

Parental Care: The Key to Understanding Endothermy and Other Convergent Features in Birds and Mammals

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ABSTRACT: Birds and mammals share a number of features that are remarkably similar but that have evolved independently. One of these characters, endothermy, has been suggested to have played a cardinal role in avian and mammalian evolution. I hypothesize that it is parental care, rather than endothermy, that is the key to understanding the amazing convergence between mammals and birds. Endothermy may have arisen as a consequence of selection for parental care because endothermy enables a parent to control incubation temperature. The remarkable ability of many birds and mammals to sustain vigorous exercise may also have arisen as a consequence of selection for parental care because provisioning of offspring often requires sustained vigorous exercise. Because extensive parental care encompasses a wide range of behaviors, morphology, and physiology, it may be a key innovation that accounts for the majority of convergent avian and mammalian characters.

Keywords: parental care, endothermy, thermogenesis.

One of the most intriguing aspects of vertebrate evolution is the large number of morphological, physiological, and behavioral characters that mammals and birds share. The similarity of these features is so strong that it has led to the suggestion that the two groups must be closely related (Owen 1866; Gardiner 1982; Løvtrup 1985). However, fossil data indicate that birds and mammals arose independently from basal amniotes and have had separate evolution histories since the Carboniferous, approximately 340 million years ago (Gauthier et al. 1988; Lombard and Sumida 1992; Sumida 1997). Hence the shared features must be the result of convergent evolution. This pattern can result from similar selective pressures working inde-

pendently among groups and. In this article, I identify a common focus for selection that could account for this convergence: parental care.

Much previous work has attributed the similarity of birds and mammals to their both being endothermic (a thermoregulatory strategy whereby a warm body temperature is maintained in the face of a cool environmental temperature through internal heat sources). Although endothermy provides an explanation for a few of the similarities (e.g., the presence of body insulation), I propose that a better explanation is that the broad convergence is a result of selection for parental care and that endothermy is just one character among many related to parental care. Consider the limitations of previous explanations for the evolution of endothermy. Of the purported selective advantages of an endothermic metabolism, two have received the most attention: an expanded thermal niche (Crompton et al. 1978; McNab 1978; Block 1991) and the ability to sustain vigorous exercise (Regal 1975; Heinrich 1977; Bennett and Ruben 1979). Critics of the former idea have argued that small increments in metabolism incur an energy cost, whereas metabolism has to increase substantially before conferring a significant thermoregulatory advantage (Cowles 1946; Bennett and Ruben 1979), although Block has shown this is not the case in some marine fishes (Block 1991; Block and Finnerty 1994). The problem with the latter idea is that there is no mechanism that explains why endothermy would be essential to sustain vigorous exercise (Bennett and Ruben 1979; Bennett 1991; Hayes and Garland 1995). Indeed, there is no reason to think that basal metabolism is tied in a mechanistic way to activity metabolism. The elevated metabolism associated with endothermy in mammals is produced by leaky membranes in the visceral organs (Ishmail-Beigi and Edelman 1970; Else and Hulbert 1985; Hulbert 1987; Hulbert and Else 1990; Else et al. 1996). In contrast, the elevation in metabolism associated with vigorous activity is a function of the energy used by skeletal muscles to produce physical work. Thus the association of expanded thermal niche and the ability to sustain vigorous exercise with endothermy

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may not reflect the selective pressures that led to the evolution of endothermy.

The hypothesis that selection for parental care may be responsible for the convergent evolution of endothermy and other features of birds and mammals is distinct from the thermal niche and sustained activity hypotheses in several ways. First, endothermy is postulated to have evolved as a means to provide a parent with the ability to control incubation temperature through thermogenesis (the production of heat) rather than for adult thermal niche expansion or sustained vigorous exercise. With this scenario, even small increases in metabolism could potentially be favored by selection. Second, with parental care as the focus of selection, a plausible mechanism that could account for the evolution of thermogenesis exists. The initial thermogenesis of endothermy could have involved an elevation in basal (standard) metabolism that resulted from the secretion of thyroid and other hormones during the reproductive period. Third, sustained vigorous exercise is postulated to have evolved to increase a parent's ability to forage and to provision young. This would make the correlation between endothermy and sustained vigorous locomotion a consequence of selection for improved parental care rather than a causal biochemical or cellular linkage. Fourth, because extensive parental care encompasses a wide range of behaviors, morphology, and physiology, it may be a key innovation, thus providing a conceptually unifying explanation for the convergent evolution of a broad range of avian and mammalian characters.

