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Physiological correlates of natural activity and locomotor capacity in two species of lacertid lizards

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Summary. 1. Physiological factors relating to activity metabolism were measured in two species of African lacertid lizards that differ greatly in natural foraging patterns: *Eremias lineoocellata*, a sit-and-wait predator, and *E. lugubris*, a widely foraging animal.

2. Maximal oxygen consumption at 37 °C is greater in *E. lugubris* [3.22 ml O_2/(g × h)] than in *E. lineoocellata* [2.49 ml O_2/(g × h)].

3. Anaerobic scope and capacity at 37 °C are greater in *E. lineoocellata* [2.56 mg lactate/(g × min) and 1.81 mg lactate/g] than in *E. lugubris* [2.12 mg lactate/(g × min) and 1.40 mg lactate/g].

4. Relative heart mass and hematocrit are greater in *E. lugubris* than in *E. lineoocellata* (0.28% and 0.24% body mass; 30.1 and 24.4, respectively).

5. No significant interspecific differences occur in hind limb muscle mass as a percentage of body mass or in myoglobin concentration, citrate synthase or myofibrillar ATPase activity of hind limb skeletal muscle.

6. No significant interspecific differences occur in isometric contractile properties (twitch and tetanic tension, twitch rise time and half-relaxation time, and fatigue response to tetanic stimulation) of the iliofibularis muscle.

7. Organismal metabolic patterns of aerobic and anaerobic capacity reflect differences in locomotor capacity and natural foraging patterns of these species.

Introduction

Eremias lineoocellata and *E. lugubris* are sympatric species of lacertid lizards from the Kalahari semi-desert in southern Africa. Both species are insectivorous, similar in size and in activity temperatures (36–37 °C) (Huey et al. 1977) and occupy the same sand dune-face habitat. Nevertheless, these species differ strikingly in their patterns of field activity and foraging modes. *Eremias lineoocellata* is a sit-and-wait predator, moving only 14% of its active period; in contrast, *E. lugubris* is a widely foraging lizard, walking during 57% of its active day (Huey and Pianka 1981; Huey et al.). *Eremias lineoocellata* consequently expends far less energy in its foraging behavior than does *E. lugubris* (44 vs 214 J/h, respectively) and significantly less on a daily basis (544 vs 800 J/day, respectively) (Nagy et al.). Although both lizards walk at 0.5 km/h when active in the field, *E. lineoocellata* has considerably less behavioral endurance and can sustain this speed for only a few minutes. *Eremias lugubris* has greater stamina and can walk at this speed for indefinite periods (Huey and Pianka 1981; Huey et al.). On the other hand, *E. lineoocellata* has a significantly greater burst speed and acceleration from a standing start (Huey et al.). Thus, the widely-foraging lizard sustains greater levels of field activity and has greater stamina than does the sit-and-wait predator, which expends less energy on locomotory activities and has a greater capacity for burst activity.

We undertook studies on these species to determine whether their differences in field activity patterns and locomotor capacities are correlated with differences in physiological capacities. It might be hypothesized that *Eremias lugubris*, a widely-foraging animal with greater stamina, would possess greater aerobic scope and oxygen transport abilities and that *E. lineoocellata*, a sit-and-wait predator, would have a greater capacity for anaerobically supported activity. Alternatively, one could hypothesize that these closely related species would be identical in their functional capacities but em-

phasize different portions of a similar physiological repertoire during their natural activity and behavior.

To determine which, if any, physiological factors correlate with field locomotor patterns, we examined a series of organismal and tissue properties related to activity capacity. We measured maximal oxygen consumption and aerobic scope as indices of aerobic work capacity, and the rate and amount of lactic acid formation to determine anaerobic scope and capacity. The animals are unfortunately too small for a detailed examination of cardiorespiratory functions, but we measured relative heart size and hematocrit as indices of these. In hind limb muscle, we determined myoglobin content, an indicator of oxygen stores and diffusion capacity (Hemmingsen 1963; Cole 1982), and the activities of citrate synthase and myofibrillar ATPase, indices of aerobic capacity (Holloszy et al. 1971) and maximal shortening velocity (Bárány 1967), respectively. We also measured isometric contractile properties (twitch and tetanic tension, twitch rise and half-relaxation time, and resistance to fatigue) of the iliofibularis muscle, a small parallel-fibered muscle that flexes the lower limb during locomotion (Putnam et al. 1980). The combination of these properties of skeletal muscle indicate whether the locomotory muscle tissue is similar or dissimilar in functional capacity in these two species. An abstract of this work has been published previously (Bennett et al. 1982).

