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Chapter 9

HETEROCHRONY AND THE EVOLUTION OF AVIAN FLIGHTLESSNESS

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INTRODUCTION

In his landmark work on heterochrony, Gould (1977, p. 346) noted the phenomenon of delayed breeding in tropical seabirds, polygamous New World blackbirds (Icteridae), and grouse (Tetraonidae), and concluded:

> These cases do not involve neoteny: birds, when adult, do not retain juvenile features (so far as the literature records), and there is no delay of somatic development relative to reproduction.

The inclusiveness of this statement is doubly remarkable in light of the historical thoroughness that otherwise typified Gould's (1977) review. On the contrary, however, there is a long tradition of citing "neoteny" in the ornithological literature, one intertwined with the related concept of recapitulation.

Perhaps the earliest diagnosis of avian heterochrony, and one of the most compelling, was that by Strickland and Melville (1848, p. 4) concerning the extinct, flightless dodo (Columbiformes: *Raphus cucullatus*), which was described as having:

> . . . wings too short and feeble for flight, the plumage loose and decomposed, and the general aspect suggestive of gigantic immaturity.

These authors continued (1848, pp. 33–4):

> We cannot form a better idea of it than by imagining a young Duck or Gosling enlarged to the dimensions of a Swan. It affords one of those cases . . . where a species, or a part of the organs in a species, remains permanently in an underdeveloped or infantine state. Such a condition has reference to peculiarities in the mode of life of the animal, which render certain organs unnecessary, and they therefore are retained through life in an imperfect state, instead of attaining that fully developed condition which marks the mature age of the generality of animals.

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. . . And lastly, . . . the Dodo is (or rather was) *a permanent nestling*, clothed with down instead of feathers, and with the wings and tail so short and feeble,,as to be utterly unsubservient to flight [emphasis in original].

Unfortunately, like the dodo, ornithological study of heterochrony has remained in a protracted infancy, retarded in part by a poor appreciation of the diversity of processes involved in the phenomenon, as well as a confusion between pattern and process. Also, study of the evolutionary role of ontogeny in avian flightlessness suffered collateral damage from contemporary scientific debates concerning continental drift, homology, recapitulation and morphological convergence. With the exception of recent investigations of anatomical heterochrony in a few flighted species of birds (Fry, 1983; Dawson *et al.*, 1994) and the study of heterochrony of plumage and behaviour (Lawton and Lawton, 1986; McDonald and Smith, 1990, 1994), ornithological interest in heterochrony continues to centre on flightless species. In this paper I review the study of the ontogenetic basis of avian flightlessness, with an emphasis on the history of study and most promising directions for future research.

DIVERSITY OF FLIGHTLESS BIRDS

Flightless birds of the Cretaceous

Fossil remains of large, flightless, foot-propelled diving birds—the Hesperornithiformes—were first described in detail by Marsh (1880). Two families are recognized (Table 9.1). Members of the group currently are considered to represent one of the earliest branches in the class Aves (Gingerich, 1973; Cracraft, 1986). A flighted ancestor generally is assumed for the Hesperornithiformes, but this is not essential to the currently inferred phylogenetic position of the order (Cracraft, 1986). Members of the order are highly specialized for foot-propelled diving (Marsh, 1880; Martin and Tate, 1976). Available skeletal elements, including the comparatively distal elements described by Martin and Tate (1976), substantiate the radically shortened pectoral limbs of the Hesperornithiformes.

Lowe (1935, p. 410) considered *Hesperornis* to be:

. . . as reptilian as it was possible to be without losing its claim to be avian . . . an aquatic palæognath, just as the Ostriches (Struthiones) were cursorial palæognathes . . . there is little reason to think that either had volant ancestors . . .

Lowe (1935, p. 410) also likened *Hesperornis* to a "swimming ostrich" and later (1942, p. 17) included *Hesperornis* among the "aquatic or swimming palæognaths". Preliminary consideration of the probable ontogenetic mechanism(s) involved in producing the uniquely derived body form of this group indicates pectoral paedomorphosis combined with significant non-pectoral peramorphosis, but absence of developmental data and a flighted ancestral morphotype precludes detailed inferences.

