CAROLINE M. POND

PARENTAL FEEDING AS A DETERMINANT OF ECOLOGICAL RELATIONSHIPS IN MESOZOIC TERRESTRIAL ECOSYSTEMS

POND, C. M.: Parental feeding as a determinant of ecological relationships in Mesozoic terrestrial ecosystems. Acta Palaeontologica Polonica, 28, 1—2, 215—224, 1983.

The comparative physiology of living mammals strongly suggests that lactation was an early and fundamental feature of mammals. Because the young are fed on the mother's body secretions, supplying food to the neonates can be much more independent of the available food resources than is the case for reptiles or for birds, whose parents must find food for them in the immediate environment.

Mammals are therefore particularly well suited to breeding in environments in which there is insufficient diversity of food available to support a breeding population of large birds or large reptiles. Mammals also sustain a very high rate of postnatal growth, because it is the larger and more experienced parents which are doing most of the work to obtain the food which supports the growth of the young. The interval between conception and sexual maturity is very short in many mammals, very much shorter than the same interval for reptiles and most birds.

It is concluded that current thinking about the ecological relationships between Mesozoic mammals, birds and reptiles may place too much emphasis on endothermy and viviparity, and not enough emphasis on lactation and other forms of parental feeding.

K e y   w o r d s: lactation, parental feeding, reproductive habit, colonizing species, energy storage, growth rate, reptiles, mammals, Mesozoic.

Caroline M. Pond, Department of Biology, The Open University, Walton Hall, Milton Keynes, MK7 6AA, Bucks, England. Received: November 1981.

INTRODUCTION

For the first two thirds of their history, mammals were small, dainty creatures, living in a world dominated by much larger reptiles. The Permian ancestors of mammals, the diadectomorphs and *Dimetrodon* were of moderate size, up to about 170 Kg, but from the middle Triassic onwards therapsids and mammals became smaller and most of the large terrestrial vertebrates were reptiles. This situation persisted — the reptiles became larger but the mammals remained small throughout the

Cretaceous. The fact that Jurassic and Cretaceous mammals were small does not necessarily mean that they were also rare. Mammalian fossils from these periods are widely distributed (Clemens et al. 1979).

Physiologists have recently joined palaeontologists in a lively discussion about why large reptiles were so prevalent in the Mesozoic fauna, but are comparatively insignificant in the Cenozoic. Most of the discussion has focussed upon only one physiological difference between mammals and reptiles — the fact that the former are mostly endothermic, while the latter are ectothermic. All the discussion of metabolic differences between mammals and reptiles has tended to direct attention away from another difference between the two groups — their mode of reproduction. The aim of this paper is to outline some important features of reptilian and mammalian reproduction and to emphasize how the reproductive habits can be related to differences in energy storage, energy metabolism, and ecological habit.

Although reptiles are structurally very diverse as adults, the anatomy of the egg and physiology of early development is remarkably uniform in all living members of the Class. Animals as varied in structure and ancestry as snakes, turtles, and crocodiles lay large, yolky, shelled eggs which hatch into a juvenile similar in form to the adult. The few ovoviviparous species are clearly derived from this primitive condition. Some crocodilians and squamates guard the nest and newly-hatched young, but no living reptile brings food to the nest. Once their yolk sac is exhausted young reptiles must forage for themselves, and because the young of large species are so much smaller than their parents, their diet is necessarily different. For example, newly hatched crocodiles have hardly an item of diet in common with large adults; the young take food of gradually increasing size, starting with insects, crustaceans and amphibians and may be more than 10 years old before they share the same food supply as their parents (Cott 1961).

There is no reason to suggest that the mode of reproduction of Mesozoic reptiles was fundamentally different to that of living forms. Several species are known to have laid eggs in nests (Kielan-Jaworowska and Dovchin 1969) and to have had juveniles which moved about (and hence were presumably feeding) independently of the adults (Currie 1983). Young Mesozoic reptiles probably also had diets different from that of their parents. So like living crocodilians and big snakes, a breeding population could only become established in a habitat in which food for all growth stages was available.

Mammals are different; all living mammals, including the most primitive, provide food for the newborn or newly hatched young, either secreted from their own tissues, as in lactation, or by bringing suitable food to the nest and processing it in such a way that it is readily chewed and digested by the juveniles. The evolution of lactation must have

preceded the evolution of viviparity. The egg-laying monotremes lactate heavily; in the case of the duckbilled platypus, the mother supplies all necessary nutrients in the form of milk to the young which remain in the nest until they are more than half grown (Griffiths 1978). There is every reason to believe that lactation, and possibly other forms of parental care, are an early and fundamental character of mammals, probably evolving during the Triassic.