Thermoregulation for the Purpose of Reproduction

Vertebrate embryos are adversely affected by small deviations in incubation temperature in at least four ways. First, a deviation in temperature from an optimal range, a shift that may be easily tolerated by an adult, is generally lethal for an embryo (reviewed in Packard and Packard 1988). For example, the eggs of most avian species studied cannot tolerate an exposure of several hours to temperatures outside the range of 36°–39°C (Webb 1987). Embryos of the lizards *Sceloporus undulatus* and *Iguana iguana* do not tolerate temperatures beyond the ranges of 25°–35°C and 28°–32°C, respectively (Licht and Moberly 1965; Sexton and Marion 1974). *Chelonia mydas*, *Caretta caretta*, and *Chelonia depressa* tolerate a range of approximately 25°–33°C (Bustard and Greenham 1968; Yntema and Mrosovsky 1980; Miller 1982). Crocodylian eggs generally will not hatch if mean incubation temperatures vary outside of 28°–34°C (Ferguson 1985). Second, incubation temperatures at the extremes of the viable range commonly result in developmental defects. For example, in fish both the number of vertebrae and the number of fin rays are

determined by developmental temperature of the larvae (Taning 1952). In reptiles, typical deformations that occur from developmental temperatures that deviate too greatly from the optimum are limb malformation, abnormalities of the central nervous system and eyes, loss of the lower jaw, facial clefting, abnormal formation of the vertebral column causing the loss of the tail, increased numbers of vertebrae in the trunk, and ventral hernias (Yntema 1960; Webb 1977; Webb et al. 1983; Ferguson 1985; Burger et al. 1987; Deeming and Ferguson 1991). Similar abnormalities resulting from deviation in developmental temperatures are found in birds (Romanoff 1972). Third, the thermal environment during embryonic development is a determinant of developmental period. For example, an increase in developmental temperature from 28°C to 32°C shortens the incubation period by 27 d in the lizard *Dipsosaurus dorsalis* (Muth 1980). Incubation period and timing are important because the risk of predation and disease can vary with the incubation period and timing can be important in matching hatching with seasonal food supplies. Fourth, in some ectothermic amniotes, incubation temperature influences a suite of characters that are under the control of the hypothalamus: posthatching thermal preferences, embryonic and posthatching growth rates, sex, molting cycles, pigmentation patterns, scalation, and behavior (Fox 1948; Osgood 1978; Packard and Packard 1988 and references therein; Deeming and Ferguson 1991 and references therein; Norris 1996 and references therein; O'Steen 1998). Thus, vertebrate embryos are very sensitive to temperature.

Perhaps because temperature is important during development, the ability to control temperature during reproduction has evolved independently in remarkably diverse organisms. Consider the many examples of insulation used for heat retention during reproduction. Body insulation facilitates the elevation of body temperatures above ambient temperatures in birds and mammals (feathers, hair) and in some insects (setae of gypsy moth caterpillars and pile of bumblebees; Heinrich 1979; Casey and Hegel 1981). Perhaps the most effective form of insulation found among insects is that provided by a nest (Seeley and Heinrich 1981). Ants, termites, wasps, bees, some caterpillars (that use the abandoned hives of bees), crocodylians, many mammals, and most birds make use of nests to help them control developmental temperatures (Wood 1971; Heinrich 1981; Lang 1987; Shine 1988; Clutton-Brock 1991; Hölldobler and Wilson 1994). Even without a nest, some organisms are able to cluster together and to use their own bodies as insulation for the purpose of stabilizing incubation temperature. For example, metabolic heat elevates the body temperature of clustering caterpillars, dramatically affecting their developmental rates. Caterpillars (*Vanessa urtica*) that are allowed to ag-

gregate pupate 67 h sooner than isolated siblings because of increased developmental temperature (Heinrich 1981). At night army ants form shelters with their own bodies in which the queen and eggs are placed centrally to be warmed by the metabolic heat of the group (Hölldobler and Wilson 1994). Vertebrates such as emperor penguins and mice huddle during reproduction for thermoregulation (Jouventin 1975; Heinrich 1979; Hill 1992).

In some lizards, snakes, and ants, adults provide heat to developing embryos by basking in the sun and then returning to the nest to transfer the warmth from their bodies to their young (Shine 1988; Hölldobler and Wilson 1990). Some lizards and ants also regulate developmental temperature by transferring their eggs to different depths of the nest (Shine 1988; Hölldobler and Wilson 1990). Furthermore, in lizards and snakes natural selection for females that can behaviorally control incubation temperature has been an important selective factor in the evolution of viviparity (retainment of embryos internally; Guillette et al. 1980; Guillette 1982; Shine 1985, 1989). Apparently there is strong selection for this trait, as viviparity has evolved independently approximately 100 times within squamate reptiles (lizards and snakes; Shine 1991).

Most significantly, thermogenesis is used in a wide variety of animals to elevate incubation temperature above ambient temperature. For example, among insects this capacity has evolved independently in honey bees, bumblebees, vespine wasps, and the European hornet *Vespa crabro* (Heinrich 1979; Seeley and Heinrich 1981). Most birds and all mammals incubate their embryos with thermogenesis and are able to increase their rates of thermogenesis to maintain appropriate incubation temperatures. For example, when incubating, an adult zebra finch is capable of more than doubling its metabolic rate if the surface temperature of the eggs cools (Vleck 1981). Mammals can also increase their heat production during reproduction (e.g., tenrecs, sloths; Dawson 1973 and references therein; Nicoll and Thompson 1987; Stephenson and Racey 1993; Poppit et al. 1994 and references therein). To direct efficiently the heat of thermogenesis straight onto the eggs, both birds and bumblebees have evolved a strikingly similar incubation patch. Both groups have an area on the abdomen that contains a specialized circulatory system and that is free of insulation. This incubation patch is placed next to the eggs to warm them (Heinrich 1979). The one squamate reptile (python) that is known to produce heat by shivering uses the heat specifically for egg incubation (Van Mierop and Barnard 1978; Shine 1989). An analogous system for embryo incubation found in some crocodylians and megapode birds is the use of heat produced by bacteria during the decomposition of organic matter to keep their eggs warm (Lang 1987; Jones et al. 1995).

