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# Raymond B. Cowles and the Biology of Temperature in Reptiles

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ABSTRACT.—**Through his imaginative work on the thermal biology of reptiles, Raymond B. Cowles fomented a revolution in thought on the biology of temperature. In this article, I review the development of Raymond Cowles' work on temperature, and show how much of its originality can be attributed to a remarkable theory on the extinction of the dinosaurs.**

Raymond Bridgman Cowles (1896–1975) substantially influenced the ways that modern biologists think about temperature. His most important scientific work on temperature dealt with reptiles. Nevertheless, the impact of his work went far beyond herpetology. It is fair to say, I think, that we are still coming to grips scientifically with the work of Raymond Cowles.

Cowles is usually remembered for the skillful blend of natural history and experimental biology that appeared in such works as "A Preliminary Study of the Thermal Requirements of Desert Reptiles," co-authored with Charles M. Bogert in 1944 (for some remembrances of Cowles, see Pough, 1974 and Brattstrom, 1977). However, the most striking feature to me of Cowles' work is its pervasive originality. When confronted with an original thinker such as Cowles, it is tempting to ask, "What drove the engines of his creativity?" In this article, I attempt to answer this question by reviewing the development of Cowles' work on the thermal biology of reptiles and placing it in its historical context. I will develop the argument that most of Cowles' original ideas on temperature derived from an inspired idea on the extinction of the dinosaurs, which dominated his thinking in one form or another from 1938 until the end of his life.

## THE BIOLOGY OF TEMPERATURE: HISTORICAL BACKGROUND

*Cold-Blooded, Warm-Blooded: Biosemantics of Temperature.*—Prior to the 20th century, animals long had been classified as either "warm-blooded" (mammals and birds) or "cold-blooded" (everything else). In the 19th century, these terms often were used as a literal description of body temperature. Thus, one of the leading zoological textbooks of the time (Agassiz and Gould, 1856) asserts that reptiles, being "cold-blooded" do not possess ". . . the power of maintaining a constant body temperature . . . [with] . . . body temperatures always as low as from 35°F to 50°F." Despite such dogmatic assertions, 19th century biologists certainly knew of striking exceptions. In the 18th century, Reaumur discovered that honeybee hives were warmed considerably by the activities of their inhabitants (for a review of early work in insect thermoregulation, see Heinrich, 1981). And in 1832, Lamarre-Picquot reported to the French Academy that a Bengalese python tending its eggs raised its body temperature by several °C above air temperature. Lamarre-Picquot's report was not well received by the Academy, his credibility being somewhat injured by his accompanying observations of a snake withdrawing "milk from the udder of a cow" (cited in Benedict, 1932). In addition, Lamarre-Picquot had been unable to differentiate heat production by the brooding python from heat produced by the fermentation of rotting eggs. Nevertheless, subsequent

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observations by other investigators vindicated Lamarre-Picquot's observations.

These early studies were hindered by the use of glass thermometers, which were unwieldy, and could significantly alter the temperature of the animal. However, once biologists began to use thermocouples routinely in the mid 19th century, far more detailed and sophisticated measurements of body temperature were possible. Increasingly, biologists found that even "cold-blooded" animals often had body temperatures quite different from air temperature, and could in fact be quite warm. These discoveries led some biologists to question the legitimacy of labels such as "warm-blooded" and "cold-blooded." Yet, the terms persisted, because they reflected undeniable differences between these two types of creatures. This was put eloquently by Sutherland in 1896:

> "There has for many years past been a tendency to diminish or ignore the distinction between the cold-blooded and warm-blooded types of animal life. Quite a number of writers adopt the habit of speaking of 'the so-called cold-blooded animals', as if the contrast were an unfounded belief that increasing knowledge is fast abolishing. Yet, the difference is one that is not only real, but in some respects, radical."

Faced with this quandary, biologists retreated to the convenient strategem of semantics, classifying animals as being either "homoiothermic" (those animals which maintain a constant, high body temperature, equivalent to the "warm-blooded" birds and mammals) and "poikilothermic" (those animals whose body temperatures vary with that of the "surroundings," usually taken to be air temperature, and essentially equivalent to "cold-blooded"). This did not provoke greater awareness of the biology of temperature, except to incorporate the obvious fact that poikilothermic animals could sometimes have warm bodies if they lived in a hot environment.

*Tolerance to High Body Temperature.*— The new dichotomy of "homoiotherms" vs. "poikilotherms" produced a curious result. The view came to prevail that temperature *regulation* was the sole province of homoiotherms, for they were continually faced with maintaining a constant body temperature. For poikilotherms, the problem of temperature regulation could not be important, because, by definition, their body temperature simply varied with that of the environment. Nowhere was this bias more strongly seen than in the writings of naturalists on desert reptiles. Reptiles had long been known to be a conspicuous fauna in the deserts of the world. Because these regions were often very hot (usually uncomfortably so for the naturalists), and because reptiles were considered poikilotherms, the inference was naturally made that desert reptiles could tolerate unusually high body temperatures. This was a cause of much wonder among naturalists. For example, Gadow (1901) wrote that ". . . dark-colored tortoises basking in the sun are sometimes so hot that they are disagreeable to touch, since they possess little mechanism for regulating their heat." Likewise, Camp (1916) thought it remarkable that collared lizards could ". . . mount rocky eminences and lie for hours in the sun during the hottest part of the day," and that chuckwallas were often seen ". . . perching on rocks so hot as to be unbearable to the hand . . ." or pursuing each other ". . . over hillsides in the middle of the hottest July days." Indeed, some reptiles seemed to love high temperatures so much that campers sometimes were said to be troubled by the persistence of snakes trying to crawl into the flames of their campfires (in Klauber, 1956)!

