(*1*). When the young follow adults for any reason, the chances increase that they will experience the same environmental contingencies as the adults. Thus, behaviors may be socially transmitted and the young learn to behave like their elders.

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References and Notes

1. S. A. Barnett, *Behaviour* **9**, 24 (1956); J. B. Calhoun, *The Ecology and Sociology of the Norway Rat* (Department of Health, Education, and Welfare, Bethesda, Maryland, 1962); P. Crowcroft, *The Life of the Shrew* (Reinhardt, London, 1957); *Mice All Over* (Fowlis, London, 1966); R. F. Ewer, *Ethology of Mammals* (Logos, London, 1968); E. S. E. Hafez, Ed., *The Behavior of Domestic Animals* (Williams & Wilkins, Baltimore, 1962); K. R. L. Hall, *Br. J. Psychol.* **54**, 201 (1963); H. L. Rheingold, Ed., *Maternal Behavior in Mammals* (Wiley, New York, 1963); W. Sluckin, *Imprinting and Early Learning* (Aldine, Chicago, 1965); V. C. Wynne-Edwards, *Animal Dispersion in Relation to Social Behavior* (Oliver & Boyd, London, 1962).
2. R. M. Church, *J. Abnorm. Soc. Psychol.* **54**, 163 (1957).
3. B. G. Galef, Jr., and M. M. Clark, *J. Comp. Physiol. Psychol.* **75**, 341 (1971); B. G. Galef, Jr., *ibid.*, p. 358.
4. R. P. Wortis, *Anim. Behav. Monogr.* **2**, 1 (1969).
5. C. B. Ferster and B. F. Skinner, *Schedules of Reinforcement* (Appleton-Century-Crofts, New York, 1957).
6. P. L. Brown and H. M. Jenkins, *J. Exp. Anal. Behav.* **11**, 1 (1968).
7. A. Bandura, *Principles of Behavior Modification* (Holt, Rinehart, and Winston, New York, 1969); A. Bandura, Ed., *Psychological Modeling: Conflicting Theories* (Aldine-Atherton, Chicago, 1971); P. Chesler, *Science* **166**, 901 (1969).
8. We thank L. Johnson for technical assistance and L. Squier, B. Wiest, G. Eaton, and C. Phoenix for their comments. Research supported by NIMH grants to A.N. and manuscript preparation supported by NIH grant RR-00163 to the Oregon Regional Primate Research Center. This is ORPRC Publication No. 728.

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Thermal Inertia versus Thermoregulation in "Warm" Turtles and Tunas

The recent report by Frair *et al.* (*1*) convinces us that large leatherback turtles (*Dermochelys coriacea*), like large pelagic fishes (*2*), can maintain body temperatures several degrees warmer than the environment. However, after cooling one turtle to determine whether the excess body temperature of another could be attributed to experimental manipulation, Frair *et al.* incorrectly computed the coefficient of temperature change, *k*. While Frair *et al.* reached a conclusion that seems substantially correct, their *k* is thermodynamically inconsistent for animals that maintain body temperatures appreciably higher than ambient temperature. Our comment is also directed to reconsideration of presumptive evidence by Carey and colleagues (*2–4*) for thermoregulation in bluefin tuna (*Thunnus thynnus*).

An object that produces no heat changes temperature at a rate proportional to the difference between its temperature (T_b) and that (T_a) of its environment:

$$dT_b/dt = k(T_a - T_b)$$

The term $T_a - T_b$ may be thought of as the driving gradient of temperature. When T_a and T_b are measured in degrees Celsius and *t* in minutes, the units of *k* are degrees Celsius per minute per degree of driving gradient.

