

COMMENTARY

Dinosaur lactation?

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Summary

Lactation is a process associated with mammals, yet a number of birds feed their newly hatched young on secretions analogous to the milk of mammals. These secretions are produced from various sections (crop organ, oesophageal lining and proventriculus) of the upper digestive tract and possess similar levels of fat and protein, as well as added carotenoids, antibodies and, in the case of pigeons and doves, epidermal growth factor. Parental care in avian species has been proposed to originate from dinosaurs. This study examines the possibility that some dinosaurs used secretory feeding to increase the rate of growth of their young, estimated to be similar to that of present day birds and mammals. Dinosaur 'lactation' could also have facilitated immune responses as well as extending parental protection as a result of feeding newly hatched young in nest environments. While the arguments for dinosaur lactation are somewhat generic, a case study for lactation in herbivorous site-nesting dinosaurs is presented. It is proposed that secretory feeding could have been used to bridge the gap between hatching and establishment of the normal diet in some dinosaurs.

Key words: nesting, parenting, crop milk, crop, birds, mammals.

Received 27 March 2012; Accepted 8 October 2012

Lactation in ancient groups

Lactation is a process normally associated with mammals. This proprietary right is based on the fact that the presence of mammary glands is a defining characteristic of the class Mammalia. The very term 'lactation' is tailored to apply to mammals as it refers to the suckling of milk normally assumed to be coming from a mammary gland. So, the precise application of the term lactation cannot accommodate other forms of similar nutritive supply from other organs in other animals. Therefore, the use of the term lactation in this document is imprecise. Interestingly, the origin of lactation predates mammals by tens of millions of years. Lactation had its roots in synapsida, a group that gave rise to the class Mammalia. The synapsids were one of two major amniote groups: the other being sauropsida, which gave rise to reptilian lineages, including dinosaurs and birds (Pough et al., 2009). It was within synapsids that the physical and chemical systems, as well as the behavioural support required for lactation in mammals originated (Oftedal, 2002). It is also possible that within the mammaliaformes and even cynodonts (antecedents of mammals), some form of lactation occurred (Lefèvre et al., 2010; Oftedal, 2002). So, lactation predates class Mammalia, but could some form of lactation also have occurred in sauropids, specifically in the non-avian dinosaurs?

Lactation in groups other than mammals

Apart from the likelihood that some form of lactation occurred in the antecedents of mammals there is no evidence of lactation in any other early vertebrate group. Of course, the big problem here is that any indication of lactation in other prehistoric groups is unlikely to be preserved in the fossil record as it involves the 'soft' tissues. Therefore, it is difficult to prove the existence of lactation in other vertebrate groups, as there is no evidence to either support or refute the idea. However, there is one group of vertebrates that

possess a form of 'lactation' that may well point to a similar use in some sauropsids, including dinosaurs.

This other form of lactation is known to occur in a number of very different extant bird species. Pigeons and doves (*via* the crop organ), flamingos (*via* the oesophageal lining), emperor penguins (*via* the oesophageal lining) and Procellariiformes (seabirds that include albatrosses, petrels and shearwaters; *via* the proventriculus) have all been reported to produce a milk-like fluid or a nutritive oil that they use to nurture their young (Dumont, 1965; Evans and Heiser, 2004; Fisher, 1972; Horseman and Will, 1984; Oka, 2011; Roby et al., 1997; Vandeputte-Poma, 1980). It is also probable that some bird species may provide varying levels of sustenance to their young *via* secretions from the upper portions of the digestive tract, but it has not been noted because it is mixed-in with the regurgitated food mass, or has simply not been observed or recognized because of the rather intimate nature of this feeding mechanism. By far the best-known and best-documented avian 'lactators' are the pigeons and doves that form the family *Columbidae*. Their 'milk' product is not formed by any cutaneous glands but is instead produced in the crop organ (a pouched area of the oesophagus that normally serves as a temporary storage area to moisten and break down food). The 'milk' formed by these birds is commonly referred to as 'crop milk' (Dumont, 1965; Horseman and Will, 1984; Vandeputte-Poma, 1980).