This species pair is a particularly favorable system to determine the correlation between physiological capacities and natural activity patterns. First, these species are very closely related, and differences in their physiological properties are likely to reflect adaptive differences. In comparisons involving phylogenetically diverse organisms, it is difficult to know which aspects are selected in a specific context and which are due to divergent developmental patterns or other factors unrelated to the phenomenon of interest. Second, in contrast to most other studies on activity physiology, extensive field observations on the ecology and natural history of these species are available (Pianka 1971; Huey et al. 1977; Huey and Pianka 1981; Nagy et al.). Thus, the physiological capacities measured can be interpreted in a natural framework.

Materials and methods

Animals. Specimens of *Eremias lineoocellata* and *E. lugubris* were collected in November 1981 near Twee Rivieren, Kalahari Gemsbok National Park, Republic of South Africa (R.S.A. Collecting Permits 461–81 and 1032–81 and permits from the Department of Nature Conservation, Botswana). They were transported by air to the United States where all experimental procedures were undertaken at the University of Chicago and the University of California, Irvine. The lizards had access to water and food (crickets and termites) and were housed in terraria equipped with incandescent lights that permitted behavioral thermoregulation for 10 h during the day. Nocturnal temperatures approximated 26 °C, normal burrow temperatures of these animals at this time of year (Nagy et al., in press). Animals were maintained on a natural African photoperiod (0600–1900 hours light period, local time). All experimental procedures were completed within 1 month of capture. Measurements of oxygen consumption and lactic acid formation were completed within 2 weeks.

Maximal oxygen consumption. Measurements of maximal oxygen consumption were made on 16 *E. lineoocellata* (mean mass = 3.99 g ± 0.18 SE) and 15 *E. lugubris* (3.98 g ± 0.15 SE) at 37 °C, the field-active body temperature of these species, during the diurnal portion of their photoperiod (1100–1300 hours). Measurements of resting oxygen consumption under these conditions have been previously reported (Nagy et al., in press). Lizards were placed in individual plastic boxes in a controlled environmental room (36–37 °C) in which all measurements were undertaken. Oxygen consumption was determined with a mask and open-flow circuit system. The mask (approx. 0.3 ml in volume) was fashioned from the closed end of a plastic centrifuge tube and was secured to the lizard's neck with a loose-fitting diaphragm made from the finger of a disposable medical glove. The lizard's head was placed through a slit in this diaphragm, which also contained additional ports for air intake. Normal ventilation was not impeded by this apparatus. An excurrent air port was drilled at the anterior end of the mask. Air was drawn through the mask and through low volume absorbent columns of Ascarite and Drierite (for removal of carbon dioxide and water vapor, respectively), a diaphragm pump, a Brooks mass flow controller, and an Applied Electrochemistry model S-3A oxygen analyzer. The latter was connected to a Honeywell dual pen stripchart recorder. Response time of the system was less than 15 s.

Lizards were manually stimulated to activity for 3 min bouts. Immediately prior to and after a bout of activity, baseline levels of oxygen partial pressure were determined through the empty mask. A lizard was removed rapidly from its container, placed in the metabolic mask, and placed in a shallow open plastic box (approximately 5 l in volume). Animals were touched on the hind limbs and tail, and they responded with intense bouts of running and struggling. The mask apparatus did not greatly impede this movement, as they were able to run around the container and hold up their heads and carry the mask around. Maximal levels of oxygen consumption were generally obtained during the first min of activity in both species. However, oxygen consumption remained high throughout the 3-min stimulation period. At the end of this stimulation, animals were removed from the mask and checked for loss of righting response. Six of 16 *E. lineoocellata* had lost this response, whereas none of the *E. lugubris* had done so.

Maximal oxygen consumption was calculated for the greatest consecutive min of oxygen consumption, regardless of the time during stimulation. All values reported are corrected to STPD conditions.

