

Neoteny and the thyroid in ratites

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The ratites (for example ostriches, emus) are neotenous descendants of flying birds. The best studied cases of neoteny among vertebrates are in the Amphibia. In this class, whether individuals metamorphose and breed as adults, or whether they become sexually mature as neotenous aquatic larvae, is controlled by the thyroid. In this review it is argued that the thyroid may have been important in the evolution of ratite neoteny. The evidence is based on characteristics of ratites that could indicate thyroid abnormality, similarities between ratites and thyroidectomized non-ratite birds, and preliminary results from a study of thyroid function in ostriches.

Paedomorphosis, the evolutionary process in which juvenile stages in the ontogeny of ancestors become the adult stages of descendants, has occurred frequently in all animal phyla. It can happen as the result of two processes: neoteny, in which the ontogeny of somatic features is retarded so that sexual maturity occurs while juvenile features are retained; and progenesis, in which sexual maturation is accelerated with respect to somatic development. The difference between these two processes, and the relative importance of each, has frequently fuelled debate among evolutionary biologists (for example, de Beer, 1958; Gould, 1977). Neoteny is not uncommon in vertebrate phylogeny. All vertebrates may be neotenous descendants of a primitive chordate in which the sessile adult stage, which still exists in tunicates, is lost (Berrill, 1955), and it has been argued that humans are neotenous descendants of apes (Bolk, 1926). One group of birds is also thought to have passed through a neotenous stage in their evolution - the ratites.

There are living ratites in all of the southern hemisphere continents: the ostrich (*Struthio camelus*) from Africa, two species of rhea (*Rhea*) from South America, the emu (*Dromaius novaehollandiae*) from Australia, three species of cassowary (*Casaurius*) from New Guinea and northeastern Australia and three species of kiwi (*Apteryx*) from New Zealand. Many extinct species have been recorded including moas and elephant birds. Contrary to earlier beliefs (for example, Young, 1962), DNA-DNA hybridization studies suggest that the ratites comprise a monophyletic taxon (Sibley and Ahlquist, 1981). A divergence occurred among them about 80 million years ago, when the southern continents drifted apart, leading to the ostrich and rheas, which themselves soon diverged, and to the Australasian species. A surprising conclusion from this is that the kiwis, which are small, nocturnal and insectivorous, with a long bill and small eyes, diverged more recently from the emu and cassowaries than did the ostrich and rheas, despite the huge size and other similarities between these other species. The kiwis may have undergone a secondary reduction in size, and Gould (1991) has suggested that this may account for the huge size, in relation to body size, of kiwi eggs.

All ratites are flightless. Ostriches and rheas have short wings which are used in display. Cassowaries and emus have only vestiges of wings, and in kiwis the remnants of wings are

barely detectable. The ratites have no keel to the sternum (hence ratite from the Latin *ratīs* for raft) to which the flight muscles of flying birds are anchored. Their flightless condition had led them to be regarded as primitive birds. However, de Beer (1956) argued that many of their apparently primitive characters were in fact juvenile rather than primitive, and that, in fact, ratites were neotenous descendants of flying birds. Of particular importance was the arrangement of the palate, which is palaeognathous. Most birds are neognathous, but pass through a palaeognathous stage in their development. Other juvenile characters are the structure of the head with very large eyes (except in kiwis), comparatively long legs (O'Connor, 1984) and downy feathers. In short, adult ostriches, for example, are simply overgrown chicks; although they grow to an enormous size, their morphology remains surprisingly unchanged. True adult avian features never develop. In de Beer's words, they are the Peter Pans of the avian world.

Thyroid and neoteny

The best studied cases of neoteny among vertebrates occur in Amphibia. Amphibians have a well-defined metamorphosis from an aquatic juvenile form to an air-breathing adult. This metamorphosis is dependent on thyroid hormones. Gudersnatsch (1912) fed horse thyroids to *Rana temporaria* tadpoles and this caused them to metamorphose. This was the first recorded function of an endocrine organ in a cold-blooded vertebrate. Conversely, hypothyroidism, as a result of congenital athyroidism, experimental removal of the thyroid glands, or treatment with goitrogens, results in tadpoles that continue to grow but never metamorphose (Dodd and Dodd, 1976).