The crop milk of pigeons and doves manifests itself as an oily, yellowish cheese-like substance that is formed into small seed-sized, rice-shaped pellets (Dumont, 1965; Gillespie et al., 2011). It is these rice-shaped milk pellets that are fed to the squabs. In penguins, the secretion is a curd-like solid (Fisher, 1972), in flamingos the milk is a fluid containing oesophageal cells plus red and white blood cells, and in Procellariiformes it is an oil-like product (Roby et al., 1997). These birds feed their chicks directly

from the oral cavity, with the exception of flamingos, which trickle their 'milk' into the open beaks of their young as a red fluid (because it contains canthaxanthin pigment, made from carotenoids they gain in their diet) that presumably helps prevent any clogging of the developing strain bristles (Evans and Heiser, 2004).

If one were looking for a model of lactation that is most likely to have occurred in dinosaurs, there is no better example than that found in birds, and, within birds, no better model to examine lactation than that present in pigeons. The crop organ of adult pigeons (normally about 0.5 g) increases in mass 5-fold, 2 days prior to hatching, and 1 week post-hatching it is 7-fold its normal size. At egg hatching the adult crop is full of crop milk and over the next 21 days of squab feeding the crop of the parents gradually contains less crop milk and is increasingly filled with seed that the squabs are progressively 'weaned' onto as they develop (Horseman and Buntin, 1995).

Histology of a lactating crop

The non-lactating crop has a histology that is typical of the digestive tube (mucosa, submucosa, muscularis externa and serosa or adventitia) but the most important layer associated with lactation is the mucosa. The pigeon crop mucosa normally consists of a stratified squamous epithelium 10–12 cells thick that, when stimulated to lactate, increases 2- to 10-fold in thickness (Dumont, 1965; Horseman and Buntin, 1995). The other notable feature indicative of lactation includes downward growths into the lamina propria of epidermal ridges commonly called 'pegs'. These pegs throw the epidermis into an increasingly folded layer with germinal lower levels, an expanded middle eosinophilic nutritive layer (rich in protein), and an upper layer where the cells increasing fill with lipid and fuse together to form the rice-shaped milk pellets of the crop. The epidermal cells within the rice pellets are still nucleated and rich in lipid droplets (Gillespie et al., 2011). Therefore, lactating birds utilize the ability of epidermal cells to rapidly multiply together with their natural ability to accumulate lipid (normally associated with waterproofing and maintenance of the epidermis) as a mechanism to augment the feeding of their young.

The formation and composition of avian milk

The milk-like products produced by birds are similar in many respects to that formed by mammals (see Table 1). This would seem reasonable based on the fact that both forms of lactation develop from epidermal origins and it might therefore be expected that any dinosaur lactator would produce a similar nutritive milk-like product. Mammalian lactation involves both merocrine (where membrane-bound vesicles release their protein-rich component into the fluid) and apocrine (apical budding of cells that provides the lipid component) secretions. In birds, milk formation is *via* holocrine secretion, which involves the sloughing off of cells. One difference between pigeon and mammal milk is that the fat in pigeon milk is accumulated by epithelial endocytosis, rather than by its synthesis as in mammalian epithelia (Horseman and Will, 1984). Another notable difference between mammalian and avian milk (at least for pigeons and flamingos) is the almost complete lack of carbohydrate in the bird milk. Pigeons feed their young exclusively on crop milk for 4 days, flamingos do so for several weeks and penguins feed their young for as long as required, or can be sustained, until the females return from the sea with available fish for regurgitation (Evans and Heiser, 2004; Fisher, 1972; Horseman and Will, 1984; Oka, 2011; Roby et al., 1997).

Table 1. Gross composition (%) of milk from various avian and mammalian species

	Fat	Protein	Carbohydrate (lactose)	Ash	Total solids
Pigeon	10	23	0		33.0
Penguin	29	59	5.5		93.5
Flamingo	18	8	0.2		26.2
Rat	14.8	11.3	2.9	1.5	31.8
Rabbit	12.2	10.4	1.8	2.0	26.4
Human	4.5	1.1	6.8	0.2	12.6
Seal	53.2	11.2	2.6	0.7	67.7
Whale	34.8	13.6	1.8	1.6	51.2

Data are from previously published studies (Schmidt-Nielsen, 1979; Park and Haenlein, 2006).

Prolactin as a lactogenic and parent-promoting hormone

One of the most important hormones associated with lactation in mammals is prolactin (Bole-Feysot et al., 1998). Prolactin promotes both mammary gland development and milk formation (Neville et al., 2002). In lactating birds, prolactin is also heavily involved in the promotion of lactation (Horseman and Buntin, 1995). In pigeons and doves, high prolactin levels precede bird lactation and then further increase to mirror the substantial thickening of the milk-producing crop epithelium that occurs in parenting birds (Horseman and Buntin, 1995). The very high level of prolactin in lactating pigeons also acts to facilitate the regurgitation reflex by increasing the sensitivity of the epithelia to crop engorgement (Horseman and Buntin, 1995). In this way, a positive feedback mechanism is produced that ensures effective lactation.

