref. 8).

To determine whether the sedentary and trained groups differed from each other, either before or after 8 wk, we used analysis of variance, again on mass-corrected and log-transformed values.

To determine whether either the sendentary or trained group differed from either January or March field-fresh animals, we used analysis of covariance, with body mass and, where appropriate (see Table 3 in Ref. 17), sex or season as covariates.

RESULTS

Sedentary and trained animals did not differ in sprint speed, endurance, or standard metabolic rate before the study. However, the group to be trained exhibited a significantly lower $\dot{V}O_{2 max}$ [analysis of covariance (ANCOVA), $F = 6.04$, $P = 0.0266$: initial $\dot{V}O_{2 max}$ of sedentary, ±SE = 110.1 ± 15.03, range = 50.4–174.2 ml O_2/h; initial $\dot{V}O_{2max}$ of trained, ±SE = 93.9 ± 12.01, range = 40.8–169.1 ml O_2/h; body masses are given in MATERIALS AND METHODS].

All of the sedentary animals remained in apparent good health and most gained or maintained weight (see Fig. 1). Five of the trained animals remained in good health. The other five trained animals appeared in normal condition, except for problems with their hindlimbs: three developed swelling of one hindlimb; two developed swelling and partial immobilization of both hindlimbs. The first incidence of swelling appeared during the 4th wk of training. On dissection, some hip joints were necrotic, with extensive overgrowth of cartilage around the joints in two individuals. We therefore weighed muscle from both thighs of each trained animal and conducted enzyme assays on both thighs as well. For individuals with either both normal or both swollen thighs, we analyzed mean values; for individuals with one normal and one swollen thigh, we analyzed the two thighs separately. Except for thigh muscle mass and enzyme activities (see below), the five trained animals with swollen thighs exhibited character variation within the range shown by the five apparently healthy trained individuals. We
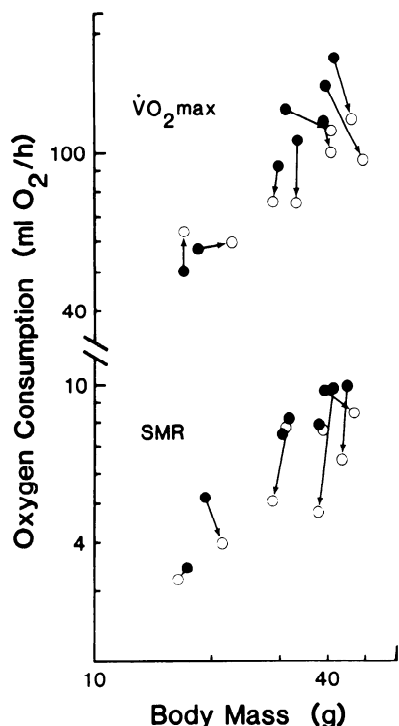
FIG. 1. $\dot{V}O_2$ of sedentary *Amphibolurus nuchalis* before (*closed circles*) vs. after (*open circles*) 8 wk of captivity; $\dot{V}O_{2\,max}$, maximal O_2 consumption; SMR, standard metabolic rate. Statistical analyses are presented in Table 1.

therefore included all trained individuals in statistical analyses for SMR and the suborganismal characters, but to be conservative we omitted the two individuals with both legs disabled from statistical consideration for speed, endurance, and $\dot{V}O_{2\,max}$.

Pretraining endurance times of the trained group ranged from 18.3 to 136.5 min, with 8 of 10 animals exceeding 30 min. Individuals varied considerably in their willingness to run 30 min on the treadmill. On a daily basis, 4–10 individuals completed the full 30 min (mean = 8.2 individuals). Postraining endurance times of the trained group ranged from 29.7 to 128.0 min. Both of the individuals with two swollen thighs exhibited an increased endurance; of those with a single swollen thigh, one showed an increase, two showed decreases.

Results of the repeated-measures analyses of variance are presented in Table 1. Sprint speed did not change significantly in the sedentary group, but decreased in all 10 trained individuals. Endurance increased, but not significantly, in both groups: at the end of the study, endurance times of both groups were intermediate between January and March field-fresh lizards and not significantly different from either (Table 2). Maximal O_2 consumption decreased significantly in the sedentary group (Fig. 1), but not in the trained lizards. Standard metabolic rate also decreased significantly in the sedentary group (Fig. 1), but did not change in trained animals.