By the 1920's, observations like these were common enough to be enshrined as textbook knowledge. For example, in a classic monograph on animal life in deserts, Buxton (1923) noted that the

> ". . . very existence of small animals on the surface of the desert at midday

is remarkable. Most of the animals—for example, the lizards and beetles—are cold-blooded, so that one supposes that their temperatures approximate to that of the air in which they find themselves at any given time . . ."

Similarly, a leading textbook of ecology of the time (Hesse, 1924, translated as Hesse, et al., 1937) stated that ". . . temperatures tolerated by desert insects and desert lizards [50–55°C] correspond closely to those endured by the animals of hot springs."

*Contrary Evidence.*—Active areas of research are always making their own dogmas obsolete, and the study of body temperature was no exception. While the simple ideas outlined above were being incorporated into leading textbooks, a large number of observations were accumulating which showed them to be inadequate. For example, occasional reports suggested that the supposed tolerance of desert reptiles to extremely high body temperatures was not universal. The most provocative was Grinnell's (1908) on the death of a rattlesnake that he forced to remain in direct sunlight while attempting to photograph it. Grinnell's surprise at the rapid death of the snake is evident from his account:

"Suddenly, his snakeship appeared to give up completely, and became perfectly quiet. He shortly opened his mouth, gasped quickly several times, assumed a tetanic rigidity and—was dead! . . . He seemed to have suffered sunstroke due to violent exercise in the hot sun!"

The low thermal tolerance of desert snakes was considered unusual for reptiles. I will return to this later, because it was crucial to the early development of Cowles' thinking on temperature.

The idea that reptiles' body temperatures were always equivalent to air temperature also was being questioned. For example, Sutherland (1896) showed that body temperature of large agamid lizards rose slightly when the animal was angered, or when it was prodded into vigorous activity. Some years later, Weese (1917, 1919) showed that horned lizards selected warm temperatures when given a choice in a thermal gradient; thus, reptiles had some active control over body temperature. Weese (1917, 1919) also showed that the body temperature of horned lizards depended more upon substrate temperature than upon air temperature. Baldwin (1925*a*, *b*) later showed that the survival of turtles in a hot environment could be significantly prolonged if evaporation from the skin lowered the turtle's body temperature. And in 1928, Pearse and Hall found that living turtles cooled more quickly than dead turtles; thus, not only evaporation, but the flow of blood in the body could influence the body temperature of a reptile. Just how complicated the body temperature of reptiles could be was shown compellingly by Benedict (1932). In an exhaustive series of experiments, he showed that the body temperature of pythons was affected by such diverse influences as air and substrate temperature, the previous thermal history of both the animal and its enclosure, the flow of air, relative humidity, digestive state, prior locomotor activity, emotional state and/or posture of the snake and amount and type of handling.

By the early 1930's, enough information had accumulated to convince some biologists that there was more to the body temperature of reptiles than the textbooks allowed. It is in the context of this unsettled situation that the contributions of Cowles must be understood. Before turning to Cowles' work directly, we must consider briefly the contributions of two herpetologists, Laurence Klauber and Walter Mosauer, who were contemporary with Cowles, and who significantly influenced his work on temperature.

*Laurence M. Klauber and the Activity of Reptiles.*—Laurence Klauber (1883–1968) is best known for his fascinating book *Rattlesnakes: Their Habits, Life Histories and Influence on Mankind.* He was one of those gifted amateur naturalists that we usually imagine to have disappeared with the 19th century. Born and raised in San Diego, he developed an early interest in herpetology through his pursuits of horned lizards, that perennial quarry of boys growing up in the West. For his higher education at Stanford University, he elected not to pursue his zoological interests, studying instead to be an electrical engineer. After graduating from the Westinghouse Graduate Apprentice program in 1910, he went to work for the San Diego Gas and Electric Company, where he was promptly put to work as a salesman. It did not take long for his talents as an engineer to be put to appropriate use, however. He had a long and distinguished career with his company, eventually succeeding to its Presidency in 1947, where he remained until his retirement in 1953. Despite his full career as a businessman, Klauber nevertheless indulged his avocational interest in herpetology through a position as Consulting Curator with the budding San Diego Zoological Garden. (Shaw, 1969).