For animals that are typically warmer than their environment, the driving gradient of temperature can be redefined to maintain logical consistency in the estimation of *k* (*5*). If a turtle or fish maintains a body temperature 1°C warmer than the water in which it lives, it will not cool at all unless put into water at least 1°C cooler than its body temperature. The body temperature that would ultimately obtain at any given water temperature may be called the equilibrium body temperature (T_e) for that water temperature. The difference, $T_x = T_e - T_a$, between equilibrium body temperature and environmental temperature has been termed the excess body temperature by Stevens and Fry (*6*). If heat production and heat transfer remain constant, the animal will cool or warm only if the environmental temperature falls or rises so that body temperature is no longer at the equilibrium temperature. Moreover, the rate at which the animal cools or warms will be proportional, not to $(T_a - T_b)$, but to $(T_e - T_b)$:

$$dT_b/dt = k(T_e - T_b)$$

If the animal physiologically regulates body temperature, T_x is not constant with respect to T_a, and the problem of evaluating *k* becomes more difficult. Either *k*, heat production, or both *k* and heat production may change as a function of T_a.

To return to leatherneck turtles, Frair *et al.* (*1*) measured the cooling rate of a 134-kg animal in Florida to establish that the 18°C excess body temperature they had measured from a 417-kg turtle in Nova Scotia was not attributable to warming or cooling during experimental manipulation. The Nova Scotian turtle had a body temperature of 25.5°C after it had been held in seawater at 7.5°C for 24 hours and then kept moist in air at 17° to 26°C for an additional hour. The Florida turtle was held at ambient temperature (?) for 6 days after capture, then cooled in a bath that decreased from 27° to 1°C in about 5 hours. The animal began the cooling experiment with a body temperature of 32°C and was still cooling at 22°C when the bath reached 1°C. The slow rate at which the Florida turtle cooled led Frair *et al.* to conclude that the large excess temperature of the Nova Scotian turtle "must have been due largely to the turtle's having been able to maintain its temperature in the cold water."

The leatherback turtle cooled by Frair *et al.* (*1*) certainly maintained an excess body temperature greater than 0°C and may actually have regulated body temperature. If one assumes that the turtle was at thermal equilibrium when the experiment started and that T_x remained constant at about 5°C throughout the experiment, then the turtle was cooling about 0.035°C per minute with a driving gradient of 16°C at the end of the experiment. Thus, *k* was about 0.0022°C min^{-1} °C^{-1}—not 0.0015°C min^{-1} °C^{-1} as concluded by Frair *et al.* If, on the other hand, this turtle regulated temperature to maintain a potential excess body temperature of 18°C at an ambient of 7.5°C (like the turtle from Nova Scotia), then *k* was about 0.009°C min^{-1} °C^{-1} when the bath was at 7.5°C (*7*). Since the two turtles were of different size and had different thermal histories, true *k* of the Florida turtle was probably nearer 0.002 than 0.009°C min^{-1} °C^{-1}.

Frair *et al.* (*1*) were right to recognize that the slow rate at which a large animal exchanges heat with its environment must be considered in any evaluation of that animal's potential for physiological thermoregulation. Among fishes, such consideration is especially appropriate for tunas (Scombridae), which have countercurrent heat ex-