In summary, incubation temperature influences embryo survival, developmental defects, the length of the developmental period, and (in some amniotes) a suite of characters controlled by the hypothalamus. A wide variety of species have independently evolved mechanisms that facilitate control of temperature during development. In at least seven groups (honey bees, bumblebees, vespine wasps, the European hornet, birds, mammals, pythons) thermogenesis is used for embryo incubation. Hence, there is a large data set to suggest that the initial selective advantage of thermogenesis in birds and mammals may have been to better control developmental temperature.

A Mechanism Linking Thermogenesis to Reproduction

A plausible mechanism exists that could account for the evolution of nonshivering thermogenesis in birds and mammals. The initial thermogenesis of endothermy could have involved an elevation in basal (standard) metabolism (and therefore thermogenesis) as a result of the secretion of thyroid and other hormones during the reproductive period. Early in the evolution of vertebrates, thyroid hormones were probably important primarily in reproduction, especially in gonadal maturation (Sage 1973). Importantly, thyroid cycles are positively correlated with reproductive cycles in most vertebrates (Sage 1973; Bonagallo et al. 1980). In some vertebrates (e.g., birds), thyroid hormones function to mobilize lipids for vitellogenesis; they affect egg weight and shell thickness as well as the laying sequence and the number of eggs laid (Sturkie 1986). In addition to functioning in reproduction, in amniotes, thyroid hormones are also involved in control of basal (standard) metabolism and thermogenesis (Sage 1973; Sturkie 1986; Hulbert and Else 1990; Silva 1995; Else et al. 1996; Norris 1996). In light of the dual role of hormones in reproduction and thermogenesis, it is not surprising to find that metabolism is fundamentally altered during reproductive periods. For example, basal (standard) metabolic rates increase during reproduction in humans, tenrecs, short-tailed opossums, elephant shrews, snakes, and lizards (Van Mierop and Barnard 1978; Guillette 1982; Birchard et al. 1983; Thompson and Nicoll 1986; Prentice and Whitehead 1987; Forsum et al. 1988; Guyton and Hall 1996; Butte et al. 1999).

Not only do some amniotes increase their thermogenic abilities during reproductive periods, but the temperature set points of the hypothalamus and thermoregulation are also altered at this time. For example, nonreproductive pythons are ectothermic, and when subjected to a cold stress, body temperature decreases with the ambient temperature. In contrast, gravid or brooding pythons are endothermic; when subjected to cold they maintain elevated body temperature through internal heat sources (Van

Mierop and Barnard 1978). During reproduction viviparous garter snakes behaviorally regulate body temperatures at higher mean body temperatures (Charland 1995), and viviparous rattlesnakes change their behavior to decrease body temperature fluctuations, whereas nonpregnant females do not (Charland and Gregory 1990). Similarly, pregnant lizards change their mean body temperature and regulate more carefully to decrease body-temperature fluctuations, whereas nonpregnant individuals do not (Beuchat 1986 and references therein). Numerous data indicate that heterothermic birds and mammals, whose body temperatures can depend largely on ambient temperature, alter their body temperature set points and thermogenic abilities when brooding and during pregnancy. For example, although hummingbirds generally become torpid at night to save energy, incubating females normally maintain endothermic homeothermy, even when nighttime temperatures dip to near freezing (Calder 1971 and references therein). Pregnancy in tenrecs causes elevated metabolic rate, increased mean body temperature, increased thermogenic ability, and decreased body temperature fluctuations with the ambient temperature (i.e., improved endothermy; Nicoll and Thompson 1987; Stephenson and Racey 1993; Poppit et al. 1994). Although sloths have a low potential for heat production and inferior ability to thermoregulate compared to most other mammals, pregnancy enhances their thermoregulatory abilities (Dawson 1973 and references therein). Similarly, pregnant bats maintain higher mean body temperatures and reduce the time spent in torpor, whereas nonpregnant and male bats do not (Audet and Fenton 1988; Hamilton and Barclay 1994). Torpor is less likely in pregnant than nonpregnant hedgehogs (Fowler 1988). Although dormant and hibernating, pregnant bears maintain a warm body temperature. Black bears maintain a body temperature of 30°C or higher, and pregnant polar bears do not drop their body temperature by $>2^{\circ}$ C (Watts and Hansen 1987). Thus, it appears that high metabolic rates and warm body temperatures are either advantageous or essential during reproduction in mammals and birds (Thompson and Nicoll 1986; Nicoll and Thompson 1987).