Anaerobic scope and capacity. Anaerobic scope, the maximal rate of lactate formation, and capacity, the total amount of lactate formed during exercise to exhaustion, were determined by measuring whole body lactate concentration of resting and exercised lizards (see Bennett and Licht 1972, for methods and

definitions). Twenty *E. lineoocellata* (mean mass = 4.08 g ± 0.16 SE) and 19 *E. lugubris* (4.04 g ± 0.14 SE) were used in these experiments. Animals were pre-weighed and housed in individual plastic boxes for several hours in the controlled temperature room at 36–37 °C, where experimental procedures were undertaken. Lizards were removed individually and either killed immediately or exercised and killed for analysis of lactate content. Animals to be exercised were placed in a 40-l glass terrarium and manually stimulated by prodding the hind quarters, tail and head with blunt-nosed forceps. The lizards responded with very intense bursts of running behavior. All lizards maintained vigorous activity for at least 30 s, but activity generally slowed between 45 s and 1 min. Animals were exercised for either 30 s or 5 min, at which time activity in all lizards had decreased greatly and some had lost their righting responses.

Exercised animals or resting animals directly removed from their boxes were killed quickly by decapitation, and their carcasses were homogenized in 10 times their volume of 0.6 N perchloric acid with a Polytron tissue homogenizer. These homogenates were refrigerated (4 °C) and subsequently filtered and analyzed for lactate content with an enzymatic test kit (Boehringer Mannheim Corp. Kit No. 149993) with an Hitachi model 191 spectrophotometer.

Lactate contents are reported as mg lactate/g body mass. Anaerobic scopes are calculated from the difference between lactate contents of resting lizards and those active for 30 s. Anaerobic capacities are calculated as the difference between lactate contents of resting animals and those exercised for 5 min.

Heart and hind limb muscle mass and hematocrit. Eight lizards of each species (mean mass = 2.29 g ± 0.141 SE, *E. lineoocellata*; 2.76 g ± 0.081 SE, *E. lugubris*) were used for determination of heart mass and total hind limb muscle mass. Hind limb muscles were used in enzymatic and myoglobin assays described below. Lizards were weighed and killed by decapitation. All the skeletal muscle on both hind limbs was dissected from the femur and tibia, weighed, and frozen directly on dry ice. Muscle samples were stored frozen at −20 °C for subsequent analysis. Blood samples for hematocrits ($n = 16$, *E. lineoocellata*; $n = 15$, *E. lugubris*) were taken from these and other lizards from the infraorbital eye sinus, the stump of an autotomized tail, or the neck of decapitated animals. Samples were collected in heparinized tubes which were centrifuged for 10 min in a laboratory bench centrifuge equipped with an hematocrit head. The proportion of red blood cell volume to total blood volume was measured immediately after centrifugation.

Enzymatic activity and myoglobin concentration of skeletal muscle. Aerobic enzymatic capacity of the skeletal musculature of the hind limbs was measured by assay of the activity of citrate synthase, a citric acid cycle enzyme. Frozen tissue samples were homogenized with a ground glass homogenizer on ice in 20 volumes of 100 mM K_3PO_4 buffer (pH = 7.4) containing 5 mM EDTA. Homogenates were frozen and thawed twice. Citrate synthase activity was measured at 36 °C by the method of Srere (1969) on a Beckman model 25 spectrophotometer. Protein contents of the muscle homogenates were measured in duplicate by the biuret method with bovine serum albumin as a standard. Citrate synthase activities are expressed both as Units per g wet mass of tissue and per g protein.

The activity of myofibrillar ATPase was measured to determine the capacity of the skeletal muscle to catabolize high energy phosphate compounds. Myofibrillar ATPase is also used as an index of maximal contractile velocity (Bárány 1967). This enzyme was prepared and assayed according to the methods of Marsh and Wickler (1982). Assays were done at 36 °C in stirred vials containing 1.5 ml of 100 mM KCl, 20 mM Tris, 2 mM $MgCl_2$, 0.25 mM $CaCl_2$, 2 mM MgATP, and approximately 0.4 mg myofibrillar protein at pH 7.4. Assays were started by addition of ATP and stopped after 30 s with 0.1 ml 30% trichloroacetic acid. Controls were run with an initial addition of trichloroacetic acid. Stopped reaction mixtures were iced and later analyzed for phosphate content. All assays were run in duplicate. Results are expressed as micromoles of phosphate formed/(min × mg myofibrillar protein).