Klauber had long realized that driving along paved roads in the early evening provided rich collecting opportunities for a variety of reptiles (Klauber, 1939). In trying to predict the most opportune times for successful collecting, Klauber soon noticed that the abundance of reptiles on the roads depended strongly upon the air temperature. Interestingly, all species of reptiles were not equally abundant at a given temperature; some species appeared more frequently on cooler nights than others.

The idea that environmental temperature somehow limited the activities of reptiles was not new. Temperature long had been thought to limit the latitudinal distribution of reptiles (Pearse, 1931; Hesse et al., 1937). Klauber's observations could be intepreted simply as a limitation of temperature on the "distribution" (i.e., the conspicuousness of active animals) of reptiles with respect to *time*. However, they actually pointed to something more profound. The differences in activities of the various species of reptiles corresponded to differences in air temperature that were much smaller than those that limited latitudinal distributions. In light of the knowledge that reptiles could behaviorally seek out environments of a certain temperature (Weese, 1917, 1919), it was a simple inference that the different species had slight differences in their "preferred" body temperatures for activity. This was a subtle shift in thinking. Yet, it would have profound consequences for prevailing views on the ecology of temperature. Temperature previously had been thought to act simply to place physical limits on what organisms could do. Klauber's observations opened the possibility that temperature could be a *resource,* one which could be exploited, partitioned and competed for by organisms.

*Walter Mosauer and the Thermal Tolerance of Squamates.*—Walter Mosauer (1905–1937) was a colleague of Cowles' at the Los Angeles campus of the University of California (UCLA). His experiments on the tolerance of lizards and snakes to high body temperature were central to Cowles' early experiments on temperature. I am indebted to C. M. Bogert (pers. comm.) for much of the following information.

Mosauer was a native of Austria, who became acquainted with herpetology through an association with Franz Werner of the University of Vienna (Mosauer, 1940). While Mosauer studied medicine at the University of Vienna, he worked as Werner's assistant, and eventually was chosen to lead the University's expedition to the Sahara in 1928. In accord with the wishes of his family, who wanted him to be a dentist, he completed his dental curriculum in 1929. After doing so, he decided his future was brighter in herpetology. After completing his work with Werner, Mosauer emigrated to the United States, where he studied for the Ph.D. at the University of Michigan. After completing his studies in Michigan, he obtained a position as instructor in the Department of Zoology at UCLA in 1930. His Ph.D. was granted by the University of Michigan in 1931.

The enthusiasm for deserts which he had developed in Africa quickly carried over to the deserts near Los Angeles. He spent a great deal of time in the desert with both Cowles and Bogert, working mostly on snake locomotion. His medical training made him one of the few herpetologists of the time with the expertise and temerity to attempt an anatomical explanation of how snakes move.

Mosauer became interested in temperature through observations on the quick deaths that snakes suffered when forced to remain in direct sunlight, a phenomenon he may have been introduced to by Cowles. Because prevailing views held that desert reptiles could tolerate very high body temperatures, such sensitivity was considered unusual by many herpetologists. Various explanations were advanced for this, among them the possibility that nocturnal reptiles could not tolerate body temperatures as high as diurnal ones, or that snakes were unusually sensitive to wavelengths of light found only in solar radiation (Mosauer and Lazier, 1933; Blum and Spealman, 1933). Unfortunately, no one had done any measurements of body temperatures of snakes when they succumbed from exposure to sunlight. Mosauer decided to examine this phenomenon more closely, and built some crude environmental chambers for laboratory tests of thermal tolerance. Mosauer, along with Edgar Lazier (Mosauer and Lazier, 1933) found that the body temperatures of rattlesnakes (*Crotalus atrox* and *C. cerastes*) were always close to 46°C at death—high, but not as high as they had been led to expect. Mosauer and Lazier (1933) believed that snakes were unusual, considering:

"... the extreme sensitivity to sunlight of these nocturnal creatures ... [in] ... contrast with the tolerance of certain diurnal reptiles, such as *Uma notata*, which, in exactly the same habitat, plays and thrives on sand at 55–60°C" (Mosauer and Lazier, 1933).

A few years later, however, Mosauer extended these observations to desert lizards (Mosauer 1936), and found that lizards, like snakes, were not especially tolerant to high body temperature. Mosauer also conducted field and laboratory experiments to show how cooler microclimates were important in enabling these animals to live in such apparently hot environments. It is interesting to speculate on the potential contributions of this interesting man had not leukemia claimed his life at an early age.

## RAYMOND B. COWLES AND THE THERMAL BIOLOGY OF REPTILES

Raymond Cowles was a naturalist *par excellence.* Born of missionary parents in what is now Natal South Africa, he was immersed in nature from the time he was a boy. He almost certainly gained an early appreciation of natural history from his mother, an amateur ornithologist who supplemented her family's income by mounting and selling bird skins to universities and museums. He writes eloquently of his African boyhood and of his later experiences in Africa in his book, *Zulu Journal* (Cowles, 1959*a*), an unappreciated classic in natural history writing. He became interested in reptiles through a concern with the effects of snake venoms, helped along perhaps by a close call he had with a venomous snake. He had a brief flirtation with immunology in the hopes of developing an antivenin. Fortunately for herpetology, when he discovered that antivenin had already been invented, he gave up and became interested in the natural history of the birds and reptiles of his homeland (R. B. Huey, pers. comm.).