Several species of urodele amphibian are neotenous; they become sexually mature as aquatic larvae and do not metamorphose into air-breathing adults. In some cases entire genera (for example, *Necturus*, *Proteus* and *Amphiuma*) are obligately neotenous and hence permanently aquatic. Permanent neoteny tends to occur where the aquatic environment is stable and favourable but surrounded by a hostile terrestrial environment. Some species are facultative neotenes and these are associated with aquatic habitats that may occasionally become unfavourable. Whether neoteny occurs depends on environmental

conditions. Within the salamander genus, *Ambystoma*, there are several species that always metamorphose, some that do occasionally, and the axolotl, *Ambystoma mexicanum*, which is always neotenus (Brandon, 1989).

The absence of metamorphosis in neotenus species, and whether metamorphosis occurs in facultative neotenes, is dependent on thyroid hormones. In the genera of obligate neotenes, treatment with large amounts of thyroxine fails to induce metamorphosis, implying that their tissues are insensitive to thyroxine. In contrast, in facultatively neotenus species, treatment with exogenous thyroxine always results in an adult form. This is also true of several species that are naturally always neotenus, *Eurycea tynerensis*, *E. neotenes*, *Gyrinophilus palleucus*, *Typhlomolge rathbuni* and the axolotl (Kühn and Jacobs, 1989), and results in adult forms that are not known in nature. Treatment of the salamander, *Hynobius retardus*, which has been reported as being occasionally neotenus in the wild, with a goitrogen not only prevented metamorphosis but also accelerated spermatogenesis markedly (Wakahara, 1994).

Although concentrations of triiodothyronine and thyroxine are low in the axolotl, failure to metamorphose cannot be attributed to an inability of the thyroid to secrete these hormones, because treatment with thyroid-stimulating hormone (TSH) does induce metamorphosis (Kühn and Jacobs, 1989). Nor is it due to a lack of endogenous TSH in the pituitary or thyrotrophin-releasing hormone (TRH) in the hypothalamus. Rather, it may be due to an inability to secrete TRH or of TRH to stimulate TSH release. However, this conclusion must remain tentative because the degree to which TRH stimulates TSH release even in non-neotenic amphibians remains unclear.

Thyroid in birds

Since the early work of Voitkewitsch (1940), many studies on several species of bird have shown that thyroid hormones are required for the expression of appropriate reproductive responses to photoperiodic cues. For example, thyroidectomy prevents the onset of photorefractoriness (the profound switching off of the reproductive system in the hypothalamus induced by long days) in starlings (Wieselthier and van Tienhoven, 1972; Goldsmith and Nicholls, 1984; Dawson *et al.*, 1985) and tree sparrows (Wilson and Reinhart, 1993), and relative photorefractoriness (a potential switch off induced by long days, not manifest until daylength decreases) in Japanese quail (Follett and Nicholls, 1985). Conversely, thyroidectomy of birds that have already become photorefractory on long days causes the termination of photorefractoriness and consequent gonadal maturation. This specific effect of thyroidectomy may reflect a general requirement of thyroid hormones for all photoperiodic responses (Dawson, 1993). Indeed, the effects on reproduction may simply be symptomatic of widespread general effects of thyroidectomy on the central nervous system (McNabb and King, 1993).

In most birds, the annual moult is associated with termination of breeding, and this too is abolished by thyroidectomy (Voitkewitsch, 1966). As with the other effects of thyroidectomy, this can be reversed by treatment with exogenous thyroxine. In thyroidectomized starlings, a single injection of thyroxine is sufficient to trigger a moult (Goldsmith and Nicholls, 1992), which then begins some weeks later. Consequently, the new

feathers develop long after the thyroxine has been cleared from the circulation. The result is feathers with an aberrant structure. They are longer than usual and lack the asymmetric barbules that normally link adjacent barbs together. Such feathers are therefore downy rather than stiff and planar.