Thus comparative physiology and palaeontology are consistent with the assumption that the reproductive habits of Mesozoic mammals and reptiles were similar to that of 'typical' mammals and 'typical' reptiles of the present day. It is not necessary to postulate major physiological differences between living and Mesozoic representatives of the same Class, as those who place emphasis on temperature regulation and exercise physiology have found it necessary to do. The physiology and ecology of living reptiles and living mammals can therefore be compared directly with that of Mesozoic members of these Classes.

GROWTH OF THE YOUNG

Even in climates in which it is warm throughout the year, modern reptiles grow quite slowly (Bakker 1980). The growth rate depends upon quantity and quality of food available as well as on temperature, but even under optimum conditions it seems to take a herbivorous gopher tortoise about 3 years to reach breeding size at 1 Kg, and carnivorous crocodiles about 10 years to grow 50 Kg. The interval between conception and sexual maturity can be very much shorter in mammals, as little as three months in the case of some small rodents, and only about one year for many medium-sized ungulates and carnivores (Pond 1977). The difference is not due to the fact that newly born mammalian babies are particularly large; when viviparous mammals and viviparous reptiles are compared it is found that the ratio of the weight of the clutch at birth to the mother's weight is higher in some reptiles than in mammals (see Pond 1977: Table 3). Some snakes and chameleon lizards give birth to broods up to 50% of the mother's weight, but the largest recorded clutch size in mammals is 38% of the mother's weight and the majority are 5—20% of the mother's weight. Nor do mammals have particularly short gestation times; the growth of mammals *in utero* is often surprisingly slow, particularly when the high, constant body temperature is taken into account. In humans for example, it takes about 9 months to produce a 4.5 Kg infant, an average rate of 0.5 Kg per month, which is less than 1% per month increase in the mother's weight. The habit of parental feeding alters the ecological requirements for reproduction in some very

important ways. Its effect on the young is to relieve the newborn mammal is the need to find, subdue, masticate and digest its own food until it is weaned. The young can rely upon a more or less constant food supply which is free from chemical and bacterial contaminants does not need to be chewed is a balanced diet and is easy to digest. As far as its feeding and digestive organs are concerned it can continue to grow in an embryonic manner for some weeks after birth. This may be particularly important for hard tissues such as the teeth which depend upon the exact apposition of the jaws for their proper function.

In many mammals, particularly the more primitive of the living forms such as insectivores, *Tupaia* and most monotremes and marsupials, the young does not run about while it is suckling but remains in a nest or in a pouch until it has reached a substantial fraction of the adult weight. Growth in weight during the suckling phase if often extremely fast, also always much faster than during gestation and after weaning (see Pond 1977: Tables 2 and 4). In many mammals the young is born with very little fat, i.e. with very little energy store, in contrast to the newly hatched reptiles which have large yolk sacs, but mammalian adipose tissue grows very fast during suckling and for many mammals the fattest periods of their lives is when they are about to be weaned (Pond 1981). This store of body fat helps them through the final phase of growth when they are first out of the nest and foraging for themselves.

LACTATION AND THE PHYSIOLOGY OF THE MOTHER

Lactation has several important effects on the physiology of the mother, it means that although gestation may be long due to the slow growth of the young *in utero*, the clutch is not excessively heavy at birth. Female reptiles of viviparous species give birth to clutches of young which are a much greater fraction of the mother's own weight than is the case with mammals (Pond 1977). Such females are often unable to feed and retire for long periods before giving birth, but almost all mammals are able to feed normally and remain with the herd until a few days before giving birth. Most mammals show no noticeable increase in food intake during gestation, hence no extra food gathering activity is required while she is carrying the young. The really heavy metabolic demand is during the lactation period, when large quantities of calories, proteins and minerals such as calcium are supplied to the growing young. But this period of heavy demand can be met in part from fat and mineral stores built up during pregnancy and stored elsewhere in the body, for example, in adipose tissue and as calcium stores in the bones. When the animal is foraging for additional food during lactation it is not encumbered

with the weight of the young, which are normally left in a nest. The lactation thus has the advantage to the young that it can remain inactive and continue to grow in an embryonic manner for sometime after birth. It has a steady, nutritious food supply, but at the same time the mother is not encumbered with carrying around her offspring at later stages in their development when they are heavy. And if necessary she can withdraw fats, proteins and minerals from her own body tissues to supply the young with milk. The lactation habit therefore means that by the time the young mammal has to feed for itself it can consume the same diet as its parents. There is no need for special food to be available for the juveniles. Furthermore, the juveniles do not suffer if there are temporary food shortages during their phase of most rapid growth, because the mother can meet at least part of the metabolic demands of lactation from her own body reserves. Because lactation requires a very high rate of synthesis of protein, sugars and fat, it will tend to promote anatomical and physiological adaptations to energy storage and metabolism. Mammals differ from reptiles in both the quantity and distribution of storage fats (Pond 1978) particularly the role of the skin and subcutaneous tissues in the storage and metabolism of fats.