Liver mass increased in both groups (Fig. 2 and Table 2). Heart mass decreased in both groups (Fig. 2 and Table 2). Thigh muscles of sedentary animals were similar in weight to those of field-fresh lizards (Fig. 2 and Table 2). Normal thighs of trained animals were significantly lighter than those of either sedentary or field-

fresh animals (Table 2), but swollen thighs of the trained animals were significantly heavier (Fig. 2).

Hematocrit and hemoglobin tended to be higher in both sedentary and trained lizards at the end of the experiment; however, the increase was statistically significant only for hematocrit of trained animals (Table 2).

Trained animals showed a significant increase in both liver pyruvate kinase and heart citrate synthase activities (Table 2), both in comparison with the sedentary group and in comparison with field-fresh animals. Relative to trained lizards, sedentary animals had higher thigh enzyme activities (Table 2 and Fig. 3). However, their thigh enzyme activities were not higher than those measured in March field-fresh lizards. The swollen thighs of trained animals (Fig. 2) exhibit reduced enzyme activities (Fig. 3).

DISCUSSION

Treadmill endurance running capacities did not change significantly in either the trained or the sedentary control group, either in relation to prestudy values or in relation to field-fresh lizards. The positive though insignificant increases in endurance seen in both groups (Table 1) may be *1*) related to increased glycogen and/or lipid storage in liver (Fig. 2; cf., Ref. 2) or *2*) a parallel of the significant increase in endurance seen in March compared with January field-fresh lizards (17).

Sprint speed was unchanged in the sedentary group, but decreased in all 10 trained individuals. This decrease may be partly attributable to motivational changes: some trained lizards seemed quite habituated to handling after 8 wk of treadmill running. However, some of the trained individuals appeared to be maximally exerting themselves during sprint speed trials. The significant decrease in thigh muscle mass in trained lizards (Fig. 2) may also be related to their decrease in sprint speed. We know of no studies in the mammalian literature that have looked for an effect of endurance training on sprint speed. Sprint training has been reported to have no effect on endurance in rats (12).

Maximal O_2 consumption has been considered "the single most objective indication of a training effect" (Ref. 19, p. 568 and Ref. 32, p. 232). Rather than increasing, $\dot{V}O_{2\,max}$ showed an 18% decrease ($P = 0.162$; see Tables 1, 2) in our trained lizards. In the sedentary group, $\dot{V}O_{2\,max}$ decreased significantly (Fig. 1), a finding consistent with studies on mammals (30–32), teiid lizards held captive 12–15 mo (8), and Cuban iguanas (*Cyclura nubila*: K. A. Christian and K. Conley, personal communication). Gleeson (18), on the other hand, found no decrease in $\dot{V}O_{2\,max}$ in *Sceloporus occidentalis*, and John-Alder (23) concluded that "laboratory housing itself is insufficient to cause a decline in energetic capacities" in another iguanid lizard, *Dipsosaurus dorsalis*. We conclude that captivity alone can result in a decrease in $\dot{V}O_{2\,max}$ in lizards, but that this effect may vary among species.

Standard metabolic rate did not change in the trained group, but decreased significantly in our sedentary animals (Fig. 1). No change in SMR occurred in *S. occidentalis* (18). The mammalian literature includes conflicting

TABLE 1. *Repeated measures analysis of variance of organismal characters*

Character	Units	Mean ± SE		Change	F	P
		Before	After			
Sedentary group						
Speed ($n = 7$)	$\log_{10} \dfrac{\text{km/h}}{\text{g } 0.161}$	0.781±0.0220	0.785±0.0253	+0.9%	0.15	0.716
Endurance ($n = 8$)	$\log_{10} \dfrac{\text{s}}{\text{g } 0.648}$	2.412±0.0999	2.684±0.1214	+86.8%	4.94	0.062
$\dot{V}O_{2\,max}$ ($n = 8$)	$\log_{10} \dfrac{\text{ml } O_2/\text{h}}{\text{g } 0.958}$	0.599±0.0234	0.482±0.0271	−23.7%	8.54	0.022
SMR ($n = 8$)	$\log_{10} \dfrac{\text{ml } O_2/\text{h}}{\text{g } 0.831}$	−0.373±0.0187	−0.490±0.0291	−23.6%	10.70	0.014
Trained group						
Speed ($n = 8$)	$\log_{10} \dfrac{\text{km/h}}{\text{g } 0.161}$	0.733±0.0244	0.570±0.0430	−31.2%	16.80	0.005
Endurance ($n = 8$)	$\log_{10} \dfrac{\text{s}}{\text{g } 0.648}$	2.596±0.0907	2.729±0.0982	+35.7%	2.14	0.187
$\dot{V}O_{2\,max}$ ($n = 8$)	$\log_{10} \dfrac{\text{ml } O_2/\text{h}}{\text{g } 0.958}$	0.484±0.0359	0.402±0.0391	−18.1%	2.44	0.162
SMR ($n = 10$)	$\log_{10} \dfrac{\text{ml } O_2/\text{h}}{\text{g } 0.831}$	−0.411±0.0149	−0.404±0.0143	+1.0%	0.12	0.739