Myoglobin contents of muscle tissue were measured by the method of Reynafarje (1963). Muscle tissue was ground in 19 volumes of 100 mM K_3PO_4, 5 mM EDTA at pH 7.4 with a ground glass homogenizer. Homogenates were frozen and thawed twice and stored at −20 °C. At the time of assay, the homogenates were thawed and centrifuged at 28,000 *g* for 50 min at 0–4 °C. Carbon monoxide was bubbled through the supernatant solution for 8 min, and a small amount of sodium dithionite was added to insure complete reduction of the solution. Optical density was read at 538 and 568 nm on a Beckman model 25 dual beam spectrophotometer. Myoglobin concentrations are expressed as mg myoglobin/g wet mass of muscle.

Contractile properties of skeletal muscle. Isometric contractile properties (twitch and tetanic tension, twitch rise and half-relaxation times, and fatigue response) were measured in four *E. lineoocellata* and five *E. lugubris*. Lizards were killed by decapitation and the iliofibularis muscle (mean mass = 7.6 mg ± 0.61 SE for *E. lineoocellata* and 7.3 mg ± 0.44 SE for *E. lugubris*) was isolated and removed with a section of the pelvic girdle. A light-weight silver chain was tied to the distal tendon and the pelvis was secured with silk suture thread to a stainless steel support. The chain was attached to the lever of a Cambridge Instruments model 300H servo-controlled ergometer. Force output from the ergometer was displayed on a Tektronix model 5111 storage oscilloscope and photographed with a Tektronix model C-5C camera. The length of the muscle was adjusted to achieve maximal tension during a tetanus.

The muscle was bathed in Ringer's solution at 36 °C in a recirculating system consisting of a 50 ml chamber containing the muscle which was connected to a 1-l reservoir. The large reservoir was bubbled with 95% O_2 and 5% CO_2 and maintained in a temperature controlled water bath. The Ringer's solution consisted of 145 mM NaCl, 4 mM KCl, 2.5 mM $CaCl_2$, and 20 mM imidazole at pH 7.54.

Stimuli of supramaximal voltage were delivered to the muscle via a pair of platinum wire electrodes placed in the bath on either side of the muscle. Stimuli were square wave pulses of 0.2 ms duration. A 30 ms train of these pulses at 450 Hz was used to tetanize the muscle. After 1 h equilibration in the

Table 1. Lactate contents of two species of lacertid lizards during rest and activity at 37 °C. Tabular values are mean values (mg lactate/g body mass) ± SE; numbers of animals per group are given in parenthesis. Probability levels are evaluated by Student's *t*-tests

Species	Activity		
	Resting	30 s	5 min
Eremias lugubris	0.42 ± 0.078 (5)	1.48 ± 0.076 (8)	1.82 ± 0.122 (6)
Eremias lineoocellata	0.50 ± 0.050 (5)	1.78 ± 0.079 (7)	2.31 ± 0.072 (8)
Probability	0.58	0.016	0.003

Table 2. Enzymatic activity and myoglobin concentration in hind limb muscle of two species of lacertid lizards. Mean values ± standard errors are reported; the number of observations is given in parentheses. Species values are compared with Student's *t*-tests

Species	Citrate synthase		Myofibrillar ATPase μmoles phosphate/(min × mg myofibrillar protein)	Myoglobin concentration mg/wet muscle-mass
	U/g wet muscle mass	U/g protein		
Eremias lineoocellata	16.7±1.26(7)	82.9±5.95(7)	1.33±0.094(8)	1.20±0.29(7)
Eremias lugubris	16.9±0.96(8)	81.9±3.62(8)	1.31±0.072(8)	1.36±0.34(7)
Probability	0.90	0.89	0.91	0.72

Table 3. Isometric contractile properties of the iliofibularis muscle of two species of lacertid lizards ($n=4$ for *E. lineoocellata* and $n=5$ for *E. lugubris*). Mean values ± standard errors. Species comparisons are made by Student's *t*-tests

Species	Twitch tension (g/cm²)	Twitch time (ms)	One half relaxation time (ms)	Response to fatigue		
				Tetanic tension (g/cm²)	% original tension at 1 min	% original tension at 2 min
Eremias lineoocellata	957±86	8.0±0.46	8.62±0.47	1,840±191	68±3.8	39± 5.9
Eremias lugubris	695±89	7.8±0.41	8.44±0.78	1,690±52	65±6.5	39±11.0
Probability	0.07	0.75	0.85	0.56	0.77	> 0.95

apparatus, first the twitch response of the muscle was measured and then the tetanic response. Time-to-peak twitch was measured from the first point of the contractile response; half-relaxation time was measured as the time from peak twitch to one-half its value. Finally, the muscle was fatigued with tetanic impulses delivered one per second for 3 min, and the contractile tension was measured throughout the stimulation.