The sequence of events that led to thermogenesis for the sake of embryo incubation could have been as simple as a continued elevation of thyroid hormones or other reproductive hormones that increase metabolism after oviposition in a species in which a female guarded her nest. Keep in mind the important role thyroid hormones play in gonadal maturation, vitellogenesis, in determining egg weight and shell thickness (Sage 1973; Sturkie 1986) and the effect of thyroid hormones on metabolism in adult vertebrates (Sage 1973; Sturkie 1986; Hulbert and Else 1990; Silva 1995; Else et al. 1996; Norris 1996). The heat produced from the elevated metabolism could then have

benefited embryonic development because of the close proximity of the female to her eggs. This scenario could be corroborated by identifying and monitoring the hormones that control reproduction and thermogenesis in those heterothermic mammals that alter their thermogenic abilities during reproduction (e.g., tenrecs) as well as in the facultative endotherms (e.g., pythons) and by comparing their hormone profiles to those of closely related ectotherms.

Provisioning Offspring with Warmth and Nutrition Requires Sustained Vigorous Exercise

In addition to selection for parental care leading to the convergent evolution of endothermy in birds and mammals, selection for parental care also offers an explanation for many other convergences found in these groups. One similarity that has received a great deal of attention is the ability of birds and mammals to sustain vigorous exercise (endurance; Pough 1980). To sustain vigorous exercise ATP must be synthesized at high rates through aerobic pathways. This, in turn, requires many specialized morphological features that function in the oxygen cascade (Weibel 1984; Perry 1993; Farmer 1999; Hicks and Farmer 1999). It is widely assumed that the capacity to sustain vigorous exercise entails a maintenance cost for this specialized machinery in the form of a high basal metabolic rate and an endothermic thermoregulatory physiology (Regal 1975; Heinrich 1977; Bennett and Ruben 1979; Pough 1980). Although in amniotes a broad correlation does exist between an endothermic physiology and an exceptional ability to sustain vigorous exercise, a cause and effect relationship has never been established (Bennett and Ruben 1979; Bennett 1991; Hayes and Garland 1995).

Another explanation for the "correlation" between endothermy and the ability to sustain vigorous exercise is that they have a common cause: parental care. While endothermy may have evolved to maintain a constant incubation temperature for developing embryos, vigorous sustained exercise may have evolved to enable parents to secure the resources they need to warm and to feed developing young. Procuring food for offspring is a major facet of parental care in all mammals and for the majority of birds. There are several advantages to providing offspring with food. First, adults can make use of food sources that are unavailable to juveniles either because they cannot digest them or because they cannot obtain them for lack of adult strength and skill (Pond 1977; Ricklefs 1979). For example, ontogenetic limitations in wing growth appear to play a role in determining fledging time in birds and to constrain flight in hatchling and young birds (Carrier and Auriemma 1992). Therefore, juveniles cannot use flight to forage on their own, and food obtained by this

means must be provided by an adult. Second, there is an inverse relationship between growth rate and mature locomotor function; the young of altricial birds grow three- to four fold faster than those of precocial birds because altricial offspring are able to devote a greater percentage of their energy budget to growth rather than to maintenance (Ricklefs 1979). Since predation rates are often many fold higher in juveniles than in adults, natural selection may favor mechanisms that reduce the time spent in the vulnerable juvenile period (Williams 1966). Therefore, parents may increase the fitness of their offspring by providing food to them because this enables offspring to devote a greater percentage of their energy budget to growth rather than to maintenance and decreases the time spent in the dangerous juvenile life-history stage.

Although there are clearly advantages to parental provisioning of offspring, it requires that parents obtain extra food. For example, to feed their young, avian parents generally need to obtain from three- to five-fold more energy than nonreproductive adults and must therefore increase foraging efforts (Walsberg 1983). These foraging efforts are often staggering. When gathering food for offspring the common swift of Europe flies $1,000 \text{ km d}^{-1}$. The great tit makes about 990 trips to the nest in a single day to feed its young. To raise a brood from hatching to fledging, the European pied flycatcher makes approximately 6,200 foraging trips (Gill 1995). Energy demands on reproductive mammals are no less impressive. Lactation in mammals can increase the mean daily energy requirements severalfold over nonreproductive individuals (from 400% to >1,000% of the basal metabolic rate); hence lactating females often increase foraging efforts (Lee and Cockburn 1985; Clutton-Brock 1991; Thompson 1992; Rydell 1993). Thus, it is not unreasonable to suggest that the extra energy expense incurred by this parental feeding of offspring is of sufficient magnitude to cause selection for an increased ability to sustain vigorous exercise.

An ability to sustain vigorous exercise requires high rates of transport of oxygen and carbon dioxide between the atmosphere and the metabolically active skeletal muscles. The lineages that gave rise to birds and mammals independently evolved a similar suite of characters that facilitate their high aerobic capacity. Both groups share anatomical features, such as parasagittal limb posture, that enable high rates of minute ventilation during locomotion (Carrier 1987*a*, 1987*b*), a large pulmonary diffusion capacity (Perry 1983, 1989, 1993; Weibel 1984), high oxygen-carrying capacity of the blood (Snyder and Sheafor 1999), a large tissue diffusion capacity (Weibel 1984), a completely divided cardiac ventricle (Goodrich 1930), an extensive coronary circulation and compact myocardium (Farmer 1997, 1999), high systemic blood pressure (Johansen 1972), and a single aorta (Goodrich

1930). The convergent evolution of these characters may be due, at least in part, to selection for an ability to sustain vigorous exercise, which is requisite for birds and mammals to provision their offspring.