ECOLOGY OF EARLY MAMMALS

These reproductive habits make mammals ideally suited as colonising organisms: animals which can flourish in a disturbed or fluctuating habitat and reproduce rapidly to build up a large population quickly when a new food supply opens up. They are like weeds in the plant world; small, adaptable, rapidly reproducing species which are quick to colonize habitats which more slowly reproducing organisms with more stringent ecological requirements simply cannot do. Permanently impoverished environments such as mountain ranges, high latitudes, or temporarily disturbed areas such as the aftermath of floods, volcanic activity and extensive fires, would favour mammals. Ecologically complex, stable habitats, such as temperate plains and the lowland tropics, which were extensive during the Mesozoic, would favour, or rather not be a disadvantage to, large reptiles. The fauna and flora would be diverse enough for there to be food available for all sizes of juveniles. As the climate gradually became cooler and drier, and the upland areas increased relative to the swamps and lowlands, the mammals gradually became more numerous, though not larger, and dinosaurs, particularly the very largest species, became fewer in number.

It is interesting that some of the very earliest mammals, *Morganucodon watsoni* and *Kuehneotherium praecursoris* seem to have occurred as

small populations on islands (Lillegraven, Kraus and Brown 1979). Detailed studies by Schankler (1981) on fossils from the Willwood formation of early Eocene age suggest the condylarth *Phenacodus* was locally abundant during relatively brief periods of geological time, then became extinct, the same species reappearing elsewhere or at a later time again in significant numbers. These observations are consistent with the suggestion that these mammals were able to colonise small areas and build up populations relatively rapidly.

REPRODUCTIVE ECOLOGY OF BIRDS

The birds were another group which increased in abundance and diversity during the second half of the Mesozoic (Elżanowski 1983). Anatomically they are very similar to archosaurs (Ostrom 1973; Hecht and Tarsitano 1983), but they have several physiological and behavioural characters which are similar to mammals. The most widely discussed of these characters is endothermy, but equally important for their ecology is parental feeding of the young. Parental feeding in birds has three important differences with parental feeding in mammals; it is rudimentary among the most primitive living members of the Class: the ratites, the hoatzin and some of the shore birds, and best developed among passerines, psittaciformes and other specialized groups. Secondly, both parents guard the nest and the food is gathered or caught from the environment just before it is brought to the nest. With the exception of pigeons (which secrete 'pigeon milk') and perhaps penguins, the food supplied to the young is not derived from metabolic reserves within the parent's body. An animal's own metabolic reserves within its body could have been built up some time before being donated to the young. But when food brought to the nest must be gathered or caught just before it is eaten by the young, storage of food materials obtained at a more remote time or place is not possible.

Many birds which eat seeds or other plant materials as adults feed the young on insects, and an important function of seasonal migrations is to enable birds to breed in areas where there are temporarily a very large number of insects. The very rapid increase in insect abundance in the spring and summer is high latitudes means that the population is much greater than the food requirements of the resident insectivores. The 'surplus' insects are easily harvested by seasonal populations of birds. Even so it is well known that a cold spell in spring which delays the emergence of insects can cause high mortality among swift nestlings (Lack 1968) and there is nothing the parent birds can do about it, because they cannot move the nestlings or supply alternative foods. The prevalence

of migrations among so many different kinds of birds, in spite of the high mortality and enormous energy demands of the journey, suggests that many birds can only breed where there is a temporary abundance of food suitable for the young. If they could breed successfully in their winter residence, presumably they would do so, and save much time and energy. It has been suggested (Hotton 1980) that *Plateosaurus* and other dinosaurs found as fossils at high latitudes may have been seasonal migrants, perhaps also migrating for breeding in areas where small food items were temporarily easy to come by. It is not known whether dinosaurs brought food to their young, as most birds do. All mammals, including the most primitive, lactate, and the most primitive living mammals are among those which lactate most heavily and for the longest time (Pond 1977). These facts suggest that parental feeding may also have been a feature of the reptilian ancestors of mammals. But among birds parental feeding is best developed in the anatomically most advanced groups, which suggests that parental feeding was not a feature of their reptilian ancestors.