Analyses based on mass-corrected values; see text for details and explanation of sample sizes. Percentage change of mass-corrected values on an arithmetic scale. $\dot{V}O_{2\,max}$, maximal O_2 consumption; SMR, standard metabolic rate.

TABLE 2. *Analysis of covariance comparing sedentary or trained group with field-fresh lizards and ANOVA comparing sedentary with trained animals*

Character	Significance of Difference vs. Field-Fresh*		Significance of Difference Sedentary vs. Trained	Conclusion for Group Effect
	Sedentary	Trained		
Speed	0.986	**<0.001 (−)**	**0.001**	Trained decrease
Endurance	0.716	0.335	0.777	No effect
	0.227	0.300		
$\dot{V}O_{2\,max}$	**0.006 (−)**	**0.020 (−)**	0.118	Sedentary decrease,
	0.001 (−)	**<0.001 (−)**		trained may decrease[†]
SMR	**0.003 (−)**	0.458	**0.031**	Sedentary decrease
Liver	**0.041 (+)**	**0.037 (+)**	0.839	Both increase
Heart	**0.007 (−)**	**0.030 (−)**	0.592	Both decrease
Thigh	0.123	**<0.001 (−)**	**0.010**	Trained decrease
Hematocrit	0.128	**0.0496 (+)**	0.937	(Trained increase)
Hemoglobin	0.095	0.276	0.479	No effect
CS Liver	0.480	0.493	0.962	No effect
PK Liver	0.634	**0.005 (+)**	**0.005**	Trained increase
CS Heart	0.949	**<0.001 (+)**	**0.013**	Trained increase
PK Heart	0.726	0.497	0.641	No effect
LDH Heart	0.610	0.885	0.678	No effect
	0.061	**0.023 (−)**		
CS Thigh	**0.001 (+)**	0.152	**0.041**	Sedentary higher than trained
	0.425	0.321		
PK Thigh	**0.006 (+)**	0.819	**0.017**	Sedentary higher than trained
	0.404	**0.034 (−)**		

Significant probabilities are in boldface. $\dot{V}O_{2\,max}$, maximal O_2 consumption; SMR, standard metabolic rate; CS, citrate synthase; PK, pyruvate kinase; LDH, lactate dehydrogenase. * For characters that varied seasonally (see Refs. 16, 17), upper probability is for comparison with January, lower for comparison with March field-fresh lizards. For characters that did not vary seasonally, values are significance of difference compared with pooled field-fresh lizards. Sign following probability indicates whether experimental group was higher (+) or lower (−). [†] Trained group was significantly lower than sedentary group before training regimen began (see RESULTS), and repeated-measures ANOVA is insignificant for trained group (Table 1).

reports as to the effects of training on basal metabolic rate (27, 33).

Liver mass increased in both groups, due perhaps to increased glycogen and/or lipid storage. Liver mass has shown both increases and decreases with training in rats (19).
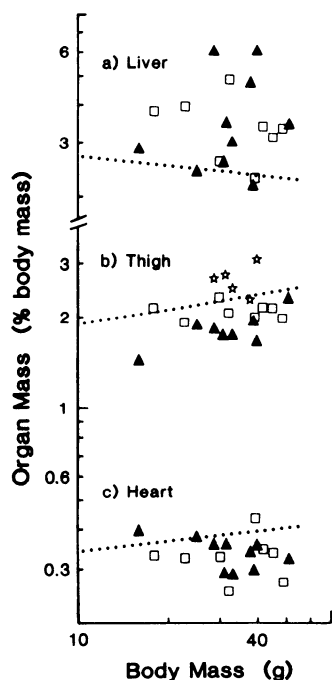
FIG. 2. Relative organ masses of sedentary (*open boxes*) and trained (*triangles*) vs. field-fresh lizards (*regression lines* from Ref. 17). *Stars* represent swollen thighs of some trained animals (see text). Statistical analyses are presented in Table 2.
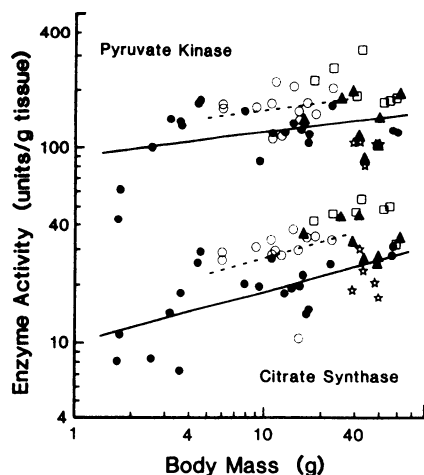