Prolactin is an ancient hormone, with more actions than all other pituitary hormones combined, including effects on the immune system, growth and development, metabolism and, importantly, parenting behaviours (Bole-Feysot et al., 1998). Prolactin can increase aggressive and defensive behaviours, food intake, and nest care and attendance of parenting birds (Horseman and Buntin, 1995). In mammals, prolactin can decrease the latency (rather than having a direct stimulatory effect) in behaviours associated with nest building, gathering, cleaning, and crouching over and nursing of young (Freeman et al., 2000). There is great similarity between the prolactins of reptiles and birds, with sequence identity ~90% between crocodile, alligator, chicken and turkey (Noso et al., 1992), plus reptilian and avian prolactin receptors share tandem-repeat regions in their extracellular domains (Kato et al., 2005). So, prolactin was undoubtedly present in dinosaurs, and was probably similar to that present in reptiles and birds, and available to support lactation and parenting behaviours.

Potential benefits of lactation in dinosaurs

Although there are some extant reptiles with complex levels of parental care, most have little to do with their young and it is largely a set (eggs)-and-forget approach where young reptiles must survive without ongoing support from their parents (Rosenblatt, 2003). This simple model of parenting behaviour has in the past served as the model for dinosaurs. However, more recently, avian parental care including nest construction, collective nesting sites, potential brooding, egg guarding and feeding of young have all been suggested to have originated from dinosaurs (Horner, 2000; Varricchio et al., 2008; Meng et al., 2004; Norell et al., 1995; Varricchio et al., 1997). So, although it is likely that many dinosaurs had little to do with their young, others may well have displayed complex parenting behaviours, including the feeding of

newly hatched dinosaurs in nests (Horner and Makela, 1979; Horner, 1984; Horner, 2000; Paul, 1996). A natural progression in nest-based feeding could have been the provision of nutrients and fluid *via* secretion, i.e. lactation! Lactation might free large parents from having to feed their newly hatched young the regurgitated products of their own meals (that might be unsuited for altricial young based on digestive systems unfamiliar with coarse fodder and essential nutrient requirements to promote rapid growth) and replace this with secretory products synthesized by the foregut that are more suited to supporting rapid development.

Growth

Many dinosaurs are believed to have grown rapidly to their adult size, akin to the rapid growth rates present in modern day birds and mammals, rather than those of reptiles (Padian et al., 2001). Rapid growth rate is normally associated with endothermy and there are many studies presenting data for and against this concept in dinosaurs (Seebacher, 2003). Modelling of ectothermic metabolism suggests that inertial homeothermy would produce $\geq 30^{\circ}\text{C}$ body temperatures in dinosaurs over 1500 kg (Gillooly et al., 2006). Yet, other studies using isotopic analysis of dinosaur tooth enamel (Amiot et al., 2006; Eagle et al., 2011) have suggested higher body temperatures ($33\text{--}38^{\circ}\text{C}$) in dinosaurs smaller than 1500 kg and that similar isotopic ratios between diverse dinosaur taxa *versus* the different ratios of large reptiles (crocodiles and turtles) argue for some level of endothermy (Amiot et al., 2006). These arguments, however, do not tell us whether the rapid growth of very small, newly hatched dinosaurs was as a consequence of endothermy (e.g. being based on the bones, body mass and teeth of larger adult animals) or other factors. What we do know is that, where examined (e.g. in an ontogenetic series of the hadrosaur *Maisaura peblesorum*), the smallest nestlings display the highest rate of growth (Horner et al., 2000).

One possible factor that may have aided rapid growth in small newborn dinosaurs (without necessarily the need for endothermy) could have been the supply of milk-like secretions provided by parents with the potential of adding growth hormone. This is analogous to pigeon crop milk, where pigeon squabs mature at rates 2- to 3.5-fold faster than other similarly sized domesticated avian species, e.g. chickens and quail (Sales and Janssens, 2003). This rapid rate of growth is driven by the presence of epidermal growth factors in the crop milk, which enables squabs to increase their body mass ~20-fold, gaining 84% of adult body mass within 3 weeks of hatching (Vandeputte-Poma, 1980). A similar mechanism, if used by dinosaurs, could facilitate the growth of their young, allowing them to attain sizes that would make them more able to avoid predation, be independent and join herds. It is interesting that juvenile remains in the fossil record are rare and this has been interpreted as being due to predatory factors (Hone and Rauhut, 2010) but alternatively it could be the result of rapid growth rates.