"Ratites" or flightless paleognathous birds

Undoubtedly the most celebrated flightless birds are the "ratites" or flightless Paleognathiformes. Named for the flat, raft-like conformation of their sterna (Feduccia, 1980), "ratites" are relatively large, flightless land birds and include the ostriches, kiwis, and extinct moas. Prior to the recognition of continental drift, many ornithologists reasoned that these flightless giants of the southern continents were necessarily polyphyletic (e.g., Fürbringer, 1888; Mayr and Amadon, 1951; Storer, 1971), and evolutionary interpretations of flightlessness were made accordingly. Opinions regarding the phylogenetic relationships among ratites remain diverse, but monophyly of the group remains the favoured hypothesis (e.g., Bock, 1963; Parkes and Clark, 1966; Cracraft, 1974, 1986; Prager *et al.*, 1976; Sibley and Ahlquist, 1990; Stapel *et al.*, 1984; Bledsoe, 1988). Eight taxonomic families are recognized (Mayr and Amadon, 1951), distributed throughout the southern hemisphere (Table 9.1). Although varying in cursorial abilities, all ratites are (were) strictly terrestrial.

Often popularly considered to typify the flightless avian morphotype, ratites are diverse and combine profoundly primitive features (indicating an early divergence from most other modern birds) with a variety of extremely derived, often unique characters (only some of which are related to flightlessness). There is considerable variation in body size among the families of ratites; kiwis (Apterygidae) average 1–3 kg in total body mass, whereas the other extant ratites have mean body masses of 30–100 kg. Variation among ratites in osteology (especially the paleognathous palate) and the integument, widely interpreted as the result of divergence subsequent to common ancestry, has been cited as evidence of the polyphyly of ratites by several systematists (Fürbringer, 1888; Pycraft, 1900; McDowell, 1948; Houde, 1988; Bock and Bühler, 1990).

Flightless "carinate" (neognathous) birds

Neognathes, traditionally referred to as "carinates" because of the presence of a keel or carina on the sternum (Newton, 1896), include flightless members from a number of taxonomic orders, most of which show significant reduction of this purportedly diagnostic feature (Table 9.1). Unlike ratites, the higher-order phylogenetic relationships of flightless neognaths (possibly excluding the penguins) have not been a significant source of confusion, and most systematic issues have concerned the lesser determination of the closest flighted confamilials of each flightless species for purposes of comparison. The Gruiformes (cranes, rails, and allies) include the greatest number and diversity of flightless members; the rails (Rallidae) alone account for roughly one-third of the known flightless neognaths (Table 9.1). Penguins, the only modern neognathous order in which all species are flightless, are second-highest in number of flightless species

Table 9.1 Taxonomic diversity and geographical distributions of adequately documented flightless species of birds, after Raikow (1985). Groups preceded by daggers are extinct.