Results

Oxygen consumption

Maximal levels of oxygen consumption at 37 °C are significantly greater in *E. lugubris* [3.22 ml O_2/(g × h) ± 0.20 SE, $n=15$] than in *E. lineoocellata* [2.49 ml O_2/(g × h) ± 0.13 SE, $n=16$] ($P<0.001$, Student's *t*-test). Resting levels of oxygen consumption at 37 °C are not different between these species [*E. lugubris*, 0.25 ml O_2/(g × h) ± 0.017 SE, $n=8$; *E. lineoocellata*, 0.24 ml O_2/(g × h) ± 0.015 SE, $n=8$] (Nagy et al.). Consequently, aerobic scope is greater in *E. lugubris* than in *E. lineoocellata* [2.97 vs 2.25 ml O_2/(g × h)], as is the maximal factorial increment in oxygen consumption (12.8 × vs 10.4 ×).

Anaerobic scope and capacity

Lactate contents of the experimental groups are reported in Table 1. Lactate contents of resting animals are not significantly different. However, they are significantly greater in active *E. lineoocellata* than in *E. lugubris*, both after 30 s and 5 min of activity. Anaerobic scope, the maximal rate of lactate formation, is 2.56 mg lactate/(g × min) in *E. lineoocellata* and 2.12 mg lactate/(g × min) in *E. lugubris*. Anaerobic capacity, the total lactate formed during exhaustive activity, is 1.81 mg lactate/g in *E. lineoocellata* and 1.40 mg lactate/g in *E. lugubris*.

Heart mass and hematocrit

Mean heart masses in *E. lineoocellata* and *E. lugubris* were 5.2 mg ± 0.27 SE and 7.7 mg ± 0.55 SE, respectively. As the *E. lugubris* in this group were significantly larger than the *E. lineoocellata* (see Methods), heart mass was also expressed as a percentage of body mass and compared after arc sine transformation. Heart mass was significantly smaller in *E. lineoocellata* than in *E. lugubris* (0.25% and 0.28%, respectively) ($P=0.02$ by Student's *t*-test after transformation).

Hematocrit was significantly greater in *E. lugubris* than in *E. lineoocellata* (30.1 ± 1.02 SE and 24.4 ± 1.03 SE, respectively) ($P<0.001$, Student's *t*-test).

Mass, enzymatic activity, and myoglobin concentration of skeletal muscle

Total hind limb muscle masses were 149.0 mg ± 8.00 SE in *E. lineoocellata* and 176.1 mg ± 11.23 SE in *E. lugubris*. As the specimens of the former species were larger, hind limb muscle mass was expressed as a percentage of body mass and compared after arc sine transformation. Percentage values are 6.63% for *E. lineoocellata* and 6.35% for *E. lugubris;* these are not significantly

different ($P=0.64$ by Student's t-test after transformation).

Enzymatic activities and myoglobin concentration are reported in Table 2. There are no significant differences in either citrate synthase activity, myofibrillar ATPase activity, or myoglobin concentration in the hind limb muscles of these two species.

Contractile performance of skeletal muscle

Isometric contractile variables measured for these two species are reported in Table 3. There are no significant differences in tetanic tension, speed of twitch contraction or relaxation, or fatigue ability in the iliofibularis muscles of these species. Twitch tension is somewhat greater in *E. lineoocellata*, but not significantly so. Maximal isotonic contractile velocities of these muscles are likewise not different (Marsh and Bennett, unpublished data).