It is instructive to compare the ecological requirements for breeding in modern birds and mammals. The adults of scavenging species such as the maribou stork *Leptoptilos crumeniferus* can live in a wide variety of habitats on diets ranging from big game carrion to human domestic refuse, but their breeding requirements are very specific: they cannot reproduce successfully without access to a plentiful supply of small vertebrates such as frogs and fish which they bring whole to the nest for the young. Breeding is thus restricted to a few areas during the dry season, when suitable prey are concentrated in small pools (Kahl 1966). Similarly *Griffon vultures* (*Gyps* spp.) can live for long periods on offal, which contains only about 0.01% calcium, but bone fragments are an essential item of diet for nestlings. A shortage of suitable bone fragments may be a major factor limiting reproduction in *Gyps africanus* (Houston 1978).

Many mammals, particularly small species raising large litters also develop a specific appetite for calcium and other minerals (see Pond 1977), during gestation and lactation. But at least part of the demand for these minerals can be met from reserves within the mother's body which may have been built up a long time before conception took place, and which may be replenished after depletion to feed the offspring, during an indefinite period after the young are weaned. Birds are dependant upon finding all essential nutrients in the immediate neighbourhood of the nest at the time the young are on the nest; they cannot utilize body energy or mineral reserves to feed the growing young, even in an emergency. Because of the lactation habit, mammals can use body food reserves to provision the young before and after birth, thus donating to the young, during a brief period, nutrients which may have been acquired by the mother over a much longer period. For many mammals breeding is more

independent of the temporal and spatial distribution of resources than is the case for many living birds, particularly the larger species. So, while the adult of the species may be very widely distributed, successful breeding may only occur in a restricted area where there is a reliable supply of food suitable for the young. The greatest burden of food gathering will fall on parents with dependent young, while weanlings and non-reproducing adults only need to obtain enough food to support themselves. In other words the burden of obtaining food to support postnatal growth is transferred from the neonates themselves to their older and hence more experienced parents, an ecological strategy which will promote the importance of learning and the development of more complex feeding techniques and strategies.

For birds with highly developed parental feeding the young become extremely fat towards the end of the nestling period and may remain in the nest while they continue rowing after the parents have abandoned them. Some migratory species may also become very fat just before migration begins, but in this latter case, they become so fat that they have difficulty taking off from the ground. Many normally solitary species may form large flocks during the pre-migratory period which may increase protection from predators (see Pond 1978). But bird parents are not particularly obese while they are bringing food to the nestlings; perhaps it is not possible to achieve a distribution of fat which permits agility while gathering food, does not impede take-off, landing and flight, and which nonetheless allows large quantities of fat to be carried in the body. The problem appears to have been solved among mammals, for females of many species are able to combine increased foraging activity with increased fat and mineral reserves within the body, without noticeable ill-effect.

The Columbiformes parallel the mammals most closely in the physiology of parental feeding. In this order, both parents produce a deciduous tissue in the throat which, in the case of the domestic pigeon, consists of a nutritious mixture of fats, proteins and hormones and is fed to the young for about four days after hatching. Thus compared to mammals of similar size, 'lactation' in pigeons is very brief; nothing is known of the physiological basis for this difference between birds and mammals, but presumably it must have something to do with the way nutrients, particularly fats, proteins and minerals are stored and reclaimed within the body. The fact that even highly endothermic, metabolically active birds 'lactate' very little makes it very unlikely that their Mesozoic relatives, endothermic or not, did so.

Nothing is known of when extensive parental feeding became widespread among birds, but it is unlikely to have been earlier than the beginning of the Cretaceous, at least 50 million years after the trait was well-established in mammals.

CONCLUSION

My suggestion therefore is that lactation is an early and fundamental character of mammals and one which has been a major determinant of their ecological role since early Triassic times. For the first two thirds of their history mammals were opportunist species, rapidly colonizing areas which the more slowly reproducing reptiles could not invade. Mammal populations built up relatively rapidly but they may have been hunted out or competitively displaced by reptiles which were better able to maintain a population when the environment became more stable and the fauna and flora more diverse. Even when larger mammals evolved in the Tertiary, the group retained the potential for rapid postnatal growth and short generation time, perhaps inherited from the long period of their history when the ability to build up a population rapidly was a key factor in their success.