FIG. 3. Citrate synthase and pyruvate kinase activities in thigh muscle of *Amphibolurus nuchalis*. *Closed circles* and *solid regression lines* are January animals; *open circles* and *dashed lines* are March animals (17); *open boxes* are sedentary group; *triangles* are trained animals; *stars* represent swollen thighs of some trained animals. Statistical analyses are presented in Table 2.

Heart mass appeared to decrease significantly in both sedentary and trained *A. nuchalis*. Ventricular mass did not change in *S. occidentalis* (18). Heart mass often increases in response to endurance training in mammals, but variable responses, including decreases, have been reported (19, 32, 34). Heart mass may increase with endurance training in fishes (5), but did not increase in an amphibian (24). Scheuer and Tipton (Ref. 32, p. 232) conclude that "an increase in (cardiac) mass is not a sensitive indicator of a training effect." It is also of interest to note that drug-induced cardiac enlargement

does not necessarily affect whole-animal performance (2).

Thigh muscle mass decreased significantly in trained but not in sedentary *A. nuchalis* (Fig. 2 and Table 2). Decreases as well as increases in muscle mass have been noted in rats in response to training (19).

Hematocrit and hemoglobin tended to be higher in both groups than in field-fresh animals, but the difference is statistically significant only for hematocrit in the trained group (Table 2). These characters were not measured in *S. occidentalis* (18), so there are no comparable data for lizards. Increases, decreases, and no changes in hematocrit and hemoglobin have been reported in mammals (32, 34), and increases with endurance training have been reported in birds (26) and fishes (5).

Oxidative enzymes in skeletal muscle generally increase in response to endurance training in mammals (Refs. 4, 30, 31, but see Ref. 25), amphibians (Ref. 11, but see Ref. 24), and fishes (5). Glycolytic enzymes, in contrast, generally show at most modest changes, and in some cases decreases, in mammals, but generally increase in fishes (previous references). Neither the present study nor Gleeson (18) found any changes in skeletal muscle oxidative capacity in response to training in lizards. Both citrate synthase and pyruvate kinase activities were higher in thigh muscles of our sedentary animals, compared with the trained group, but this "increase" was similar to that seen in field-fresh animals at the end of the study (Table 2 and Fig. 3). Citrate synthase activity in heart seemed to show a real increase in the trained group, but pyruvate kinase and lactate dehydrogenase (measured in direction of lactate oxidation) activities were unchanged. In contrast, most mammalian studies report little or no change in heart oxidative capacity, with increases in glycolytic capacities perhaps more common (4, 32). The effects of endurance training on liver oxidative and glycolytic enzymes are not often studied. Our trained lizards showed a significant increase in liver pyruvate kinase activity (Table 2).

Critique of exercise regimen. With regard to the results found commonly in mammals, the endurance training regimen used in the present study was expected to elicit significant increases in endurance, $\dot{V}o_{2\,max}$, heart mass, hematocrit and hemoglobin, and/or tissue oxidative capacities (3, 4, 12, 13, 19, 20, 25, 30–34); decreases might have been expected in the sedentary group. Surprisingly, however, endurance changed significantly in neither group, $\dot{V}o_{2\,max}$ did not increase in trained animals, heart mass decreased in both groups, and thigh enzyme activities were lower in trained than in sedentary animals.