After some home schooling and one

year of public school in South Africa, Cowles' parents sent him to the United States for the rest of his education, before "endocrine changes [made him] susceptible to the blandishments of the adventurous native 'maidens'" (Cowles, 1959). He graduated from Pomona College with the B.A. degree in 1921. He then went to Cornell University to study for the Ph.D. under the direction of A. H. Wright, and returned to Natal in 1925 for his research. While there, he returned to a serendipitous discovery he had made as a boy, that the Nile monitor lizard (*Varanus niloticus*) uses the mounds of a termite as incubators for its eggs (Cowles, 1928, 1930). He came back to the United States from South Africa in 1927 and completed the Ph.D. at Cornell University in 1928. After joining the faculty at UCLA in 1927, he published widely on the natural history of African and American vertebrates. While his work on *Varanus* nesting habits must have impressed Cowles with the subtle ways a reptile could exploit its environment for heat, there is little evidence of the pervasive interest in temperature that is found in his later papers. This was soon to change dramatically.

Cowles' first decade at UCLA must have been a stimulating one, because his colleagues came to include a large number of people with common interests in problems of temperature, particularly of reptiles in the host environment of the desert. They included Walter Mosauer, Sarah Rogers Atsatt, Charles Bogert (as a graduate student) and Laurence Klauber. It is difficult to sort out the scientific relationships of these researchers, to see who stimulated what ideas, but one thing is clear from Cowles' own recollections (R. B. Huey, pers. comm.). The research that was most provocative to Cowles was Mosauer's experiments on tolerance of reptiles to high body temperature (Mosauer, 1936; Mosauer and Lazier, 1933). Cowles had no trouble believing that desert reptiles were not unusually tolerant to high body temperature. However, he found hard to believe Mosauer's claim that nocturnal rattlesnakes and diurnal lizards did not differ appreciably in their temperature tolerances. Klauber's (1939) observations had suggested to Cowles that even different species of nocturnal reptiles had subtle differences in the ways that environmental temperature affected their activities. In addition, Cowles had serious doubts about both the design of Mosauer's chambers, and the applicability of the data obtained from them to the problems of reptiles living in nature. Finally, some of Cowles' own writings and personal recollections hint at a touch of professional rivalry between the two men. In any event, Cowles was prompted to repeat Mosauer's experiments, but in a way that he considered more meaningful, that is, under relatively natural conditions in the field. In the late 1930's, therefore, he began an intensive program of research in the Coachella Valley of California, studying the body temperatures of desert reptiles confined in field enclosures.

Cowles soon confirmed one of Mosauer's basic findings; like snakes, the tolerance of desert lizards to high body temperature was by no means exceptional. Nevertheless, Cowles did find that lizards were tolerant to higher body temperatures than were snakes. However, the most important result of these experiments concerned the ranges of tolerated body temperatures both above and below the "voluntary" or "preferred" body temperature. If body temperature rose by as little as 2–3°C above the preferred temperature, the animal would be incapacitated, and would quickly die unless rescued. In contrast to the narrow range of temperatures that reptiles could tolerate above the voluntary temperature, temperatures far below the voluntary temperature had no apparent ill effects (Cowles, 1939, 1940; Cowles and Bogert, 1944). The contrast between the upper and lower ranges of tolerated body temperatures led Cowles to one of the major ideas of his scientific career, his speculations on the extinction of the dinosaurs.

*Extinction of the Dinosaurs.*—While pondering the significance of this wholly unexpected result, the idea came to Cowles in a "serendipitous flash" (Cowles and Bakker, 1977) that it may explain the extinction of the dinosaurs. The prevailing theories of the day held that the end of the Cretaceous had become cooler than the rest of the Mesozoic. The dinosaurs, being reptiles and hence "cold-blooded," supposedly could not tolerate these cooler climates. The homoiothermic mammals and birds, with their warm bodies and coats of insulation, might be more tolerant of a cool climate, and so would inherit the earth from the decimated ruling reptiles. Yet, all of Cowles' results on desert reptiles had shown them to be very tolerant to low temperatures. Rather, it was high temperatures they could not tolerate. Perhaps, Cowles reasoned, the dinosaurs had been driven to extinction by *increased* temperatures at the end of the Mesozoic?

This single idea would dominate Cowles' thinking on temperature for the rest of his career. It was bold, even rash speculation, which had no supporting evidence other than his observations on the thermal tolerance of extant reptiles. Yet, many of Cowles' later publications had this theory, or theories derived from it, as central themes. It was in the context of these theories that many of Cowles' sophisticated insights into the biology and ecology of temperature regulation arose. In fact, the body of Cowles' published works on temperature can be considered a unified series of papers to support these theories, or to deal with criticisms of them. In the sections that follow, I will outline some of these contributions, and show how Cowles related them to his unusual theories.