The birds are the most numerous and diverse of the living descendants of the diapsid reptile stocks; their success is usually attributed to the fact that, like mammals, they are endothermic. Equally important, however, may have been that the birds imitated the mammalian condition by evolving increased parental care, including the bringing of food to the nestlings. In our attempts to understand the physiology and ecological relationships of Mesozoic mammals, birds and reptiles, we may be placing too much emphasis on endothermy and viviparity, and not enough emphasis on lactation and other forms of parental feeding.

REFERENCES

BAKKER, R. T. 1980. Dinosaur heresy-dinosaur renaissance: Why we need endo-thermic archosaurs for a comprehensive theory of bioenergetic evolution. In: R. D. K. Thomas and E. C. Olson (eds.), A Cold Look at Warm-Blooded Dinosaurs. — AAAS Selected Symposium, 28, 351—462. Westview Press. Boulder, Colorado.

CLEMENS, W. A., LILLEGRAVEN, J. A., LINDSAY, E. H. and SIMPSON,.G. G. 1979. Where, When and What — A survey of known Mesozoic mammal distri-bution: In: J. A. Lillegraven, Z. Kielan-Jaworowska and W. A. Clemens (eds.), Mesozoic Mammals — The First Two-Thirds of Mammalian History, 7—58. University of California Press, Barkeley. Ca.

COTT, H. B. 1961. Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (Crocodylus niloticus) in Uganda and Northern Rhodesia. — Trans. Zool. Soc. London, 29, 211—256.

CURRIE, P. 1983. Dinosaur tracks. In: Z. Kielan-Jaworowska and H. Osmólska (eds.), Second Intern. Symp. Mesozoic Terrestrial Ecosystems, Jadwisin 1981. — Acta Palaeont. Polonica, 28, 1—2, 63—73.

ELŻANOWSKI, A. 1983. Birds in Cretaceous ecosystems. *In*: *ibidem*, 75—92.

GRIFFITH, M. 1978. The Biology of Monotremata, 367 pp. Academic Press, New York.

HECHT, M. and TARSITANO, S. 1983. *Archaeopteryx* and its paleoecology. *In*: Z. Kielan-Jaworowska and H. Osmólska (eds.), Second Intern. Symp. Mesozoic Terrestrial Ecosystems, Jadwisin 1981. — *Acta Palaeont. Polonica*, **28**, 1—2, 133—136.

HOTTON, N. 1980. An alternative to dinosaur endothermy: the happy wanders. *In*: R. D. K. Thomas and E. C. Olson (eds.), A Cold Look at Warm-Blooded dinosaurs. — AAAS Selected Symposium, **28**, 311—350. Westview Press, Boulder Colorado.

HOUSTON, D. C. 1978. The effect of food quality on breeding strategy in *Griffon vultures Gyps* spp. — *J. Zool. London*, **186**, 175—184.

KAHL, M. P. 1966. A contribution of the ecology and reproductive biology of the Marabou stork *Leptoptilos crumeniferus* in East Africa. — *J. Zool. London*, **148**, 289—311.

KIELAN-JAWOROWSKA, Z. and DOVCHIN, N. 1969. Narrative of the Polish-Mongolian Palaeontological Expeditions. *In*: Z. Kielan-Jaworowska (ed.), Results Pol.-Mong. Palaeont. Expeds., I. — *Palaeont. Polonica*, **19**, 171—191.

LACK, D. 1968. Ecological Adaptations for Breeding in Birds, 409 pp. Methuen, London.

LILLEGRAVEN, J. A., KRAUS, M. J. and BROWN, T. M. 1979. Palaeogeography of the world of the Mesozoic. *In*: J. A. Lillegraven, Z. Kielan-Jaworowska and W. A. Clemens (eds.), Mesozoic Mammals: The First Two-Thirds of Mammalian History, 277—308. University of California Press. Berkeley. Ca.

OSTROM, J. H. 1973. The ancestry of birds. — *Nature*, **242**, 136.

POND, C. M. 1977. The significance of lactation in the evolution of mammals. — *Evolution*, **31**, 177—199.

— 1978. Morphological aspects and the ecological and mechanical consequences of fat deposition in wild vertebrates. — *Ann. Rev. Ecol. Syst.*, **9**, 519—570.

— 1981. Storage. *In*: C. R. Townsend and P. Calow (eds.), Physiological Ecology: An Evolutionary Approach to Resource Use. 190—219. Blackwell Scientific Publications, Oxford.

SCHANKLER, D. M. 1981. Local extinction and ecological re-entry of early Eocene mammals. — *Nature*, **293**, 135—138.