Discussion

Natural field activity and locomotor capacity are accurately correlated with organismal metabolic patterns of these two species. *Eremias lugubris*, a lizard of greater endurance and field foraging activity (Huey and Pianka 1981; Huey et al., in press), has a substantially greater maximal oxygen consumption and aerobic scope. In contrast, *E. lineoocellata*, which relies on rapid bursts of activity to capture prey and is otherwise largely sedentary, has a greater burst speed and anaerobic scope and capacity. Parallel differences in metabolic and locomotor capacities among phylogenetically diverse organisms are well demonstrated (e.g., Ruben 1976a; Bennett and Ruben 1979; Ruben and Battalia 1979; Gleeson et al. 1980), and the ecological and behavioral implications of such differences are apparent (Regal 1978; Bennett 1980; Pough 1980). However, the potential for differences in metabolic and locomotor capacities among closely related species is less well documented (Taigen et al. 1982). Such differences have considerable significance for patterns of adaptive radiation of different groups. Their documentation also has theoretical importance to models relating physiology to behavior and ecology (Huey et al., in press). For instance, current models of foraging behavior usually assume that physiological capacities do not differentially constrain the behavioral and ecological options of animals. This assumption may not be universally true.

The greater maximal oxygen consumption of *E. lugubris* correlates with its larger heart mass and greater hematocrit. These factors may reflect greater stroke volume and blood oxygen carrying capacity in this species, and more detailed comparisons of the respiratory and cardiovascular properties of both lacertids would seem warranted. Our findings provide indirect comparative evidence that the cardiovascular system may be the first aspect of physiology to respond to an evolutionary change in activity level. The relative importance of oxygen transport in controlling maximum oxygen consumption has been implicated in experimental studies (Saltin 1973; Shephard 1976; Gleeson et al. 1980; di Prampero 1981) as well. Other aspects of physiology (e.g., lung structure, activities of metabolic enzymes, muscle fiber composition) which correlate with activity level in comparisons involving distantly related taxa (e.g., Bennett 1972; Ruben 1976b; Else and Hulbert 1981) may respond subsequent to changes in the cardiovascular system.

The skeletal muscle tissue of these two species appears to be very similar in its physiological properties. Specific adaptation to foraging mode is not apparent in the locomotory muscles of these lizards. There has been no detectable differentiation in fiber type, contractile performance, or aerobic capacity of the muscle tissue examined. Differences in organismal anaerobic performance have not been accounted for, but may reside in differences in glycolytic enzymatic activity or buffering capacity (Castellini and Somero 1981) which we did not investigate. In a companion study (Huey et al., in press), we found an inverse relationship between endurance capacity and burst speed in several species of Kalahari lacertids. These correlations suggest a necessary evolutionary dichotomy that a lizard must sacrifice one function for the other. A simple hypothesis to explain this relationship would have been differential muscle fiber composition, aerobically-biased in the species with greater endurance and anaerobically-biased in sprinters. Our present data suggest that this is not the case. Whatever are the physiological and/or morphological foundations of this differential locomotor capacity, they are not based in the physiological capacities of skeletal muscle that we examined in the present study.

We cannot presently state with certainty whether the organismal differences in aerobic and anaerobic capacity are due to genetic differences between the species or are the result of differential conditioning under natural circumstances. As *E. lugubris* is much more active in the field, its greater aerobic capacity might merely reflect natural training. We are inclined against this view for two reasons. First, a training response has not been found in the one lizard species examined (Gleeson 1979). Second, endurance training regimes generally result in an increased aerobic capacity of skeletal

muscle (Holloszy 1973; Holloszy and Booth 1976), and such an increment is not present in the muscles of *E. lugubris*. Consequently, it is our opinion that most of the differences between these species are not due to differential activity regimes, but rather reflect genetic differences between the species.

Our findings emphasize the utility of multi-level, comparative approaches to physiological ecology. A study attempting to deduce organismal metabolic and locomotor capacities of these species from enzymatic or muscle-contractile data alone would have necessarily emphasized physiological similarities, whereas an examination of cardiovascular indices alone would have emphasized the potential for physiological differences. The capacities of constituent parts are sometimes unreliable indicators of the whole. Consequently, behavioral and ecological capacities are most appropriately determined directly from whole-animal measurements rather than from lower-level capacities (Bartholomew 1964; Huey 1982). Conversely, one cannot deduce any particular mechanistic and physiological property of an animal from an examination of its organismal properties alone. A variety of lower-level systems must be examined to appreciate the mechanistic limits and dynamics underlying whole-animal physiological capacities.

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