Taxonomic group			Flightless members			No. flightless species	
Order	Family	Subgroup(s)	Common name(s)	Period of occurrence	Distribution	(Sub)fossil	Modern
†Hesperornithiformes	Hesperornithidae	—	—	Cretaceous	Europe, N. and S. America	4+	—
	Baptornithidae	—	—	Cretaceous	N. (possibly S.) America	2+	—
Paleognathiformes	Casuariidae	—	Cassowaries	Pleistocene–Recent	Australia, New Guinea	0	3
	Dromaiidae	—	Emus	Pleistocene–Recent	Australia	1	2
	Apterygidae	—	Kiwis	Pleistocene–Recent	New Zealand	0	3
	†Dinornithidae	—	Moas	Miocene–Recent	New Zealand	11	0
	†Aepyornithidae	—	Elephant birds	Pleistocene–Recent	Madagascar (Africa, Europe)	2–9	—
	Struthionidae	—	Ostriches	Pliocene–Recent	Eurasia, Africa	5+	1–2
	Rheidae	—	Rheas	Eocene–Recent	S. America	1	2
	†Dromornithidae[a]	—	Mihirung birds	Miocene–Recent (?)	Australia	8	—
Galliformes	Megapodiidae	†*Sylviornis*[b]	—	Recent	New Caledonia	1	0
Anseriformes	†Cnemiornithidae	*Cnemiornis*	New Zealand geese	Pleistocene–Recent	New Zealand	2	—
	Anatidae	*Anser, Branta*	Typical geese	Pleistocene	Hawaii	2	0
		Three genera[c]	†Moa-nalos	Pleistocene	Hawaii	4	—
		Tachyeres	Steamer-ducks	Recent	South America	0	3
		Anas	Dabbling ducks	Recent	New Zealand, Amsterdam I.	1+	1+
		†*Chendytes*	"Diving geese"	Pleistocene	Pacific N. America	2	—
		Mergus	Mergansers	Recent	New Zealand	1	1
Sphenisciformes	Spheniscidae	—	Penguins	Eocene–Recent	Southern hemisphere	18+	18
Podicipediformes	Podicipedidae	Involves three genera[d]	Grebes	Recent	Central and S. America	0	3
Pelecaniformes	Phalacrocoracidae	*Compsohalieus*	Marine cormorants	Recent	Galápagos Islands	0	1
	†Plotopteridae	—	—	Oligocene/Miocene	N. Pacific	3	—
Ciconiiformes	Threskiornithidae	†*Apteribis*	Ibises	Pleistocene	Hawaii	2	—
		†*Xenicibis*	Ibises	Pleistocene	West Indies	1	—
†Gastornithiformes[e]	Gastornithidae	*Gastornis*	—	Paleocene	Europe, Asia	3	—
	Diatrymidae	*Diatryma*	—	Eocene	Europe, N. America	4+	—
Gruiformes	Mesitornithidae[f]	*Mesitornis, Monias*	Roa-talos	Pleistocene–Recent	Madagascar	0	3
	†Phorusrhacidae	—	—	Eocene(?)–Pliocene	N. and S. America, Europe	10+	—
	†Bathornithidae	*Paracrax*, others(?)	—	Eocene–Miocene	N. America	3+	—
	Rhynochetidae[f]	*Rhynochetos*	Kagus	Pleistocene–Recent	New Caledonia	1	1
	†Apterornithidae	*Apterornis*	Adzebills	Pleistocene–Recent	New Zealand	2	0
	Gruidae	*Grus*	Cranes	Pleistocene	Cuba	1	0
	Rallidae	Involves 16+ genera[g]	Rails	Pleistocene–Recent	Oceanic islands worldwide	25+	30+
Charadriiformes	Alcidae	†Mancallinae	Lucas auks	Miocene–Pleistocene	Pacific N. America	8	0
		†*Pinguinus*	Great auks	Pliocene	Coastal N. Atlantic	1	1
Strigiformes	Strigidae	†*Ornimegalonyx*	Cave owls	Pleistocene	Cuba	1+	0
Psittaciformes	Psittacidae	*Strigops habroptilus*	Kakapo or owl parrot	Recent	New Zealand	0	1
Columbiformes	†Raphidae	*Raphus, Pezophaps*	Dodo and solitaire	Recent	Mascarene Islands	0	2+
Passeriformes	Acanthisittidae	Several genera	New Zealand wrens	Pleistocene–Recent	New Zealand	3	1
	Atrichornithidae[f]	*Atrichornis*	Scrub-birds	Recent	New Zealand	0	2
	Menuridae[f]	*Menura*	Lyretails	Recent	Australia	0	2

[a] Inclusion among Paleognathiformes provisional.
[b] Classification tentative.
[c] Relationships of the three extinct genera—*Thambetochen* (2 spp.), *Ptaiochen* (1 sp.) and *Chelychelynechen* (1 sp.)—within the Anseriformes remain controversial.
[d] *Rollandia microptera, Podilymbus gigas* and *Podiceps taczanowskii*.
[e] Composition and position of this order remain controversial.
[f] Actually weakly flighted.
[g] Flightless species (many extinct) in a number of genera, including *Porphyrio* (swamphens), †*Nesotrochis*, †*Aphanapteryx*, †*Diaphorapteryx*, *Habroptila*, *Tricholimnas*, *Rallus* (typical rails), *Gallirallus* (wekas), *Atlantisia*, *Porzana* (crakes), *Amaurornis* (bush-hens), *Tribonyx* (water-hens) and *Fulica* (coots).

(Table 9.1; Livezey, 1989a). Flightlessness has evolved in at least three genera of grebes (Livezey, 1989b), nine different lineages of waterfowl (Livezey and Humphrey, 1986; Livezey, 1989c, 1990, 1993a), and several genera of auks (Livezey, 1988). Most other instances of flightlessness among carinates are limited to comparatively few species (Table 9.1), but include members of such diverse groups as the cormorants (Livezey, 1992a), parrots (Livezey, 1992b), and dodos (Livezey, 1993b).