Carotenoids and antibodies

In the same way that some pigeons and doves add growth hormone to their milk-like secretions, they also add other factors including carotenoids and antibodies (Eraud et al., 2008; Tizard, 2002). Carotenoids, apart from their role in coloration and the potential benefit of camouflaging young, also act as antioxidants and as regulators of the immune system (Rock, 1997). Carotenoids cannot be synthesized by vertebrates and are acquired in the diet (Eraud et al., 2008). Parents supply carotenoids to their young in the egg yolk or in the foods they provide following birth. The provision of carotenoids in crop milk is analogous to the supply by mammals in

the colostrum of breast milk. In pigeons, it has been estimated that the level of carotenoids obtained by squabs from crop milk in the first 5 days amounts to about half that supplied in their egg yolk (Eraud et al., 2008). One obvious advantage of carotenoids in dinosaurs would have been their use in skin camouflage. However, an intact sample of preserved skin from *Psittacosaurus* (a small Cretaceous dinosaur) suggests that melanin(s) pigmented the skin (Lingham-Soliar and Plodowski, 2010). This conclusion was based on pigment colour and the resistance of melanins to degradation. Therefore, carotenoids could have been present but had simply degraded in the sample.

Crop milk is also used to supply antibodies to newly hatch birds (Tizard, 2002), just as plasma cells and lymphocytes in the connective tissue around the glandular tissue of the mammary glands add antibodies (mainly IgA) to the milk of mammals. Antibody levels are particularly high in colostrum during the first few days of lactation and this is believed to aid in immune protection until the young can generate their own effective immune defence; not surprisingly, though, there is no literature on this subject for dinosaurs.

Adaptable to species need

Lactation in mammals can be highly variable to accommodate the requirements of the individual species. For example, the lactation period in mammals is normally allometrically linked, with larger mothers lactating for longer (Lefèvre et al., 2010). Yet, one of the shortest lactating periods, as little as 4–5 days, occurs in seals, which provide their young with copious amounts of fat-laden milk (as feeding grounds for the mothers can be hundreds of kilometres away), whereas some primates lactate for up to 900 days (Lefèvre et al., 2010). The composition of milk can also be changed to meet the differing demands of the developing young. This is nicely demonstrated in marsupials, where different-aged young attached to different teats at the same time in the same pouch feed on milk of different composition. Likewise, mammals generally adjust the composition of their milk as their young develop (Lefèvre et al., 2010). Bird lactation has its own special advantages, being able to be mixed with natural foods or concentrated into a semisolid, as it is not delivered directly as a glandular secretion. Other vertebrate groups, including dinosaurs, would thus obtain a similar benefit if lactation occurred. One of the most important features of bird lactation is that unlike mammalian lactation it is not restricted to females of the species but can occur at the same time in both males and females. This allows either parent to provide fluid and sustenance to the young (as well as parental protection) while the other parent is foraging.

If lactation occurred in dinosaurs, it could have been used to accommodate the feeding of young away from normal feeding grounds, providing fluid as well as nutritive substrates without the need to leave the protection of a nest and/or a protective parent. It could allow parents to share the burden of parenting and feeding, and provide a means of getting around any special morphology of the young and/or parents (e.g. the filtration bristles of flamingos). Plus, 'dinosaur milk' could be mixed with natural foods to move feeding towards the normal preferred diet of the species. Of course, one of the problems in presenting a concept like lactation in dinosaurs is that many of the arguments are generic, so how might it have worked in dinosaurs?

Which dinosaurs lactated?

Clearly, it is not possible to examine all dinosaur taxa for their potential to lactate. However, a case study of a candidate group for

which there is a large volume of information is feasible. Such a case study can be made for hadrosaurs, and one of the largest compilations of information on this subject is that presented by Paul (Paul, 1996). According to this source, hadrosaur colonies regularly nested at the same sites. These sites were exposed, being devoid of trees (similar to those of ground-nesting birds). The hadrosaur nests were banked conical-shaped depressions (3 m across and 1 m deep) with a raised rim, separated from one another by about an adult's width (Horner, 1984; Paul, 1996). The thermal environment of the nest was considered to have been harsh, with high ground temperatures, cool nights and full exposure to precipitation (Paul, 1996).