*The Evolution of Terrestriality.*—If dinosaurs were driven extinct by high temperatures, then they probably had a lower tolerance for high body temperatures than the lines of reptiles which survived the Mesozoic. In fact, Cowles felt that vertebrate evolution was marked by "... the adoption of progressively higher body temperatures with an increasingly unfavorable susceptibility to cooling" (Cowles, 1939). By this logic, if archosaurs were more "primitive" than modern lizards, then they probably were more tolerant of cold, and at least not more tolerant of heat, than were extant lizards. Cowles regarded this as an important argument for his theory that a warm climate and not cold drove the dinosaurs to extinction (Cowles, 1940).

It also suggested to Cowles an alternative hypothesis on the origin of terrestriality during the evolution of the tetrapods. It was widely believed at the time that the terrestrial tetrapods arose in a warm and increasingly arid environment, in which small ponds and lakes began to dry up, forcing their inhabitants into overland journeys to find other bodies of water. Cowles felt that such events were probably too rare and catastrophic (to the fish) to provide a favorable setting for evolution to occur. He suggested, rather, that the climate of the Devonian was relatively cool. In keeping with the idea that vertebrates adopted progressively higher body temperatures during their evolution, Cowles proposed that the Devonian fishes would be continually "striving" to attain higher and higher body temperatures. To do this in a cool environment, they may have adopted the habit of basking at the surface of the water. The increased absorption of solar radiation may have raised body temperatures above that of fishes that remained submerged. The drive to attain higher and higher body temperatures would have lead eventually to partial and then full terrestriality (Cowles, 1940, 1949).

*Body Size and Temperature.*—In living reptiles, rates of temperature change seemed to have clear ecological consequences. If high body temperature conferred advantages on an animal, as Cowles had suggested in earlier papers, anything that would enable it to attain a high body temperature quickly, and to keep it there longer, would be advantageous. Body size clearly would be important in this regard, because it would significantly affect how fast an animal's body temperature could change, and on the availability of microclimates for an animal to exploit. For example, spring and fall in the deserts were usually cooler, and characterized by rapid and unpredictable changes in levels of solar radiation. In such a circumstance, being able to change temperature quickly and to exploit small microclimates might be extremely important. Cowles felt this might explain why small lizards often were more active than large lizards during these seasons. Summers in the desert, however, were usually hotter overall than either spring or fall, and the levels of solar radiation were more intense and constant. During this season, large lizards like the desert iguana and chuckwalla were more conspicuous than small lizards, and could extend feeding activities into hotter parts of the day than could smaller lizards (Cowles, 1939, 1940).

Using this logic, Cowles asked what could body size tell us about thermal biology during the evolution of the vertebrates? Put another way, could fossil animals be used as biological "thermometers," as indicators of the climates in which they lived? Among endotherms, the link between body size and temperature found its expression in "Bergmann's rule" (body size tends to be larger at higher, and hence colder, latitudes and elevations). An explanation for Bergmann's rule that was popular at the time (and still is) held that large body size helped endotherms conserve expensive metabolic heat in colder climates (the energetic explanation for Bergmann's rule sparked a sharp controversy in the 1950's; see Scholander, 1955 and Mayr, 1956). Cowles suggested that ectotherms often were faced with the opposite problem of having to take heat up from the environment as quickly as possible. Thus, Cowles felt that a "reverse Bergmann's rule" might apply to ectotherms. In more variable and cooler climates, where an ectotherm would have to heat quickly, small animals would be expected. Conversely, in warmer and more stable climates, where high body temperatures could be maintained easily, larger animals could exist. Thus, many of the largest extant reptiles were found in equable semitropical or tropical climates. Desert reptiles, inhabiting an environment characterized by wide and rapid excursions of temperature, were usually much smaller than their tropical counterparts (Cowles, 1945*a*).

Cowles suggested that if the energetic explanation for Bergmann's rule was accepted, then it could not be rejected a priori as an explanation for the changes of body size through evolutionary time. For example, an increase in body size during the evolution of a lineage of endotherms might indicate that its evolution occurred in a cooling climate. By the same logic, the "reverse Bergmann's rule" for changes in body size during the evolution of a lineage of ectotherms could not be dismissed lightly. Thus, the tendency to gigantism in the archosaurs suggested to Cowles that the Cretaceous was characterized by a steady warming of the climate. If this climatic trend continued to temperatures that were intolerably high for the dinosaurs, their evolutionary fate was sealed, because their large size precluded them from finding shelter against sunlight or from cooling of quickly during the night (Cowles, 1945*a*).

*Body Color and Heat Exchange.*—For the first part of the 20th century, the phenomena of mimicry, aposematic coloration, and cryptic coloration had dominated the study of animal color. The decade of the 1930's was witness to a vigorous debate over whether animal coloration (as expressed in these phenomena) had "adaptive significance" (i.e., arose through natural selection) or was simply an accident of genetics with no biological importance (Huxley, 1940). In this concern with the interactions of animal color with the biotic environment, more physical interactions, such as the effect of color on heat transfer by radiation, were ignored (Cole, 1943). While many biologists, like Klauber (1939), could agree that variation in color might affect reptiles' body temperatures, they nevertheless felt that the demands for camouflage were far more important.