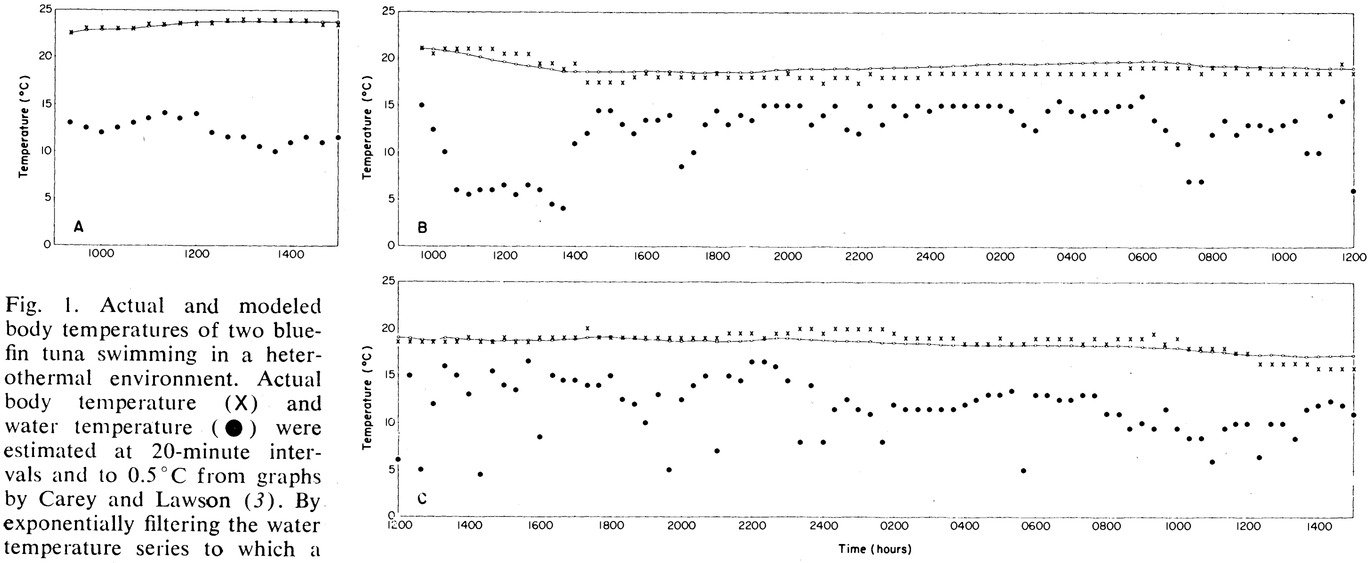

Fig. 1. Actual and modeled body temperatures of two bluefin tuna swimming in a heterothermal environment. Actual body temperature (X) and water temperature (●) were estimated at 20-minute intervals and to 0.5°C from graphs by Carey and Lawson (*3*). By exponentially filtering the water temperature series to which a constant temperature had been added, modeled body temperatures (-o-o-) were generated under the hypothesis that each fish had a constant coefficient of heat exchange and produced heat at a constant rate, that is, did not physiologically regulate body temperature. Lack of substantial physiological thermoregulation is suggested by how closely the model, optimized with reasonable values of the parameters, could be made to fit the data. (A) Muscle temperature, bluefin tuna No. 8. (B and C) Stomach temperature, bluefin tuna No. 14.

changers in their circulatory systems (*2*) and therefore might be expected to have k's approaching those of air-breathing aquatic animals and considerably smaller than the k's of typical fishes.

Large bluefin tuna have smaller excess body temperatures when caught in warm waters than when they are taken in cold water (*8*). Thus, bluefin tuna would appear to be capable of considerable physiological thermoregulation, at least when exposure to a given environmental temperature persists for the days or weeks necessary for acclimatory adjustments. On the basis of telemetry experiments, Carey and his associates (*2–4*) have carried the case for physiological thermoregulation in the bluefin further, suggesting that large bluefin subjected to rapid temperature fluctuations are capable of rapid physiological thermoregulation in the same sense as mammals. We believe the thermoregulation evident in these telemetry data was more physical than physiological—that is, that the observed responses of body temperature to changes in water temperature can be largely accounted for by a hypothesis of constant but small k coupled with constant heat production to produce a constant T_x.

To test our contention, we analyzed body temperature responses of two bluefin tuna tracked by ultrasonic telemetry through water of varying temperature. These 250-kg fish, Nos. 8 and 14, yielded what Carey and Lawson (*3*) considered the best evidence of physiological regulation of muscle and stomach temperature, respectively, among 14 bluefin tuna they monitored.

For each of the two fish, we first estimated, at 20-minute intervals and to 0.5°C, body and water temperatures from the graph of Carey and Lawson (*3*). Then, an assumed excess temperature was added to each water temperature and the resulting series of supposed equilibrium body temperatures was smoothed with an exponential filter (*9*) of the form ke^{kt} $(t \leq 0)$, where k was the coefficient of temperature change (assumed to be the same for cooling and warming) and t was time in minutes. The only actual fish temperature entering into the model was the first in the series, 22.5°C at 0920 hours for bluefin No. 8 and 21.0°C at 0940 (first day) for bluefin No. 14.