The ability to sustain vigorous exercise is linked with many ecological, behavioral, and morphological factors (Taigen et al. 1982). Consequently, such things as food source and distribution, conspecific competition for mates, predator-prey interactions, and migratory patterns may also be related to patterns of aerobic-exercise metabolism. Although factors besides parental care may have played a contributing role in the evolution of the features that enable sustained vigorous exercise, parental provisioning of offspring is one of the most distinct differences between ectothermic and endothermic amniotes. Therefore, hypotheses aimed at understanding why birds and mammals are generally better at sustaining vigorous exercise than ectotherms should consider the extra energy expense incurred by parental warming and feeding of offspring.

Broader Implications

Extensive parental care is central to the biology of both birds and mammals. It is a key innovation in these groups. Although this article has been restricted to a discussion of how parental care could account for the evolution of mammalian and avian endothermy and the ability to sustain vigorous exercise, many other convergent features may also be explained by this reproductive strategy. Parental care requires parent-offspring interaction and gives rise to complex social structures (Pond 1977). Furthermore, vocal signaling is an important component of these parent-offspring interactions (Walser 1997 and references therein; Bradbury and Vehrencamp 1998). Hence, I suggest the exceptionally keen hearing and vocal communication that is found in archosaurs and mammals (Wever 1978; Fay and Popper 1985) may have been influenced by parental care. Extensive parental care is multifaceted and therefore has the potential to provide a conceptually unifying explanation for more of the convergent features of mammals and birds than any other single hypothesis proposed to date.

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Literature Cited

- Audet, D., and M. B. Fenton. 1988. Heterothermy and the use of torpor by the bat *Eptesicus fuscus* (Chiroptera: Vespertilionidae): a field study. *Physiological Zoology* 61:197–204.
- Bennett, A. F. 1991. The evolution of activity capacity. *Journal of Experimental Biology* 160:1–23.
- Bennett, A. F., and J. A. Ruben. 1979. Endothermy and activity in vertebrates. *Science (Washington, D.C.)* 206:649–654.
- Beuchat, C. A. 1986. Reproductive influences on the thermoregulatory behavior of a live-bearing lizard. *Copeia* 1986:971–979.
- Birchard, G. F., C. P. Black, G. W. Schuett, and V. Black. 1983. Influence of pregnancy on oxygen consumption, heart rate and hematology in the garter snake: implications for the “cost of reproduction” in live bearing reptiles. *Comparative Biochemistry and Physiology* 77A:519–523.
- Block, B. A. 1991. Endothermy in fish: thermogenesis, ecology and evolution. Pages 269–311 in P. W. Hochachka and T. P. Mommsen, eds. *Biochemistry and molecular biology of fishes*. Vol. 1. Elsevier, New York.
- Block, B. A., and J. R. Finnerty. 1994. Endothermy in fishes: a phylogenetic analysis of constraints, predispositions, and selection pressures. *Environmental Biology of Fishes* 40:283–302.
- Bona-Gallo, A., P. Licht, D. S. MacKenzie, and B. Lofts. 1980. Annual cycles in levels of pituitary and plasma gonadotropin, gonadal steroids, and thyroid activity in the Chinese cobra (*Naja naja*). *General and Comparative Endocrinology* 42:477–493.
- Bradbury, J. W., and S. L. Vehrencamp. 1998. *Principles of animal communication*. Sinauer, Sunderland, Mass.
- Burger, J., R. T. Zappalorti, and M. Gochfeld. 1987. Developmental effects of incubation temperature on hatchling pine snakes *Pituophis melanoleucus*. *Biochemistry and Physiology* 87A:727–732.
- Bustard, H. R., and P. Greenham. 1968. Physical and chemical factors affecting hatching in the green sea turtle, *Chelonia mydas* (L.). *Ecology* 49:269–276.
- Butte, N. F., J. M. Hopkinson, N. Mehta, J. K. Moon, and E. O. Smith. 1999. Adjustments in energy expenditure and substrate utilization during late pregnancy and lactation. *American Journal of Clinical Nutrition* 69:299–307.
- Calder, W. A. 1971. Temperature relationships and nesting of the calliope hummingbird. *Condor* 73:314–321.
- Carrier, D. R. 1987a. The evolution of locomotor stamina in tetrapods: circumventing a mechanical constraint. *Paleobiology* 13:326–341.
- . 1987b. Lung ventilation during walking and running in four species of lizards. *Experimental Biology* 47:33–42.
- Carrier, D. R., and J. Auriemma. 1992. A developmental constraint on the fledging time of birds. *Biological Journal of the Linnean Society* 47:61–77.
- Casey, T. M., and J. R. Hegel. 1981. Caterpillar setae: insulation for an ectotherm. *Science (Washington, D.C.)* 214:1131–1133.
- Charland, M. B. 1995. Thermal consequences of reptilian viviparity: thermoregulation in gravid and nongravid garter snakes (*Thamnophis*). *Journal of Herpetology* 29:383–390.
- Charland, M. B., and P. T. Gregory. 1990. The influence of female reproductive status on thermoregulation in a viviparous snake (*Crotalus viridis*). *Copeia* 4:1089–1098.
- Clutton-Brock, T. H. 1991. *The evolution of parental care*. Princeton University Press, Princeton, N.J.
- Cowles, R. B. 1946. Fur and feathers: a result of high temperatures? *Science (Washington, D.C.)* 103:74–75.
- Crompton, A. W., C. R. Taylor, and J. A. Jagger. 1978. Evolution of homeothermy in mammals. *Nature (London)* 272:333–272.
- Dawson, T. J. 1973. “Primitive” mammals. Pages 1–46 in G. C. Whitrow, ed. *Comparative physiology of thermoregulation*. Vol. 3. Special aspects of thermoregulation. Academic Press, New York.
- Deeming, D. C., and M. W. J. Ferguson. 1991. Physiological effects of incubation temperature on embryonic development in reptiles and birds. Pages 147–171 in D. C. Deeming and M. W. J. Ferguson, eds. *Egg incubation: its effects on embryonic development in birds and reptiles*. Cambridge University Press, Cambridge.
- Else, P., D. J. Windmill, and V. Markus. 1996. Molecular activity of sodium pumps in endotherms and ectotherms. *American Journal of Physiology* 271:R1287–R1294.
- Else, P. L., and A. J. Hulbert. 1985. An allometric comparison of the mitochondria of mammalian and reptilian tissues: the implications for the evolution of endothermy. *Journal of Comparative Physiology B* 156:3–11.
- Farmer, C. 1997. Did lungs and the intracardiac shunt evolve to oxygenate the heart in vertebrates? *Paleobiology* 23:358–372.
- Farmer, C. G. 1999. The evolution of the vertebrate cardiopulmonary system. *Annual Review of Physiology* 61:573–592.
- Fay, R. R., and A. N. Popper. 1985. The octavolateralis system. Pages 291–316 in M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake, eds. *Functional vertebrate morphology*. Belknap, Cambridge, Mass.
- Ferguson, M. W. J. 1985. The reproductive biology and embryology of crocodylians. Pages 329–491 in C. Gans,