In starlings, the reproductive system of juveniles is essentially the same as that of photorefractory adults. This led to the question as to whether thyroidectomy soon after hatching would lead to premature sexual maturation. Indeed it did (Dawson *et al.*, 1987, 1994). However, not only did the gonads develop prematurely, but somatic development was slowed and eventually ceased. These birds were therefore apparently neotenus. The juvenile features that became permanent were the structure of the skull (the form of the palate and lack of fusion between the sutures), the short bill and large eyes, and the ratio of leg length to body length. The feathers of these birds were downy as described above. In addition, these birds had learning difficulties; learning to feed and to perch took much longer than in euthyroid controls.

Thyroid and ratites

The ratites are neotenus descendants of flying birds. Could thyroid dysfunction have been involved in this evolutionary step in an analogous way to that which occurs in Amphibia? There are two lines of circumstantial evidence that suggest this may have been the case. First, several features of thyroidectomized neotenus starlings resemble characteristics of ratites; and second, there are several aspects of ratite biology that suggest abnormal thyroid function.

Several somatic and behavioural features of neotenus thyroidectomized starlings resemble features found in ostriches: the chick-like head with large eyes, the lack of fusion of skull sutures and the juvenile structure of the palate. The downy structure of the feathers is also similar, as is the distribution of feathers over the body. In thyroidectomized starlings, feathers develop only along the central axes of the major feather tracts, leaving large areas of the body unfeathered, remarkably similar to the situation in ostriches. One obvious somatic difference, however, is that growth of thyroidectomized starlings ceases before adult size is attained, resulting in permanently small birds, whereas most ratites are huge. There are also behavioural similarities. Thyroidectomized starlings are slow to learn, which is presumably an effect of hypothyroidism on the development of the central nervous system. Such effects in humans (cretinism) have been known for centuries (McNabb and King, 1993) and have been widely documented in other mammals. Ostriches are anecdotally famous for their lack of intelligence. As young birds, many have difficulty learning to feed, and even older birds often ingest totally inappropriate items (Degen *et al.*, 1989; Deeming and Dick, 1995). The innate curiosity shown by young of other precocial species of bird appears to be retained by ostriches throughout life.

Information from free-living ratites is scarce, but both ostriches and emus are farmed commercially. Several aspects of animal husbandry, which present serious commercial problems, could be indicative of thyroid abnormality. However, whether such problems are restricted to farmed birds, and therefore are the result of inbreeding rather than being symptomatic of their natural physiology, is unclear. As well as the behavioural

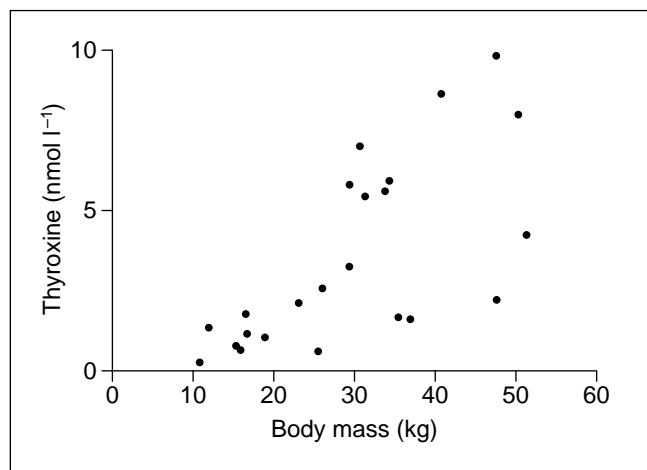


Fig. 1. Plasma thyroxine concentration plotted against body mass for a group of 23 five-month-old ostriches.

