

motor program are apparent despite the undifferentiated periphery and immaturity of hindlimb motoneurons.

The early appearance of the pattern generator for coordination between the hindlimbs, activation of this pattern generator only during operation of the locomotor program for tail oscillations, and the rigid phase and frequency locking between bursts of primary and hindlimb motoneurons all suggest that the two pattern generators may be identical or share common neuronal elements. However, the experiments are only suggestive and do not rule out the possibility that the tail and developing hindlimbs are coordinated by separate, discrete mechanisms that are phase coupled and activated by a common source. In either case, the late-developing bilaterally synchronous bursting of the hindlimb motoneurons probably represents a modification or addition to the mechanisms coordinating alternate stepping.

A behavioral parallel to the sequence of electrophysiological activity described here is found in the successive development of axial muscle flexions during swimming, alternate stepping, and then frog kicks (8). The sequential appearance of lateral trunk flexions, lateral trunk flexions accompanied by limb movements, and limb movements without lateral trunk flexions has been amply documented in humans and other species (9, 15). Thus, the results of further experiments with this preparation may provide insights into the organization and early development of locomotion in other vertebrate species.

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References and Notes

1. S. Grillner, *Physiol. Rev.* **55**, 247 (1975); J. Gray, *Animal Locomotion* (Weidenfeld & Nicolson, London, 1968).
2. D. J. Stehouwer and P. B. Farel, *Brain Res.* **195**, 323 (1980).
3. ———, *ibid.* **218**, 131 (1981).
4. A. C. Taylor, *Anat. Rec.* **87**, 379 (1943).
5. C. J. Forehand and P. B. Farel, *J. Comp. Neurol.* **209**, 386 (1982); E. D. Pollack and J. J. Kollros, *J. Exp. Zool.* **192**, 299 (1975).
6. A. C. Taylor and J. J. Kollros, *Anat. Rec.* **94**, 7 (1946).
7. E. H. Dunn, *J. Comp. Neurol.* **10**, 218 (1900); W. P. Lombard and F. M. Abbott, *Am. J. Physiol.* **20**, 1 (1907). The complex actions of some frog hindlimb muscles innervated by profundus anterior and profundus posterior may produce rotation and both flexion and extension, depending on the angle of the joints on which they act. Some muscles act on only the hip, whereas others act on both the hip and knee.
8. D. J. Stehouwer and P. B. Farel, in preparation.
9. J. Barcroft and D. H. Barron, *J. Comp. Neurol.* **77**, 431 (1942); J. D. Decker, *Science* **157**, 952 (1967); V. Hamburger, M. Balaban, R. Oppenheim, E. Wenger, *J. Exp. Zool.* **159**, 1 (1965).
10. B. A. Campbell, L. D. Lytle, H. C. Fibiger,

Science **166**, 635 (1969); B. A. Campbell and D. J. Stehouwer, in *Ontogeny of Learning and Memory*, N. E. Spear and B. A. Campbell, Eds. (Erlbaum, Hillsdale, N.J., 1979), pp. 67–100; G. Paulson and G. Gottlieb, *Brain* **91**, 3 (1968).

11. M. C. Dickerson, *The Frog Book* (Dover, New York, 1969), pp. 227–240.
12. D. G. Dunlap, *J. Morphol.* **119**, 241 (1966); M. S. Letinsky, *Dev. Biol.* **40**, 129 (1974).
13. I.-W. Chu-Wang, R. W. Oppenheim, P. B. Farel, *Brain Res.* **213**, 307 (1981).
14. A. R. Beaudoin, *Anat. Rec.* **121**, 81 (1955); P. B. Farel and S. E. Bemelmans, *Neurosci. Lett.* **18**, 133 (1980).
15. D. Hooker, *The Origin of Overt Behavior* (Univ. of Michigan Press, Ann Arbor, 1944); M. B.

McGraw, *J. Pediatr.* **15**, 485 (1939); G. E. Coghill, *Anatomy and the Problem of Behavior* (Macmillan, New York, 1929), pp. 5–38; V. H. Hamburger, *Dev. Biol. Suppl.* **2**, 251 (1968); D. Hooker, *The Prenatal Origins of Behavior* (Univ. of Kansas Press, Lawrence, 1952), pp. 3–53.