If the hypothesis of no physiological thermoregulation were plausible, some combination of constant k and constant T_x should exist to yield a smoothed series closely approximating the actual series of body temperature. For each fish, we tried several values of k and T_x; the combination we judged optimum was that which minimized the sum of squared residual errors and gave the smallest maximum residual error. Optimal k and T_x were 0.0020°C min^{-1} °C^{-1} and 13°C for bluefin No. 8 and 0.0014°C min^{-1} °C^{-1} and 6°C for bluefin No. 14. Comparison of actual and modeled body temperatures suggests that the thermal responses of these fish were generally consistent with the hypothesis of no physiological thermoregulation; maximum residual errors were only 0.3°C for bluefin No. 8 and 1.4°C for bluefin No. 14 (Fig. 1).

Moreover, the values of k and T_x giving best fit are, on independent grounds, quite reasonable. A k near 0.001 to 0.002°C min^{-1} °C^{-1} would be predicted for a 250-kg tuna by extrapolation of data summarized by Stevens and Fry (*10*) for smaller aquatic vertebrates, in conjunction with the value for the leatherback turtle cooled by Frair *et al.* (*1*). An excess muscle temperature of 13°C lies within the range expected for bluefin tuna living in water with surface temperatures between 10° and 15°C (*8*); excess stomach temperatures of bluefin range from 0°C to that of the warmest muscle (*2*).

Although our model adequately describes the major features of the bluefin data and is reasonable in its parameters, it does not eliminate the possibility that bluefin tuna can, in fact, rapidly regulate body temperature. To resolve this issue will require at least (i) careful, long-term monitoring of body temperature and activity of bluefin in heterothermal environments, together with rigorous analysis of results; and (ii) critical examination of circulatory physiology, including heat transfer and blood flow patterns, in restrained bluefin exposed to thermal stimuli.

Whether or not bluefin tuna and leatherback turtles can regulate body temperature by physiological means, their thermal inertia makes possible a kind of physical thermoregulation. Heat generated from metabolism is retained to produce advantageous (*3*) excess body temperatures, and the tissues are effectively protected from fluctuations of environmental temperature lasting even several hours. Such animals should enjoy a distinct ecological advantage over those that must rely solely on behavioral thermoregulation to maintain their tissues at the thermal optimum.

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References and Notes

1. W. Frair, R. G. Ackman, N. Mrosovsky, *Science* **177**, 791 (1972).
2. F. G. Carey, J. M. Teal, J. W. Kanwisher, K. D. Lawson, J. S. Beckett, *Am. Zool.* **11**, 137 (1971).
3. F. G. Carey and K. D. Lawson, *Comp. Biochem. Physiol.* **44A**, 375 (1973).
4. F. G. Carey, *Sci. Am.* **228**, 36 (Feb. 1973).
5. An alternative approach was developed by G. A. Bartholomew and V. A. Tucker [*Physiol. Zool.* **36**, 199 (1963)] in work on heat exchange by lizards. Essentially, *k*'s calculated from the relation

$$dT_b/dt = k(T_a - T_b)$$

were adjusted for metabolic heat production estimated independently from oxygen consumption data.
6. E. D. Stevens and F. E. J. Fry, *Can. J. Zool.* **48**, 221 (1970).
7. Assuming T_e was 25.5°C when T_a was 7.5°C,

$$k = \frac{dT_b/dt}{T_e - T_b} \simeq \frac{\Delta T_b/\Delta t}{T_e - T_b} \simeq \frac{-0.022\text{°C min}^{-1}}{(25.5 - 28)\text{°C}} \simeq 0.009\text{°C min}^{-1}\ \text{°C}^{-1}$$

8. F. G. Carey and J. M. Teal, *Comp. Biochem. Physiol.* **28**, 205 (1969).
9. J. L. Holloway, Jr., *Adv. Geophys.* **4**, 351 (1958).
10. E. D. Stevens and F. E. J. Fry, unpublished manuscript. We will supply on request a graph summarizing the relationship between *k* and body size for a number of aquatic vertebrates.
11. We thank F. E. J. Fry for his comments on a preliminary draft of the manuscript.