- F. Billet, and P. F. A. Maderson, eds. *Biology of the reptilia: development A*. Vol. 14. Wiley, New York.
- Forsum, E., A. Sadurskis, and J. Wager. 1988. Resting metabolic rate and body composition of healthy Swedish women during pregnancy. *American Journal of Clinical Nutrition* 47:942–947.
- Fowler, P. A. 1988. Thermoregulation in the female hedgehog, *Erinaceus europaeus*, during the breeding season. *Journal of Reproductive Fertility* 82:285–292.
- Fox, W. 1948. Effect of temperature on development of scutellation in the garter snake, *Thamnophis elegans atratus*. *Copeia* 1948:252–262.
- Gardiner, B. 1982. Tetrapod classification. *Zoological Journal of the Linnean Society* 74:207–232.
- Gauthier, J., A. G. Kluge, and T. Rowe. 1988. Amniote phylogeny and the importance of fossils. *Cladistics* 4: 105–207.
- Gill, F. B. 1995. *Ornithology*. W. H. Freeman, New York.
- Goodrich, E. S. 1930. *Studies on the structure and development of vertebrates*. Macmillan, London.
- Guillette, L. J., Jr. 1982. The evolution of viviparity and placentation in the high elevation, Mexican lizard *Sceloporus aeneus*. *Herpetology* 38:94–103.
- Guillette, L. J., Jr., R. E. Jones, K. T. Fitzgerald, and H. M. Smith. 1980. Evolution of viviparity in the lizard genus *Sceloporus*. *Herpetology* 36:201–215.
- Guyton, A. C., and J. E. Hall. 1996. *Textbook of medical physiology*. 9th ed. Saunders, Philadelphia.
- Hamilton, I. M., and R. M. R. Barclay. 1994. Patterns of daily torpor and day-roost selection by male and female big brown bats (*Eptesicus fuscus*). *Canadian Journal of Zoology* 72:744–749.
- Hayes, J. P., and T. G. Garland. 1995. The evolution of endothermy: testing the aerobic capacity model. *Evolution* 49:836–847.
- Heinrich, B. 1977. Why have some animals evolved to regulate a high body temperature? *American Naturalist* 111:623–639.
- . 1979. *Bumblebee economics*. Harvard University Press, Cambridge, Mass.
- . 1981. Ecological and evolutionary perspectives. Pages 235–302 in B. Heinrich, ed. *Insect thermoregulation*. Wiley, New York.
- Hicks, J. W., and C. G. Farmer. 1999. Gas exchange potential in reptilian lungs: implications for the dinosaur-avian connection. *Respiration Physiology* 117:78–83.
- Hill, R. W. 1992. The altricial/precocial contrast in the thermal relations and energetics of small mammals. Pages 122–159 in T. E. Tomasi and T. H. Horton, eds. *Mammalian energetics: interdisciplinary views of metabolism and reproduction*. Comstock, Ithaca, N.Y.
- Hölldobler, B., and E. O. Wilson. 1990. *The ants*. Belknap, Cambridge, Mass.
- . 1994. *Journey to the ants*. Harvard University Press, Cambridge, Mass.
- Hulbert, A. J. 1987. Thyroid hormones, membranes and the evolution of endothermy. Pages 305–319 in H. McLennan, J. R. Ledsome, C. H. S. McIntosh, and D. R. Jones, eds. *Advances in physiological research*. Plenum, New York.
- Hulbert, A. J., and P. L. Else. 1990. The cellular basis of endothermic metabolism: a role for “leaky” membranes? *News in Physiological Sciences* 5:25–28.
- Ishmail-Beigi, F., and I. S. Edelman. 1970. Mechanism of thyroid calorigenesis: role of active sodium transport. *Proceedings of the National Academy of Sciences of the USA* 67:1071–1078.
- Johansen, K. 1972. Heart and circulation in gill, skin and lung breathing. *Respiration Physiology* 14:193–210.
- Jones, D. N., R. W. R. J. Dekker, and C. S. Roselaar. 1995. *The megapodes: Megapodiidae*. Oxford University Press, Oxford.
- Jouventin, P. 1975. Mortality parameters in emperor penguins *Aptenodytes forsteri*. Pages 435–446 in B. Stonehouse, ed. *The biology of penguins*. Macmillan, London.
- Lang, J. W. 1987. Crocodilian behavior: implications for management. Pages 273–300 in G. J. W. Webb, S. C. Manolis, and P. J. Whitehead, eds. *Wildlife management: crocodiles and alligators*. Surrey, Beatty, Chipping Norton.
- Lee, A. K., and A. Cockburn. 1985. *Evolutionary ecology of marsupials*. Cambridge University Press, Cambridge.
- Licht, P., and W. R. Moberly. 1965. Thermal requirements for embryonic development in the tropical lizard *Iguana iguana*. *Copeia* 1965:515–517.
- Lombard, R. E., and S. S. Sumida. 1992. Recent progress in understanding early tetrapods. *American Zoologist* 32:609–622.
- Løvtrup, S. 1985. On the classification of the taxon Tetrapoda. *Systematic Zoology* 34:463–470.
- McNab, B. K. 1978. The evolution of homeothermy in the phylogeny of mammals. *American Naturalist* 112:1–21.
- Miller, J. D. 1982. *Embryology of marine turtles*. Ph.D. diss. University of New England, Biddeford, Maine.
- Muth, A. 1980. Physiological ecology of desert iguana (*Dipsosaurus dorsalis*) eggs: temperature and water relations. *Ecology* 61:1335–1343.
- Nicoll, M. E., and S. D. Thompson. 1987. Basal metabolic rates and energetics of reproduction in therian mammals: marsupials and placentals compared. *Symposia of the Zoological Society of London* 57:7–27.
- Norris, D. O. 1996. *Vertebrate endocrinology*. Academic Press, San Diego, Calif.
- Osgood, D. W. 1978. Effects of temperature on the development of meristic characters in *Natrix fasciata*. *Copeia* 1978:33–37.