Yet, experiments by Atsatt (1939) had shown that changing the body temperature of many of the desert reptiles that inhabited southern California brought about some very interesting changes in body color. For example, some of the iguanid lizards Atsatt worked with were dark-colored while they were cool, or while they were being warmed from a cool body temperature. Yet, at a critical body temperature, the animal would abruptly lighten in color, as if to restrict the absorption of radiant energy. This, of course, raised a pregnant question: if animal coloration had little thermoregulatory significance, why did they change color in this way?

The results of Cowles' field experiments had impressed him with how body color could affect a lizard's rate of temperature change which would in turn have important ecological consequences (Cowles, 1939, 1940). By the same token, if the rate of warming could be limited once a favorable body temperature had been reached, perhaps by becoming lighter in color, the allowable time for activity while exposed to solar radiation might likewise be increased. Thus, color's ecological significance and its effect on thermoregulation did not have to be separate, and their interaction could be expected to have played a role in the evolution of the vertebrates.

Cowles (1939, 1940) proposed that the early fishes were dark mostly for purposes of camouflage. During the Devonian, dark color was co-opted for raising body temperature quickly while basking at the surface of the water. He also proposed that early amphibians and reptiles did not have the ability to change color; there would be no need because the cool climate would always favor maximum absorption of solar radiation. The ability to change color would have to await the supposedly hot and sunny climes of the end of the Cretaceous, when reflecting solar radiation might be necessary to avoid overheating. Those animals which had this ability, for example the predecessors of squamate reptiles, would have survived. However, Cowles believed that archosaurs probably could not change color, because their closest living relatives, the crocodilians, did not have this ability. Thus, most of the archosaurs presumably perished because they could not limit radiation heat uptake (Cowles, 1939, 1940).

*Feathers and Fur.*—Just as the ability to change color may have ensured the survival of lepidosaurians through the end of the Cretaceous, so Cowles felt that the development of feathers in another line of Mesozoic reptiles might have ensured their survival (Cowles, 1946). It was widely thought that feathers and fur had evolved for heat conservation. Cowles believed that endothermy could only have evolved after the evolution of an insulating coat. Thus, the origin of feathers or fur must have occurred in the ectothermic predecessors of birds and mammals where heat conservation made little sense. It was Cowles' contention that the development of feathers or fur in an ectotherm also made little sense unless it was used to limit the rates of heat *uptake*. Such animals would only seek to do this if the environment had become intolerably hot. Under such conditions, external insulation would:

"... enable the animal to extend its

mid-day excursions for longer periods of time . . . [while in the evening] . . . it would retard the loss of heat and . . . extend the animals' post-warming periods of activity" (Cowles, 1946).

*The Temperature Relations of Alligators.*—Some of these sweeping speculations prompted a vigorous response from Edwin H. Colbert, then at the American Museum of Natural History (Colbert et al., 1946, and pers. comm.). The supposition that an excessively high body temperature drove the dinosaurs to extinction was flawed on two accounts, he argued. First, the available evidence suggested a drop in temperature at the end of the Cretaceous, although other interpretations were possible until new evidence came to light. Second, it was unknown just how tolerant the archosaurs were to high body temperature. Even if the end of the Cretaceous was warm, Colbert argued that Cowles' theory would fail if archosaurs were unusually tolerant to high body temperature. Experiments on the thermal tolerance of modern lepidosaurian reptiles probably would not shed much light on this question, because most modern lepidosaurians are small, and assume postures that put them close to the ground, where body temperatures could be influenced greatly by ground temperature. Archosaurians, on the other hand, were often large, and had more upright postures than lizards; some were even bipedal (Colbert et al., 1946). Colbert suggested that experiments on the thermal tolerance of alligators, which are more closely related to the dinosaurs, would be instructive.

In 1944, Cowles joined Colbert and Bogert at the Archbold Biological Station in Florida, where they conducted experiments on the temperature tolerance of the American alligator (*Alligator mississippiensis*). These experiments were important, because they showed dramatically how body size could affect thermoregulation. The range of body sizes with which they worked (47.5 g to 24.5 kg) was orders of magnitude greater than the lizards Cowles and Bogert previously had worked with. Animals this large were substantially homeothermic; they estimated that a 9000 kg dinosaur would require nearly 86 hours for its body temperature to change by 1°C if it was standing in full sunlight (there were subsequent disputes about this figure; see Colbert et al., 1947). While homeothermy in an ectotherm might have been beneficial in some ways, a large ectotherm would have been at a severe disadvantage if the climate warmed even slightly. Small animals could always exploit microclimates to avoid the consequences of a sunnier climate, and if they got very hot during the day, they could always cool off quickly at night. Large body size precluded animals from either of these strategies, and large animals would be in severe trouble when faced with long periods of hot, sunny weather, particularly if this was accompanied by a reduction in sheltering vegetation. Thus, if the end of the Cretaceous was marked by an even slightly sunnier and more arid climate, as Cowles was suggesting, it was at least possible that the larger dinosaurs could have suffered hyperthermia and death.