problems already mentioned, farmed ostriches are particularly susceptible to a variety of diseases: they often have variable growth rates, problems with ossification and difficulties with absorption of food from the gut (Deeming *et al.*, 1993; Kreibich and Sommer, 1995; Sales and Mellett, 1995). All of these could be symptoms of thyroid abnormality. Hypothyroidism in birds increases susceptibility to disease and decreases the mass of the avian lymphoid organ, the bursa of Fabricius (Harms *et al.*, 1994). Conversely, treatment with thyroxine increases bursa mass and increases numbers of lymphocytes (Haddad and Mashaly, 1990). Incidentally, the bursa of ostriches does not develop to the adult form seen in other birds (Von Rautenfeld and Budras, 1982), possibly another feature of their neoteny. Hypothyroidism reduces growth rates (King and May, 1984; Decuyper and Kühn, 1988; McNabb and King, 1993), and TRH in birds is a potent inducer of growth hormone release (Harvey, 1990). Thyroid hormones are involved in ossification (King and May, 1984) and, finally, hypothyroidism can result in malabsorption syndrome (Rudas *et al.*, 1985).

Current research

None of the above is proof of thyroid dysfunction in ratites, but taken together they were compelling enough to encourage me to begin a study of thyroid function in ostriches. Initial results tend to confirm that thyroid function is abnormal. Growth rate in ostriches is relatively slow compared with that of other birds, and full skeletal size is not attained until at least 12 months. Perhaps more significantly, growth rate varies markedly between individuals. In the first group of birds examined, which were 5 months old, body mass ranged from 10 kg to 52 kg. The coefficient of variation (CV) was 42%, which is extraordinary compared with other birds in mid-growth. Mean plasma thyroxine in these birds was 3.1 nmol l⁻¹, which is low compared with values reported for other species of bird. But again, it was the range of values, from 0.2 nmol l⁻¹, which is extremely low, to 6.5 nmol l⁻¹ (CV 90%), that was particularly striking. There was a close correlation between plasma thyroxine concentration and body mass in these birds (Fig. 1).

In Amphibia, neoteny does not appear to be simply correlated with low thyroxine but rather with a lack of hypothalamic control of thyroxine secretion. In birds, it appears that the thyroid operates more independently of hypothalamic control than it does in mammals (Batten and Ingleton, 1987) but again, the evidence is far from conclusive. There are conflicting reports, for example, as to whether TRH causes release of TSH and thyroxine in adult birds (Scanes, 1974; Sharp and Klandorf, 1985; Batten and Ingleton, 1987; Kühn *et al.*, 1987). Whether the wide range of thyroxine values found in ostriches is indicative of even less hypothalamic control in ratites than in other birds is the focus of current research. Another line of research is much more applied – whether treatment of farmed ostriches with exogenous thyroxine could ameliorate some of the problems encountered in rearing this species.

Demonstration of abnormal thyroid function in ratites will not prove that this was a factor in the evolution of their neoteny. Unlike the situation in Amphibia, where some species remain facultative neotenes and are therefore available for experimentation, the neotenuous stage in ratite evolution was complete at least 80 million years ago. Why the ratites evolved in this way is open to speculation. It may be significant that their ancestors occurred in the southern continents, where open grasslands perhaps became available as a result of climate change, where mammalian predators may have been less common, so that loss of the ability to fly did not make them easy prey.