- O'Steen, S. 1998. Embryonic temperature influences juvenile temperature choice and growth rate in snapping turtles *Chelydra serpentina*. *Journal of Experimental Biology* 201:439–449.
- Owen, R. 1866. *On the anatomy of vertebrates*. Longman, London.
- Packard, G. C., and M. J. Packard. 1988. The physiological ecology of reptilian eggs and embryos. Pages 523–605 in C. Gans and R. B. Huey, eds. *Biology of the reptilia: defense and life history*. Vol. 16. Ecology B. Liss, New York.
- Perry, S. F. 1983. *Reptilian lungs: functional anatomy and evolution*. Springer, Berlin.
- . 1989. Structure and function of the reptilian respiratory system. Pages 193–236 in S. C. Wood, ed. *Comparative pulmonary physiology: current concepts*. Dekker, New York.
- . 1993. Evolution of the lung and its diffusion capacity. Pages 142–153 in J. E. Bicudo, ed. *The vertebrate cascade: adaptations to environment and mode of life*. CRC, Boca Raton, Fla.
- Pond, C. 1977. The significance of lactation in the evolution of mammals. *Evolution* 31:177–199.
- Poppit, S. D., J. R. Speakman, and P. A. Racey. 1994. Energetics of reproduction in the lesser hedgehog Tenrec, *Echinops telfairi* (Martin). *Physiological Zoology* 67: 967–994.
- Pough, F. H. 1980. The advantages of ectothermy for tetrapods. *American Naturalist* 115:92–112.
- Prentice, A. M., and R. G. Whitehead. 1987. The energetics of human reproduction. Pages 275–304 in A. S. I. London and P. A. Racey, eds. *Symposia of the zoological society of London*. Vol. 57. Clarendon, Oxford.
- Regal, P. J. 1975. The evolutionary origin of feathers. *Quarterly Review of Biology* 50:35–66.
- Ricklefs, R. E. 1979. Adaptation, constraint, and compromise in avian postnatal development. *Biological Reviews* 54:269–290.
- Romanoff, A. L. 1972. *Pathogenesis of the avian embryo*. Wiley-Interscience, New York.
- Rydell, J. 1993. Variation in foraging activity of an aerial insectivorous bat during reproduction. *Journal of Mammalogy* 74:503–509.
- Sage, M. 1973. The evolution of thyroïdal function in fishes. *American Zoologist* 13:899–905.
- Seeley, T., and B. Heinrich. 1981. Regulation of temperature in the nests of social insect. Pages 159–234 in B. Heinrich, ed. *Insect thermoregulation*. Wiley, New York.
- Sexton, O. J., and K. R. Marion. 1974. Duration of incubation of *Sceloporus undulatus* eggs at constant temperature. *Physiological Zoology* 47:91–98.
- Shine, R. 1985. The evolution of reptilian viviparity: an ecological analysis. Pages 605–694 in C. Gans and F. Billett, eds. *Biology of the reptilia*. Vol. 15. Development. Wiley, New York.
- . 1988. Parental care in reptiles. Pages 275–329 in C. Gans and R. B. Huey, eds. *Biology of the reptilia: defense and life history*. Vol. 16. Ecology B. Liss, New York.
- . 1989. Ecological influences on the evolution of vertebrate viviparity. Pages 263–278 in D. B. Wake and G. Roth, eds. *Complex organismal functions: integration and evolution in vertebrates*. Wiley, Chichester.
- . 1991. Influence of incubation requirements on the evolution of viviparity. Pages 361–369 in D. C. Deeming and M. W. J. Ferguson, eds. *Egg incubation: its effects on embryonic development in birds and reptiles*. Cambridge University Press, Cambridge.
- Silva, J. E. 1995. Thyroid hormone control of thermogenesis and energy balance. *Thyroid* 5:481–492.
- Snyder, G. K., and B. A. Sheafor. 1999. Red blood cells: centerpiece in the evolution of the vertebrate circulatory system. *American Zoologist* 39:189–198.
- Stephenson, P. J., and P. A. Racey. 1993. Reproductive energetics of the Tenrecidae (Mammalia: Insectivory). I. The large-eared tenrec, *Geogale aurita*. *Physiological Zoology* 66:643–663.
- Sturkie, P. D. 1986. *Avian physiology*. 4th ed. Springer, New York.
- Sumida, S. S. 1997. Locomotor features of taxa spanning the origin of amniotes. Pages 353–398 in S. S. Sumida and K. L. M. Martin, eds. *Amniote origins*. Academic Press, San Diego, Calif.
- Taigen, T. L., S. B. Emerson, and F. H. Pough. 1982. Ecological correlates of anuran exercise physiology. *Oecologia (Berlin)* 52:49–56.
- Taning, A. V. 1952. Experimental study of meristic characters in fishes. *Biological Reviews* 27:169–193.
- Thompson, S. D. 1992. Gestation and lactation in small mammals: basal metabolic rate and the limits of energy use. Pages 213–259 in T. E. Tomasi and T. H. Horton, eds. *Mammalian energetics: interdisciplinary views of metabolism and reproduction*. Comstock, Ithaca, N.Y.
- Thompson, S. D., and M. E. Nicoll. 1986. Basal metabolic rate and energetics of reproduction in therian mammals. *Nature (London)* 321:690–693.
- Van Mierop, L. H. S., and S. M. Barnard. 1978. Further observations on thermoregulation in the brooding female *Python molurus bivittatus* (Serpentes: Boidae). *Copeia* 1978:615–621.
- Vleck, C. M. 1981. Energetic cost of incubation in the zebra finch. *Condor* 83:229–237.
- Walsberg, G. E. 1983. Avian ecological energetics. Pages 161–220 in D. S. Farner, J. R. King, and K. C. Parkes, eds., *Avian biology*. Vol. 7. Academic Press, New York.
- Walser, E. S. 1977. Maternal behavior in mammals. Pages