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After reading Neill and Stevens' comment, I came away with the impression that the thermoregulation we observed in bluefin tuna is in some way invalid and am concerned that it may be dismissed as an artifact of poor data analysis. I would like to point out to other readers who may have gained a similar impression that Neill and Stevens do not dispute the fact of thermoregulation, but have interested themselves in the importance of thermal buffering by the heat exchange system in achieving a stable temperature. They analyzed our experiments with bluefin No. 8 and bluefin No. 14 (*1*) and show that the observed thermoregulation could be achieved through a low coefficient of temperature change. However, this does not apply to the experiment with bluefin No. 13 (*1*). Here the stomach temperature of a 270-kg bluefin tuna increased by 7°C over a 20-hour period while the fish remained in water of constant temperature. There is more involved in the ability of the fish to control its temperature than a *k* value similar to that of a Thermos bottle.

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References

1. F. G. Carey and K. D. Lawson, *Comp. Biochem. Physiol.* **44A**, 375 (1973).

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Evidently Neill and Stevens agree both that leatherback turtles can maintain body temperatures well above that of the environment and that the cooling rates (*k* values) for the larger turtles are in the order of 0.0015°C min^{-1} °C^{-1}. The only point of difference is that they suggest that a *k* value of 0.002 would have been appropriate, whereas Frair, Ackman, and Mrosovsky (*1*) used a figure of 0.0015. There seems little point in arguing about the exact *k* value on the basis of the meager data available. Whether a *k* of 0.002 or 0.0015 was appropriate makes little difference to the overall conclusions.

We agree with Neill and Stevens that, in principle, *k* values are better calculated on the basis of the equilibrium rather than the ambient temperature. However, in the present case, making this point is unhelpful because one does not know what the equilibrium temperature was. Moreover, Neill and Stevens have assumed that the excess body temperature is 5°C and that it would be the same at different ambient temperatures. Both these assumptions are unlikely. In using the 5°C difference they ignore data on temperature of leatherbacks in tropical waters (*2*). In suggesting that excess body temperatures are constant at different ambient temperatures, they ignore observations of increased activity of marine turtles in cooler water (*3*).

It would be desirable to learn more about the equilibrium temperatures of leatherbacks and also about the functioning of their recently discovered countercurrent system (*4*). Unfortunately there is little chance of someone with a suitable thermometer in hand encountering a leatherback in northern waters, or of a specimen in good condition being caught near adequate experimental facilities. We hope that if this should occur, someone will communicate with us so that arrangements can be made for obtaining fuller information on this warm-bodied turtle.

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References

1. W. Frair, R. G. Ackman, N. Mrosovsky, *Science* **177**, 791 (1972).
2. N. Mrosovsky and P. C. H. Pritchard, *Copeia* **1971**, 624 (1971).
3. S. M. McGinnis, *Am. Zool.* **8**, 766 (1968); N. Mrosovsky, *Nature (Lond.)* **220**, 1338 (1968).
4. A. E. Greer, J. D. Lazell, R. M. Wright, *Nature (Lond.)* **244**, 181 (1973).

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Screwworm Eradication Program

Calman (*1*) and Smith (*2*) comment adversely about the status of the Southwestern Screwworm Eradication Program. This program is conducted by the U.S. Department of Agriculture (USDA) with the cooperation of livestock regulatory agencies, extension services, and grower organizations in affected U.S. states and Mexico. The program is conducted by USDA's Animal and Plant Health Inspection Service (APHIS), with research support from the Agricultural Research Service (ARS).

There could be many reasons for our recent difficulty in keeping populations of the screwworm *Cochliomyia hominivorax* from growing and spreading in this country. Ecological as well as genetic and physiological factors must be considered. Abundant rainfall for the past 2 years has favored screwworm increase in the warm months. An