*Hyperthermia and Aspermia.*—The experiments with alligators (Colbert et al., 1946) had pointed out that large animals' body temperatures could respond in unexpected ways to slight warming of the climate. Yet, the paleoclimatological evidence still could not show *any* warming occurring at the end of the Cretaceous. If Cowles' theory was to be vindicated, he would have to show that the warming was so small that it could not have been detected by the available paleoclimatological methods. It was probable that an increase in temperature sufficient to kill the dinosaurs would have been large enough to be seen by the paleoclimatologists.

Biologists had known since the 1920's that the sterility that accompanied cryptorchidism (undescended testes) in mammals was caused by a slight increase in testicular temperature. It occurred to Cowles that body temperatures did not need to be high enough to kill the dinosaurs to cause their extinction; it need merely to have been high enough to render the males sterile (Cowles, 1945*b*). Since modern reptiles regulated body temperature close to their maximum tolerated body temperatures, only a very slight increase in temperature could have rendered the dinosaurs infertile, particularly if they were large (Cowles, 1945*a*, *b*). Cowles eventually found widespread evidence for heat induced sterility in a variety of organisms. For example, the scrotum of mammals was widely recognized to regulate the temperature of the testes (Cowles, 1945*b*). Lizards kept in warm temperatures quickly exhibit testicular collapse (Cowles and Burleson, 1945). Birds had developed a "scrotum" of sorts by enveloping the testes in ventilated air sacs (Cowles and Nordstrom, 1946), which could perhaps be cooled by ventilation of the lungs. And Cowles proposed that control of heat loss through the wings of bats was a way to reconcile the need to keep the testes cool with the high energetic consequences of flight (Cowles, 1947). This line of specualtion was eventually to lead to a general model on the role of temperature in evolution (Cowles, 1965).

*Dermal Blood Flow in Lizards.*—Cowles had long maintained that it was advantageous for ectotherms to elevate body temperature quickly, and to keep it high for as long as possible. However, there were certain "rules" that constrained the possible ways an ectotherm could do this. For example, conserving body heat would extend an ectotherm's period of activity in a cooling environment. Endotherms did this by developing a coat of insulation. While a layer of external insulation on an ectotherm would impede the loss of heat, it would impede its uptake as well (Cowles, 1946). Cowles proved this by wrapping a lizard in a "wrap-around" of mink fur. The insulated lizards cooled much more slowly than did uninsulated lizards, but they also warmed more slowly. Thus, a lizard with a layer of external insulation would require a very long time to attain its preferred temperature (Cowles, 1958*a*).

While color change might enable a reptile to vary the rate of heat absorption, such control would not be enough by itself. If a darkened skin was warmed quickly, for example, the absorbed heat still would have to penetrate rapidly into the body; variations in "internal insulation" also would be needed. This could be done in the same way that birds and mammals did it, that is, by varying the rates at which blood carried heat between the skin surface and the core of the body. To show that this indeed happened in a lizard, he injected small "blebs" of water beneath the skin of desert iguanas (*Dipsosaurus dorsalis*). He found that the blebs disappeared more quickly when the skin was warmed than when it was cooled. This suggested that blood flow to the skin increased when it was warmed. The changes in skin blood flow were correlated with changes in the temperature gradients within the body. Thus, lizards could control the movement of heat within the body by blood flow (Cowles, 1958*a*).

The regulation of heat exchange by blood flow to the skin was thought to be unique to endotherms. However, Cowles showed that this was not so; lizards had dermal temperature regulation as well, although it had different purposes than for endotherms. How did this ability evolve? Cowles noted that modern amphibians also have a well-developed and actively controlled dermal vascular bed, which is used for respiration. Presumably, the ancestors of amphibians had it also. When Devonian amphibians made the transition from aquatic to predominantly terrestrial life, Cowles argued they would have had to abandon dermal respiration and develop a dry skin; evaporation from a wet skin would have prevented them from attaining the high body temperatures they came out on land for in the first place (Cowles, 1940). Why, Cowles reasoned, could not these early amphibians have appropriated the dermal vascular beds from their original respiratory function for the regulation of heat exchange, just as skin color had been appropriated from camouflage from the absorption of solar radiation? Thus, Cowles proposed that the dermal temperature regulation of mammals and birds had its origins among the Permian amphibians.

## Retrospective

At the beginning of this article, I suggested that the body of Raymond Cowles' scientific contributions could not be understood fully without confronting his highly unorthodox theories on dinosaur extinction and on the origin of the tetrapods. In the case of two of his well known contributions, the connection with these theories is straightforward and explicit. His work on dermal temperature regulation in lizards (Cowles, 1958*a*) was an attempt to put his ideas on the evolution of fur and feathers (as they related to dinosaur extinction), and on the evolution of terrestriality in the Devonian to some empirical test. His work on hypthermia, aspermia and evolution (Cowles, 1965), which Cowles considered to be the crowning work of his career (R. B. Huey, pers. comm.) had its origin in an attempt to salvage his original theory on dinosaur extinction from Colbert's vigorous criticisms (Cowles, 1945*a, b*). Many of Cowles' less well remembered contributions also bear the stamp of these theories.