- 313–331 in M. Peaker, ed. Symposia of the Zoological Society of London. Vol. 41. Academic Press, London.
- Watts, P. D., and S. E. Hansen. 1987. Cyclic starvation as a reproductive strategy in the polar bear. *Zoological Society of London* 57:305–318.
- Webb, D. R. 1987. Thermal tolerance of avian embryos: a review. *Condor* 89:874–898.
- Webb, G. J. W. 1977. Abnormalities of incubation temperature in the estuarine crocodile *Crocodylus porosus*. *Australian Wildlife Research* 4:311–319.
- Webb, G. J. W., G. C. Sack, R. Buckworth, and S. C. Manolis. 1983. An examination of *Crocodylus porosus* nests in two northern Australian freshwater swamps, with an analysis of embryo mortality. *Australian Wildlife Research* 10:311–319.
- Weibel, E. R. 1984. The pathway for oxygen. Harvard University Press, Cambridge, Mass.
- Wever, E. G. 1978. The reptile ear. Princeton University Press, Princeton, N.J.
- Williams, G. C. 1966. Adaptation and natural selection. Princeton University Press, Princeton, N.J.
- Wood, L. 1971. Termites and soils. Academic Press, London.
- Yntema, C. L. 1960. Effects of various temperatures on the embryonic development of *Chelydra serpentina*. *Anatomical Record* 136:305–306.
- Yntema, C. L., and N. Mrosovsky. 1980. Sexual differentiation in hatchling loggerheads (*Caretta caretta*) incubated at different controlled temperatures. *Canadian Journal of Zoology* 60:1012–1016.

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