References

- Key references are identified by asterisks.
- *Batten TFC and Ingleton PM (1987) The hypothalamus and pituitary gland. In *Fundamentals of Comparative Vertebrate Endocrinology* pp 283–409 Eds I Chester-Jones, PM Ingleton and JG Phillips. Plenum Press, New York
 - Berrill (1955) *The Origins of Vertebrates* Oxford University Press, Oxford
 - Bolk L (1926) *Das Problem der Menschwerdung* Gustav Fischer, Jena
 - *Brandon RA (1989) Natural history of the axolotl and its relationship to other ambystomatid salamanders. In *Developmental Biology of the Axolotl* pp 13–21 Eds JB Armstrong and GM Malacinski. Oxford University Press, New York
 - Dawson A (1993) Thyroidectomy progressively renders the reproductive system of starlings, *Sturnus vulgaris*, unresponsive to changes in daylength *Journal of Endocrinology* **139** 51–55
 - Dawson A, Follett BK, Goldsmith AR and Nicholls TJ (1985) Hypothalamic gonadotrophin-releasing hormone and pituitary and plasma FSH and prolactin during photostimulation and photorefractoriness in intact and thyroidectomized starlings (*Sturnus vulgaris*) *Journal of Endocrinology* **105** 71–77
 - Dawson A, Williams TD and Nicholls TJ (1987) Thyroidectomy of nestling starlings appears to cause neotenuous sexual maturation *Journal of Endocrinology* **112** R5–R6
 - *Dawson A, McNaughton FJ, Goldsmith AR and Degen AA (1994) Ratite-like neoteny induced by neonatal thyroidectomy of European starlings, *Sturnus vulgaris* *Journal of Zoology, London* **232** 633–639
 - *de Beer GR (1956) The evolution of ratites *Bulletin of the British Museum (Natural History)* **4** 58–70
 - de Beer GR (1958) *Embryos and Ancestors* Clarendon Press, Oxford
 - Decuyper E and Kühn ER (1988) Thyroid hormone physiology in Galliformes: age and strain related changes in physiological control *American Zoologist* **28** 401–415
 - Deeming DC and Dick ACK (1995) Ingestion of metal objects by ostriches (*Struthio camelus*) *Veterinary Record* **137** 99–100
 - Deeming DC, Ayres L and Ayres FJ (1993) Observations on the commercial production of ostrich (*Struthio camelus*) in the United Kingdom: rearing of chicks *Veterinary Record* **132** 627–631