The size of the 'chicks' of different hadrosaur species varied from 0.3–0.5 kg (*Maiasaura*) to 3–4 kg (*Hypacrosaurus*), with parents weighing 2.5 to 4.4 metric tons, respectively (Paul, 1996). Between 18 and 24 eggs were laid in nests that were occupied for long periods based on the evidence of egg-shell trampling (Horner and Makela, 1979). Nest occupancy is also supported by the fact that the young were quite altricial and unlikely to be able to escape the nest with poor ossification of leg bones (up until juveniles of ~20 kg), similar to those of fetal mammals (Horner et al., 2000). Adults are assumed to have tended the nest, providing food and moisture in the form of regurgitated plant matter (rather than raw leaf matter as there is no evidence of twigs, etc., in nests) (Paul, 1996).

Although it is not known how dinosaurs fed regurgitated plant matter to their young, it would be more effective if it occurred directly from the mouth of the parent, as regurgitating into the nest would increase drying (due to trampling in a hot nest environment). In one study, 15 juvenile hadrosaurs (~1 m in length) were found in a single nest with their teeth worn down to approximately a quarter of their 'normal' height, suggesting the grinding of plant matter (Horner and Makela, 1979). The regurgitated plant matter provided by the parents is unlikely to change while the young were in the nest (based on food available from around the nesting site) and would probably be relatively coarse, as indicated by tooth wear and the fact that it is regurgitated from the anterior section of the gut. Therefore, one might question firstly, whether small newly hatched hadrosaurs (0.3 kg) had teeth and, if so, were they capable of grinding enough plant material to supply their gut with adequate quantities? Secondly, would they have had the necessary gut capacity to accommodate the volume and time required to ferment enough plant material to support sustained rapid growth?

Effective herbivory requires micro-organisms and a period to establish them in the gut. Whilst the regurgitation of plant matter from parents might act as an inoculum it may still take some time for effective fermentation to be established. It is in this early developmental period that dinosaur lactation may have been used to supply the calcium and minerals necessary for bones and teeth, and the protein required for rapid growth. The use of secretions from the anterior digestive tract would lend itself to the addition of growth hormone (as used in some birds) to facilitate rapid growth, which in the case of hadrosaurs was very rapid, allowing young nestlings to go from 0.3 kg at hatching to 20 kg as juveniles within 8 weeks (Paul, 1996; Horner et al., 2000).

Although this scenario for lactation in hadrosaurs is highly speculative, there are many other dinosaur groups that could fit the profile for lactation. The use of lactation in hadrosaurs (if it occurred) was most likely restricted to when they were very young, as juveniles and adults possessed dentition specialized for plant grinding. However, other herbivorous nesting dinosaurs including other members within the order Ornithischia lacked specialized

grinding dentition (Horner and Makela, 1979). In these animals, gut secretory feeding would be more likely to be used for longer periods of time until the young were capable of processing enough plant material. Other examples of potential lactators include some of the hypsilophodonts (i.e. crested tooth dinosaurs), which have much in common with hadrosaurs, being colony site nesters showing parental care (Paul, 1996). It is also interesting that within this group are the first discovered skeletal remains of an adult with two juveniles together in a burrow (Varricchio et al., 2007), indicating a high level of parental care that, when combined with the requirement for fast growth, lends itself to the potential for lactation in these types of dinosaurs.

Certainly, herbivorous dinosaurs form some of the most likely candidates for the feeding of gut-produced secretions to their young. Herbivory in reptiles requires much longer retention times than those in comparable mammals to extract the same amount of digestible material (Franz et al., 2011). Therefore, very small, young dinosaurs fed by large herbivorous parents would require long periods for sufficient digestion. Even using regurgitated plant matter, the energy needed to support rapid growth in young dinosaurs notionally supports the idea of secretory feeding or supplementation in some dinosaurs. In addition, the predominant plant species of the time were generally far less digestible than those available today. Gymnosperms, cycads and ferns have between 54% and 68% of the metabolizable energy yield of grasses commonly grazed by mammalian herbivores (Hummel et al., 2008). The hoatzin is the only known folivorous foregut (crop) fermenting bird. The hoatzin regurgitates (from its crop) a sticky, greenish, pre-digested plant mash rich in bacteria to its young (Del Hoyo et al., 1996). The combination of low nutrient value, the toxic nature of the food and the long digestive retention times required to gain energy from this food source (between 18 and 24 h) means that the growth rates of the hoatzin compared with those of similar sized birds is very slow (Dominguez-Bello et al., 1994), indicating that rapid growth in young dinosaurs fed by herbivorous parents may have required supplementation.