In the case of Cowles' best remembered contribution, the "Preliminary Study" (Cowles and Bogert, 1944), the connection to his theories on dinosaur extinction and the origin of the tetrapods is not so straightfoward. The "Preliminary Study" appears to be a triumph of empirical ecology (Pough, 1974; Brattstrom, 1977), and a reading of this paper by itself gives hardly a glimmer of Cowles' theorizings. In fact, Cowles' original papers outlining his theories (Cowles, 1939, 1940) are confined to a single inconspicuous citation, pointing out that ". . . the possible importance of temperature in the evolution of terrestrial vertebrates has been stressed" (Cowles and Bogert, 1944). This lack of emphasis may have been due to Bogert's influence, who regarded Cowles' speculations in the absence of more data as too adventurous (Bogert, pers. comm.). Or Cowles may have developed a sense of caution as a consequence of Colbert's criticisms of his theories. Whatever the cause for Cowles' reticence in the "Preliminary Study," his theories played an important role in both the form it eventually took in print, and perhaps even the decision to publish it. I am led to this conclusion for the following reasons.

If Cowles' popular writings on the subject are to be believed, his "serendipitous flash" occurred to him sometime during the summer of 1938. This was while he was in the "mesquite camp," early in his experiments testing the tolerances of desert reptiles to heat (Cowles and Bakker, 1977). It appears that most of the work which eventually appeared in the "Preliminary Study" was done during this bout of field work, although work done as late as 1943 also appears in the "Preliminary Study." Consequently, both Cowles' theories and the gathering of the data which later would be used in their support occurred almost simultaneously, certainly too close together to differentiate them. It would be simplistic to claim that Cowles conceived his theories and then organized his 1938 field work to gather the data necessary to support them. The same can be said of any claim that Cowles' theories followed logically from an intensive period of field observation and experiment. Rather, there seems to have occurred in 1938 an extraordinary interplay of experiment and theory; a minimal observation on temperature tolerance of desert reptiles triggered the conception of a bold theory on dinosaur extinction, which in turn led to other experiments, which themselves led to further refinements of theory. The result was that by 1940, Cowles had forged a radically new way of viewing the biology of temperature, which considered temperature as an ecological resource that could be exploited, rather than merely responded to. Reptiles no longer could be considered the slaves to their thermal environment, but rather its masters.

It is curious then that as much as five years passed between the gathering of much of the data for the "Preliminary Study," and its eventual publication. It is possible to attribute this delay to a leisurely publication schedule, in the absence of the intense "publish or perish" pressures that academics experience now. However, the fact that many of the "Preliminary Study"'s important conclusions appeared in print four to five years earlier renders this interpretation doubtful. Colbert and Bogert may have convinced Cowles by the early 1940's that his theories would not win easy acceptance. It is likely then that the decision to publish the "Preliminary Study" was motivated by the need to put the basic assumptions of his theories on a firm empirical footing. Biologists needed to be convinced that reptiles *were* more sensitive to warmth than they were to cold, and that temperature did play a dynamic and central role in their ecology. If biologists could be convinced of this, then they would have to acknowledge that adaptations for temperature and its regulation could be important in the evolution of the vertebrates. Indeed, this is the final conclusion of the "Preliminary Study."

In sifting through Cowles' writings, it is clear that we are dealing with the work of an extraordinarily creative mind. The very fact of Cowles' theory on dinosaur extinction, along with the ingenious defenses and refinements of this idea, are ample evidences of that. Yet, I am convinced that Cowles would not have brought fruit from this rash speculation had he not had other interesting character attributes. Perhaps foremost was his intensive training as a naturalist. Prior to the 1940's, biologists concerned with temperature were in the sway of arbitrary doctrines which tried to classify animals as "warm-blooded" or "homoiothermic" and "cold-blooded" or "poikilothermic." Cowles' perspective as a natural historian enabled him to see that these designations had little relevance for desert reptiles, telling us little about what the animals were doing in the "real world" (K. S. Norris, pers. comm.). However, Cowles practiced natural history with a difference. For his work on temperature, Cowles combined detailed observations of behavior with quantitative measurements of temperature. This approach enabled him to make important generalizations about thermal tolerance and temperature regulation. His field observations prompted him to think about the ways in which reptiles could control how fast their body temperatures changed. Inclusion of the dimension of time into studies of body temperature was an incisive innovation. And his field observations suggested to him possible ways for reptiles to accomplish this control and its ecological consequences. Cowles brought a perspective to natural history that was simultaneously quantitative, biophysical, physiological and ecological, which was unique among his contemporaries. Because of this, we can perhaps designate Cowles as one of the founders of physiological ecology and biophysical ecology.

Cowles was tenacious in the pursuit of an idea. He followed little threads of inquiry anywhere they happened to lead him, and he rarely hesitated where his expertise was thin (K. S. Norris, pers. comm.). This tendency perhaps accounts for some of the convoluted arguments underlying some of his ideas,