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Thermoregulation and Mate-Selection in Fowler's Toads?

Fairchild (1) has presented evidence that large male Fowler's toads (*Bufo woodhouseii fowleri*) are more often found in amplexus with females than are small males. While patterns such as this have previously been attributed to male-male competition for mates (2), Fairchild has chosen to explain this pattern as resulting from female choice of larger males. He has supported this assertion with data showing that females more frequently respond to recorded mating calls of large males than to those of small males (3). Thus, he has concluded that the assumed mate selection is based on the quality of calls made by males at the breeding site; the quality of the calls is influenced by both the size and body temperature of the male toad (4). Fairchild further suggests that males thermoregulate to make their calls more attractive to females. Specifically, he hypothesizes that males choose colder microclimates in order to cause their calls to sound like those of a larger male. However, we feel that the evidence presented to support this hypothesis is inadequate. We also believe the assertion that female Fowler's toads select large males with which to mate is not supported by the evidence presented.

Fairchild presented data [table 1 in (1)] to show that larger males were found significantly more often in cold environments. His analysis of the table gave a G statistic of $G(4) = 20.52$, $P < .005$. Using the data reported, we calculate a G statistic of $G(2) = 3.15$, $P > .10$. Thus, while five out of eight large males were found in cold environments, this pattern could have occurred if males randomly selected thermal environments.

A second line of evidence for thermoregulation was that males found in the breeding pond were significantly larger than those on adjacent banks. The breeding pond was found to have a water temperature of 20°C, whereas the air temperature above the bank was 22°C.

Aside from the fact that this modest difference in temperature was determined with a thermometer graduated to only 1°C, the explicit assumption that these measurements of the environment reflect body temperature is not warranted (5). It seems likely that the high thermal conductivity of water would have caused toads swimming in water to assume the temperature of their ambient fluid, but toads on the bank should exchange energy with their environment by convection, radiation, evaporation, and conduction. Thermal radiation to the cold night sky and evaporation easily could have caused these toads to have body temperatures more than 2 degrees below that of the ambient air (5). Thus, without measurements of body temperature, it seems that conclusions concerning behavioral thermoregulation are premature.

Finally, the pattern of large males being found in the breeding pond is consistent with several alternative hypotheses. For example, dominant (larger) males could exclude subdominants from suitable breeding sites which happen to be in the water. Thus, while Fairchild suggests that large males are found in the pond as a result of their "selecting colder calling sites," an alternative is that large males are found in the pond because the pond is the only adequate site for aquatic egg laying (6). This alternative does not require the existence of behavioral thermoregulation to explain males being found in the pond (7). Thus, alternative hypotheses exist that could explain the pattern of male-female associations and distributions of males around the pond, and none of these hypotheses have been tested.

In conclusion, announcement of "the first documented case of behavioral thermoregulation in mate selection by amphibians" seems unwarranted, and the mechanism by which large male Fowler's toads are found in amplexus more often than small males is not resolved.

Unfortunately, potentially spurious correlations and inadequately analyzed data have been substituted for sound scientific methods in investigating these very interesting questions.

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References and Notes

1. L. Fairchild, *Science* **212**, 950 (1981).
2. N. D. Davies and T. R. Halliday, *Nature (London)* **269**, 56 (1977).
3. Larger males have a call that is lower in frequency than that of small males, and females are apparently more strongly attracted to the calls of larger males (1). Fairchild points out that a male's body temperature as well as his body size can influence the frequency of his calls. But, a female's attraction to male calls depends both upon the quality of the male's call and also upon her own body temperature (D. Pettus, personal communication). Unfortunately, Fairchild did not report the body temperatures of females.
4. The frequency of the male's calls directly correlates with body temperatures of toads. Fairchild's hypothesis suggests that small males could sound larger by selecting a microclimate in which body temperature would be lower than that of large males.
5. C. R. Tracy, *Ecol. Monogr.* **46**, 293 (1976).
6. R. D. Howard, *Evolution* **32**, 850 (1978).
7. R. D. Howard suggested several additional hypotheses that are consistent with existing data and the idea that small males are found surrounding the breeding pond as a way of competing with large males for mates (personal communication).
8. We thank R. D. Howard for sharing his ideas with us as we prepared this comment and J. P. Hailman and J. S. Turner for critically reading this manuscript. Supported in part by a Colorado State University graduate fellowship and a J. S. Guggenheim Foundation fellowship.
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To explain large male mating success in Fowler's toads in terms of male competition, Christian and Tracy (1) have extrapolated mechanisms from other species and, in so doing, made invalid assumptions about Fowler's toads. I have rarely observed displacement attempts by Fowler's toads as described by Davies and Halliday (2) for common European toads, although I commonly observe such behavior in American toads. Furthermore, Davies and Halliday (2) did not find that mated males were larger than unmated males. They found that common European toads mate assortatively, that is, large males