The bird species currently known to lactate (or produce nutritive oils) tend to have only a small number of offspring. Pigeons normally have two squabs (with eggs laid 1 day apart) whereas emperor penguins, flamingos and Procellariiformes lay a single egg. The likely reason for this in the case of flamingos, penguins and Procellariiformes is that nesting sites are often far removed (distance and time) from feeding grounds. Dinosaurs seem to have laid a larger number of eggs (Horner, 2000), a characteristic indicative of reptiles as opposed to mammals and birds (Shine, 2005). However, the fact that dinosaur parents were relatively much larger in comparison to their newly hatch young would also make them more capable of supplying a greater number of offspring with secretions from the upper parts of the digestive tract.

Did dinosaurs have crops? No, at the present time there is no fossil evidence of crops ever having been present in dinosaurs. However, until recently there was no fossilized evidence of crops ever having been present in early birds, till it was reported in two early cretaceous bird species (Zheng et al., 2011). This new finding of crops in birds that flew over the heads of non-avian dinosaurs indicates that the current lack of evidence of crops in dinosaurs does not preclude their presence. It should also be pointed out that although crops are normally associated with grainivorous birds, hawks, vultures and even hummingbirds have crops (Zheng et al., 2011). The existence of crops in birds that eat meat, carrion and nectar indicates that the presence of a crop is not limited by diet. But even if dinosaurs did not have crops, or similar soft structures,

they would certainly have had an oesophageous and probably also structures similar to a proventriculus feeding into a gizzard. Therefore, dinosaurs would definitely have possessed the necessary soft structures required to produce various secretions similar to those produced by some birds.

Conclusion

There is no doubt that the presence of sealed skin (in the form of scales) in dinosaurs would have precluded the option of external epidermal glandular lactation. So, if lactation did occur in dinosaurs it would have had to involve secretions from other sources, such as a crop, oesophageal or gastric structures as found in birds. It is interesting that Oftedal in his major review of the evolution of mammalian lactation considers that if mammals had not evolved a glandular system of lactation they would have evolved one similar to that present in birds (Oftedal, 2002). Of course, the idea of lactating dinosaurs is highly speculative and it is difficult to avoid generating generic arguments. However, the fact that very different types of birds have evolved the use of a similar form of feeding and the close relationship between birds and dinosaurs makes lactation in dinosaurs seem quite plausible. So, although the concept of lactation in dinosaurs will be difficult to prove or accept, it is worthwhile reflecting on Darwin's thoughts on egg-laying mammals: 'An unbeliever in everything beyond his own reason might exclaim, "Surely two distinct Creators must have been at work"' (Darwin, 2001). Yet, egg-laying mammals lactate and display a fascinating mix of avian and mammalian characteristics, so why not lactating dinosaurs with a mix of reptilian and avian characteristics?

Acknowledgements

I would like to thank Tony Hulbert, Bill Buttemer, Adam Munn (also for hoatzin awareness) and Colin Cortie for reading various versions of the manuscript and to the two anonymous reviewers who made me think more about dinosaurs.

Funding

This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors.