- Degen AA, Kam A and Rosenstrauch A (1989) Time activity budgets of ostriches (*Struthio camelus*) offered concentrated feed and maintained in outdoor pens *Applied Animal Behaviour Science* **22** 347–358
- Dodd MHI and Dodd JM (1976) The biology of metamorphosis. In *Physiology of the Amphibia* pp 467–599 Ed. B Lofts. Academic Press, New York
- Follett BK and Nicholls TJ (1985) Influences of thyroidectomy and thyroxine replacement on photoperiodically controlled reproduction in quail *Journal of Endocrinology* **107** 211–221
- Goldsmith AR and Nicholls TJ (1984) Thyroidectomy prevents the development of photorefractoriness and the associated rise in plasma prolactin in starlings *General and Comparative Endocrinology* **54** 256–263
- Goldsmith AR and Nicholls TJ (1992) Thyroxine effects upon reproduction, prolactin secretion and plumage moult in thyroidectomised European starlings *Sturnus vulgaris Ornithologia Scandinavica* **23** 398–404
- *Gould SJ (1977) *Ontogeny and Phylogeny* Harvard University Press, Cambridge MA
- Gould SJ (1991) *Bully for Brontosaurus* Hutchinson Radius, London
- Gudersnatsch JF (1912) Feeding experiments on tadpoles. The influence of specific organs given as food on growth and differentiation. A contribution to the knowledge of organs with internal secretions *Archiv Entwicklungsmech* **35** 457–483
- Haddad EE and Mashaly MM (1990) Effect of thyrotropin-releasing hormone, triiodothyronine, and chicken growth hormone on plasma concentrations of thyroxine, triiodothyronine, growth hormone, and growth of lymphoid organs and leukocyte populations in immature male chickens *Poultry Science* **69** 1094–1102
- Harms CA, Hoskinson JJ, Bruyette DS, Carpenter JW, Galland J, Veatch JK, Wilson SC and Baier JG (1994) Development of an experimental model of hypothyroidism in cockatiels (*Nymphicus hollandicus*) *American Journal Veterinary Research* **55** 399–404
- Harvey S (1990) Thyrotropin-releasing hormone as a growth-releasing factor: a review *Journal of Endocrinology* **125** 345–358
- King DB and May JD (1984) Thyroidal influence on body growth *Journal of Experimental Zoology* **232** 453–460
- Kreibich A and Sommer M (1995) *Ostrich Farm Management* Landwirtschaftsverlag GmbH, Munster-Hiltrup
- *Kühn ER and Jacobs GFM (1989) Metamorphosis. In *Developmental Biology of the Axolotl* pp 187–197 Eds JB Armstrong and GM Malacinski. Oxford University Press, New York
- Kühn ER, Decuypere E, Iqbal A, Luysterborgh D and Michielsen R (1987) A comparison between the thyrotrophic and peripheral activities of thyrotropin and thyrotropin-releasing hormone in the chick *Medical Science Research* **15** 431–432
- McNabb FMA and King DB (1993) Thyroid hormone effects on growth, development, and metabolism. In *The Endocrinology of Growth, Development and Metabolism in Vertebrates* pp 393–417 Eds MP Schreibman, CG Scanes and PKT Pang. Academic Press, Toronto
- O'Connor RJ (1984) *The Growth and Development of Birds* Wiley, Chichester
- Rudas P, Salyi G and Szabo J (1985) Decreased thyroxine, triiodothyronine and 5-deiodination levels in malabsorption syndrome *Avian Diseases* **30** 293–297
- Sales J and Mellett FD (1995) The determination of the age of ostrich carcasses from ossification of the pectoral girdle (ossa cinguli membrii thoracici) *Animal Science* **60** 499–501
- Scanes CG (1974) Some *in vitro* effects of synthetic thyrotropin releasing factor on the secretion of thyroid stimulating hormone from the anterior pituitary gland of domestic fowl *Neuroendocrinology* **15** 1–9
- Sharp PJ and Klandorf H (1985) Environmental and physiological factors controlling thyroid function in Galliformes. In *The Endocrine System and the Environment* pp 175–188 Eds BK Follett, S Ishii A Chandola. Japan Scientific Societies Press, Tokyo
- Sibley CG and Ahlquist JE (1981) The phylogeny and relationships of the ratite birds as indicated by DNA–DNA hybridization. In *Evolution Today, Proceedings 2nd International Congress Systematics Evolutionary Biology* pp 301–335 Eds GGE Scudder and JL Reveal. Hunt Institute Botanical Documentation, Carnegie-Mellon University, Pittsburgh
- Von Rautenfeld DB and Budras K-D (1982) The bursa cloacae (Fabricii) of Struthioniforms in comparison with the bursa of other birds *Journal of Morphology* **172** 123–138
- Wakahara M (1994) Spermatogenesis is extraordinarily accelerated in metamorphosis-arrested larvae of a salamander, *Hynobius retardus* *Experientia* **50** 94–98
- Wieselthier AS and van Tienhoven A (1972) The effect of thyroidectomy on testicular size and on the photorefractory period in the starling (*Sturnus vulgaris* L.) *Journal of Experimental Zoology* **179** 331–338
- Wilson FE and Reinhart BD (1993) The thyroid and photoperiodic control of seasonal reproduction in American tree sparrows (*Spizella arborea*) *Journal of Comparative Physiology B* **163** 563–573
- Woitkewitsch AA (1940) Dependence of seasonal periodicity in gonadal changes on the thyroid gland in *Sturnus vulgaris* L *Comptes Rendus (Doklady) de l'Academie des Sciences de l'URSS* **27** 741–745
- Woitkewitsch AA (1966) *The Feathers and Plumage of Birds* Sidgwick and Jackson, London
- Young JZ (1962) *The Life of Vertebrates* Oxford University Press, Oxford