mate with large females and small males mate with small females. Mate selection in common European toads and in Fowler's toads is very different.

Citing Howard's bullfrog work (3), Christian and Tracy also suggest that large males may exclude smaller males and defend "suitable breeding sites." Bullfrogs are truly aquatic, territorial, permanent pond residents; Fowler's toads are not. Unlike bullfrogs, nearly all male Fowler's toads call; there is little movement once the chorus begins; and Fowler's toads do not defend extensive egg deposition territories as bullfrogs do. Bullfrogs and Fowler's toads are clearly quite different.

The simplest explanation of large male mating success is that female choice is an important part of mate selection. Some male competition hypotheses may be sufficient and necessary for other anuran species, but for Fowler's toads, such hypotheses are rarely sufficient because males have little contact with one another and do not defend egg deposition sites. Furthermore, these hypotheses are never necessary given the demonstrated auditory discriminatory ability of females. My hypothesis is sufficient and, in the absence demonstrated male competition, necessary to explain mate selection in Fowler's toads.

Christian and Tracy are right to question the significance of the *G*-statistic in Table 1. That statistic referred to an a posteriori test used, not as a first line of evidence as they suggest, but merely to support the more robust a priori test concerning behavioral thermoregulation presented in [figure 1 in (4)].

In the latter case, however, they suggest that convection, radiation, evaporation, and conduction all act to reduce body temperatures of bank males but have minor effects on pond males. In other words, they suggest that an operative temperature model of heat exchange should be applied to bank males, but that an ambient temperature model is sufficient for pond males. Apart from the problem of mixing models, the fact is that the dorsal surfaces of both bank and

pond males were wet and exposed to air and thus to the same thermal environment. Only the thermal environment of the ventral surfaces of pond and bank males differed.

For ventral surfaces, an operative temperature model is no better than an ambient temperature model. Factors affecting the components of heat exchange in an operative temperature model are wind speed (negligible at night), long-wave radiation not from the "cold night sky" but from the bank which was at or near ambient temperature, shortwave radiation (nonexistent at night), and ambient temperature. Thus, ambient temperature (water temperature for pond males and air temperature for bank males) is the only appreciable factor affecting the operative temperature of ventral surfaces of either pond or bank males.

The best estimate of the important parameter, body temperature, would be a direct measurement. But for small, ectothermic animals, such as Fowler's toads, direct measurements can be misleading. For example, Brown and Brown (5) found body temperature less reliable than either air or substrate temperature in predicting call characteristics of spring peepers. Consequently, I used air and substrate temperatures as predictors of body temperature. To argue that air and substrate temperatures are not accurate predictors of body temperature conflicts with past work (6).

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References and Notes

1. K. A. Christian and C. R. Tracy, *Science* **219**, 518 (1983).
2. N. D. Davies and T. R. Halliday, *Nature (London)* **269**, 56 (1977).
3. R. D. Howard, *Evolution* **32**, 850 (1978).
4. L. Fairchild, *Science* **212**, 950 (1981).
5. L. E. Brown and J. R. Brown, *Am. Midl. Nat.* **97**, 209 (1977).
6. S. Hadfield, *Copeia* **1966**, 581 (1966); p. 581; C. R. Tracy, *Ecol. Monogr.* **46**, 293 (1976); C. Carey, *Oecologia* **35**, 197 (1978).
7. I thank H. M. Wilbur, R. Alford, and R. Harris for helpful comments on an earlier draft and S. A. Mahoney for critically reading this manuscript.

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