REFERENCES

- Amiot, R., Lecuyer, C., Buffetaut, E., Escarguel, G., Fluteau, F. and Martineau, F. (2006). Oxygen isotopes from biogenic apatites suggest widespread endothermy in Cretaceous dinosaurs. *Earth Planet. Sci. Lett.* **246**, 41-54.
- Bole-Feyso, C., Goffin, V., Ederly, M., Binart, N. and Kelly, P. A. (1998). Prolactin (PRL) and its receptor: actions, signal transduction pathways and phenotypes observed in PRL receptor knockout mice. *Endocr. Rev.* **19**, 225-268.
- Darwin, C. (2001). *Charles Darwin Beagle Diary* (ed. R. D. Keynes). Cambridge: Cambridge University Press.
- Del Hoyo, J., Elliot, A. and Sargatal, J. (1996). *Handbook of the Birds of the World – Hoatzin to Auks*, Vol. 3. Barcelona, Spain: Lynx Edicions.
- Dominguez-Bello, M. G., Michelangeli, F., Ruiz, M. C., Garcia, A. and Rodriguez, E. (1994). Ecology of the folivorous hoatzin (*Opisthocomus hoazin*) on the Venezuelan plains. *Auk* **111**, 643-651.
- Dumont, J. N. (1965). Prolactin-induced cytologic changes in the mucosa of the pigeon crop during crop-'milk' formation. *Z. Zellforsch. Mikrosk. Anat.* **68**, 755-782.
- Eagle, R. A., Tutken, T., Martin, T. S., Tripathi, A. K., Fricke, H. C., Connelly, M., Cifelli, R. L. and Eiler, J. M. (2011). Dinosaur body temperatures determined from isotopic (^{13}C - ^{18}O) ordering in fossil biominerals. *Science* **333**, 443-445.
- Eraud, C., Dorie, A., Jacquet, A. and Faivre, B. (2008). The crop milk: a potential new route for carotenoid-mediated parental effects. *J. Avian Biol.* **39**, 247-251.
- Evans, H. E. and Heiser, J. B. (2004). What's inside: anatomy and physiology. *Handbook of Bird Biology*, 2nd edn. Princeton, NJ: Princeton University Press.
- Fisher, H. (1972). The nutrition of birds. In *Avian Biology* (ed. D. S. Farner), pp. 431-469. New York: Academic Press.
- Franz, R., Hummel, J., Muller, D. W. H., Bauert, M., Hatt, J.-M. and Clauss, M. (2011). Herbivorous reptiles and body mass: effects on food intake, digesta retention, digestibility and gut capacity, and a comparison with mammals. *Comp. Biochem. Physiol.* **158A**, 94-101.
- Freeman, M. E., Kanyicska, B., Lerant, A. and Nagy, G. (2000). Prolactin: structure, function, and regulation of secretion. *Physiol. Rev.* **80**, 1523-1631.
- Gillespie, M. J., Haring, V. R., McColl, K. A., Monaghan, P., Donald, J. A., Nicholas, K. R., Moore, R. J. and Crowley, T. M. (2011). Histological and global gene expression analysis of the 'lactating' pigeon crop. *BMC Genomics* **12**, 452-460.
- Gillooly, J. F., Allen, A. P. and Charnov, E. L. (2006). Dinosaur fossils predict body temperatures. *PLoS Biol.* **4**, e248.
- Hone, D. W. E. and Rauhut, W. M. (2010). Feeding behaviour and bone utilization by theropod dinosaurs. *Lethaia* **43**, 232-244.
- Horner, J. R. (1984). The nesting behaviour of dinosaurs. *Sci. Am.* **250**, 130-137.
- Horner, J. R. (2000). Dinosaur reproduction and parenting. *Annu. Rev. Earth Planet. Sci.* **28**, 19-45.
- Horner, J. and Makela, R. (1979). Nest of juveniles provides evidence of family structure among dinosaurs. *Nature* **282**, 296-298.
- Horner, J. R., De Ricqlès, A. J. and Padian, K. (2000). Long bone histology of the hadrosaurid dinosaur *Maiasaura peeblesorum*: growth dynamics and physiology based on an ontogenetic series of skeletal elements. *J. Vertebr. Paleontol.* **20**, 115-129.
- Horseman, N. D. and Buntin, J. D. (1995). Regulation of pigeon cropmilk secretion and parental behaviors by prolactin. *Annu. Rev. Nutr.* **15**, 213-238.
- Horseman, N. D. and Will, C. L. (1984). Characterization of lipid storage associated proteins induced in crop tissue by prolactin. *J. Comp. Physiol. B* **154**, 237-242.
- Hummel, J., Gee, C. T., Südekum, K.-H., Sander, P. M., Nogge, G. and Clauss, M. (2008). In vitro digestibility of fern and gymnosperm foliage: implications for sauroid feeding ecology and diet selection. *Proc. Biol. Sci.* **275**, 1015-1021.
- Kato, K., Ikemoto, T. and Park, M. K. (2005). Identification of the reptilian prolactin and its receptor cDNAs in the leopard gecko, *Eublepharis macularius*. *Gene* **346**, 267-276.