Our results are in general agreement with those of Gleeson (18), but there are several differences between the studies that are worth noting. First, Gleeson's training regimen increased over 8 wk, but consisted of sprint running for only 40 m/day during the final 4 wk (5–8) of the study. Moreover, this exercise lasted for <2 min (see Gleeson's Fig. 3). Subsequent field observations of *S. occidentalis* and other lizards (T. Garland, unpublished observations) have shown that, when active in nature, *S. occidentalis* probably moves distances of similar magni-

tude on a daily basis, though probably at lower average speeds. Hence Gleeson's training regimen might not have been stressful enough to induce adaptive changes. The present protocol, equivalent to 500 m/day, and on a 10% incline for *weeks 5–8*, seemed much more likely to induce a positive training effect. Our limited field observations suggest that *A. nuchalis* typically moves ~100–200 m/day. In addition, Bradshaw (Ref. 9, p. 1412) reports that adult *A. nuchalis* (in Western Australia) are "particularly sedentary, rarely moving more than 50 m from their first point of capture." Thus our training regimen seems clearly to have constituted a stress in excess of that experienced by free-living lizards. In summary the fact that both high-intensity short-duration (18) and low-intensity long-duration (present study) training regimens have failed to elicit the adaptive responses characteristic of mammals lends credibility to the idea that lizards are relatively inflexible metabolically in response to variation in activity levels (18).

Pathological effects in trained animals. The pathological effects in thigh muscles and hip joints exhibited by 5 of the 10 trained lizards are an apparently unique observation. These animals had no external lesions and resembled nothing we have seen before, even in other *A. nuchalis* maintained in captivity (without exercise) for over 2 yr. Such deterioration has apparently not been described in the veterinary literature on reptiles (E. R. Jacobson, personal communication). Muscle fiber necrosis and degeneration are known to occur in mammals in response to intense exercise (e.g., Refs. 1, 21, 35), but it is important to note that similar and far more intense training regimens in mammals have apparently never been associated with pathological effects as severe as seen here in lizards. We therefore tentatively conclude that training regimens that elicit adaptive responses in mammals *1*) do not generally do so in lizards and *2*) may constitute excessive stress leading to pathological deterioration of joints and muscles in lizards. It is of interest to note that high levels of lactic acid, following strenuous exercise, and concomitant reductions in blood pH, seem to "dissolve" bone in reptiles but not in mammals (29).

Might factors other than the training regimen per se account for the observed pathologies? Perhaps stress induced by the training regimen led to a general depression of immune system function in our lizards, allowing endogenous bacteria (found normally in tissues of free-living lizards) to proliferate in hip joints (E. R. Jacobson, personal communication). Another possibility is that an unknown disease may have affected only some trained animals. This seems unlikely because *1*) the unaffected sedentary group was in an immediately adjacent cage, with both cage tops open to the air and *2*) we have never seen such limb deterioration in any other captive lizards, including *A. nuchalis* held for >2 yr.

If in fact our training regimen constituted "excessive stress," then it might be argued that adaptive increases in performance and its correlates occurred early in the study, but were obscured during the last few weeks when hindlimbs of some animals began to deteriorate. However, no improvements were seen even in the five trained individuals in apparent good health at the end of the study. Moreover, there was no apparent tendency for animals to perform better or become more willing to run at any time during the training regimen.

There is currently no evidence that adaptive physiological responses to endurance training, seen typically in mammals and other vertebrates, occur in lizards (Ref. 18, this study). It is interesting to note that the $\dot{V}_{O_2 max}$ of a field-fresh, 20-g *A. nuchalis* (3.3 ml $O_2 \cdot g^{-1} \cdot h^{-1}$, from Ref. 17) is intermediate between values for adult humans before (2.3 ml $O_2 \cdot g^{-1} \cdot h^{-1}$) vs. after ($3.5$ ml $O_2 \cdot g^{-1} \cdot h^{-1}$) 10 wk of endurance training (20). This comparison suggests that differences between mammals and lizards in the response to chronic changes in levels of physical activity cannot be explained simply on the basis of differences in metabolic rate.

The pathological effects noted in trained lizards in this study are apparently unprecedented for any vertebrate, but superficially appear similar to less severe pathologies that sometimes occur in mammals in relation to intense activity. Why lizards cannot tolerate exercise regimens that mammals not only tolerate but also adapt to is worthy of further study. Perhaps these differences are related to differences in bone structure (cf., Ref. 29) and/or blood and tissue buffering capacities.

The ecological and evolutionary consequences of an apparent lack of "metabolic flexibility" in lizards, as compared with mammals, have received relatively little attention (10). Perhaps the generally lower activity levels of lizards (including a general lack of play behavior, Ref. 10) have made it evolutionarily infeasible to incorporate "natural training" as a typical and beneficial part of the life cycle (but see Refs. 11, 24). Moreover, as noted by Burghardt (10), potential physiological benefits of locomotor play could probably be realized most fully early in ontogeny, which seems inconsistent with the limited aerobic capacities and stamina of many juvenile reptiles, including *A. nuchalis* (17, Refs. therein).

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