- Lefèvre, C. M., Sharp, J. A. and Nicholas, K. R. (2010). Evolution of lactation: ancient origin and extreme adaptations of the lactation system. *Annu. Rev. Genomics Hum. Genet.* **11**, 219-238.
- Lingham-Soliar, T. and Plodowski, G. (2010). The integument of *Psittacosaurus* from Liaoning Province, China: taphonomy, epidermal patterns and color of a ceratopsian dinosaur. *Naturwissenschaften* **97**, 479-486.
- Meng, Q., Liu, J., Varricchio, D. J., Huang, T. and Gao, C. (2004). Palaeontology: parental care in an ornithischian dinosaur. *Nature* **431**, 145-146.
- Neville, M. C., McFadden, T. B. and Forsyth, I. (2002). Hormonal regulation of mammary differentiation and milk secretion. *J. Mammary Gland Biol. Neoplasia* **7**, 49-66.
- Norell, M. A., Clark, J. M. and Chiappe, L. M. (1995). A nesting dinosaur. *Nature* **378**, 774-776.
- Noso, T., Swanson, P., Lance, V. A. and Kawachi, H. (1992). Isolation and characterization of glycosylated and non-glycosylated prolactins from alligator and crocodile. *Int. J. Pept. Protein Res.* **39**, 250-257.
- Oftedal, O. T. (2002). The mammary gland and its origin during synapsid evolution. *J. Mammary Gland Biol. Neoplasia* **7**, 225-252.
- Oka, N. (2011). Differential assimilation efficiency of prey and growth of short-tailed shearwater chicks. *Ornithol. Sci.* **10**, 39-50.
- Padian, K., de Ricqlès, A. J. and Horner, J. R. (2001). Dinosaurian growth rates and bird origins. *Nature* **412**, 405-408.
- Park, Y. W. and Haenlein, F. W. (2006). *Handbook of Milk of Non-Bovine Mammals*. Carlton, Australia: Blackwell Publishing.
- Paul, G. (1996). Thermal environments of dinosaur nestlings: implications for endothermy and insulation. In *Dinosaur Eggs and Babies* (ed. K. Carpenter, K. Hirsch and J. Horner), pp. 278-287. New York: Cambridge University Press.
- Pough, H. E., Janis, C. M. and Heiser, J. B. (2009). *Vertebrate Life*. San Francisco, CA: Benjamin Cummings.
- Roby, D. D., Taylor, J. R. E. and Place, A. R. (1997). Significance of oil for reproduction in seabirds: an interspecies cross-fostering experiment. *Auk* **114**, 725-736.
- Rock, C. L. (1997). Carotenoids: biology and treatment. *Pharmacol. Ther.* **75**, 185-197.
- Rosenblatt, J. S. (2003). Outline of the evolution of behavioral and nonbehavioral patterns of parental care among the vertebrates: critical characteristics of mammalian and avian parental behavior. *Scand. J. Psychol.* **44**, 265-271.
- Sales, J. and Janssens, G. P. J. (2003). Nutrition of the domestic pigeon (*Columba livia domestica*). *Worlds Poult. Sci. J.* **59**, 221-232.
- Schmidt-Nielsen, K. (1979). *Animal Physiology: Adaptation and Environment*. New York: Cambridge University Press.
- Seebacher, F. (2003). Dinosaur body temperatures: the occurrence of endothermy and ectothermy. *Paleobiology* **29**, 105-122.
- Shine, R. (2005). Life-history evolution in reptiles. *Annu. Rev. Ecol. Syst.* **36**, 23-46.
- Tizard, I. (2002). The avian antibody response. *Semin. Avian Exot. Pet* **11**, 2-14.
- Vandeputte-Poma, J. (1980). Feeding, growth and metabolism of the pigeon, *Columba livia domestica*: duration and role of crop milk feeding. *J. Comp. Physiol. B* **135**, 97-99.
- Varricchio, D. J., Jackson, F. D. and Borkowski, J. J. (1997). Nest and egg clutches of the dinosaur *Troodon formosus* and the evolution of avian reproductive traits. *Nature* **385**, 247-250.
- Varricchio, D. J., Martin, A. J. and Katsura, Y. (2007). First trace and body fossil evidence of a burrowing, denning dinosaur. *Proc. R. Soc. B* **274**, 1361-1368.
- Varricchio, D. J., Moore, J. R., Erickson, G. M., Norell, M. A., Jackson, F. D. and Borkowski, J. J. (2008). Avian paternal care had dinosaur origin. *Science* **322**, 1826-1828.
- Zheng, X., Martin, L. D., Zhou, Z., Burnham, D. A., Zhang, F. and Miao, D. (2011). Fossil evidence of avian crops from the Early Cretaceous of China. *Proc. Natl. Acad. Sci. USA* **108**, 15904-15907.