Flightless carinates include a number of terrestrial species, mostly limited to islands, including the dodo, solitaire (*Pezophaps solitaria*), several ibises, and most flightless rails. Flightless carinates inhabiting marine coastlines include(d) surface-feeding waterfowl like the Auckland Islands teal (*Anas aucklandica*), foot-propelled diving species like the steamer-ducks (*Tachyeres* spp.) and Galápagos cormorant (*Compsohalieus harrisi*), and pelagic, wing-propelled diving species like the great auk (*Pinguinus impennis*) and the penguins. Flightless grebes, also foot-propelled diving birds, inhabit(ed) continental, freshwater lakes. Several flightless birds are capable of arboreal climbing, including the New Guinea flightless rail (*Amaurornis ineptus*) and a nocturnal parrot, the kakapo (*Strigops habroptilus*).

HETEROCHRONY AND THE EVOLUTION OF RATITES

Historical perspective

Degeneration and ontogeny

Originally grouped taxonomically on the basis of their truly "keel-less" sterna (Merrem, 1813) and short wings (Lesson, 1831), ratites are unique among birds in a variety of morphological characters, including variably "loose" plumage structure, synostosis of the scapula and coracoid, substantially reduced pectoral appendages, and powerfully developed pelvic limbs (e.g., Beddard, 1898; Pycraft, 1900; Glutz von Blotzheim, 1958; McGowan, 1982; Raikow, 1985). Most early naturalists, including Darwin (1859), attributed the diminutive pectoral limb of ratites to "disuse" or "degeneration". Other anatomists also interpreted the "degenerate" characters of ratites as the products of truncated development (T.J. Parker, 1882; Newton, 1896; Duerden, 1920; Gregory, 1935).

Eventually, the idea that adult ratites retained "juvenile" anatomical characters gained support, and the hypothesis was extended beyond the pectoral appendage to the cranium, pelvic girdle, and integument (de Beer, 1930, 1956, 1975; McDowell, 1948; Webb, 1957). Thus commenced an ornithological tradition of equating "neoteny" with the "process of retention of juvenile characters" (James and Olson, 1983, p. 31), and this term is frequently considered to include any process or outcome of heterochrony in birds (Feduccia, 1980; James and Olson, 1983; Olson, 1985). Under currently accepted nomenclature, however, most ornithological instances represent the *result* "paedomorphosis"; the underlying heterochronic *mechanism*, one plausible candidate being neoteny, generally remains undiagnosed. A growing body of evidence led to the traditional orthodoxy exposing the "neoteny" of ratites and the current consensus that the ratites evolved from flighted ancestors, thus establishing that flightlessness among Paleognathiformes is a derived condition and probably involves heterochrony.

Lowe's quandary, or "ontogeny vs. phylogeny"

An especially illuminating ornithological example of the intimate conceptual relationship between recapitulation and heterochrony is provided by the writings of Percy Roycroft Lowe, curator in the Bird Room at the British Museum (Natural History) during 1919–1935. Although vestiges of recapitulationist theory lingered in the ornithological writings of some prominent ornithologists through the turn of the century and many considered the ratites to be anatomically "archaic" or (in part) "reptilian", the relevance of recapitulation to the evolution of ratites remained controversial (W.K. Parker, 1888a; Newton, 1896; Beddard, 1898; Wiglesworth, 1900; Heilmann, 1927). Lowe (1926) initially was provoked by the Lamarckian interpretations by Duerden (1920) of the anatomy of the ostrich (*Struthio camelus*), in which a number of characters also were described as "degenerative". As evident from his earliest studies of avian anatomy, Lowe was a die-hard recapitulationist (*sensu* Haeckel, 1866). Accordingly, Lowe (1928a, p. 187) instead interpreted the retention of cranial sutures in ratites as:

> . . . a belated manifestation of a reptilian character in the "Ratite" skull.

Lowe (1928a, p. 245) recognized that:

> . . . the adults of the existing Struthiones are clothed in prepennal down and have not reached a much more advanced stage of development than the downy chick of a fowl.

However, he concluded (Lowe, 1928a, p. 244) that:

> . . . the Struthiones represent a perfectly natural group descended from some common ancestor which left the main avian stem before flight had been attained.

This interpretation of the "primary" nature of the flightlessness of ratites, combined with ancillary anatomical work on other avian groups, led Lowe (1933, p. 533) to define three subclasses of Recent birds, all of which he thought had ". . . specialized independently from a common generalized ancestor". These were:

> (1) a true aquatic, represented solely by the Penguin; (2) a cursorial, represented by such forms as the "Ostriches"; (3) a flying, represented by the Carinate division of birds.

Lowe (1935, p. 411) clarified his recapitulationist interpretation of the evolution of ratites, one combined with an almost Aristotelean reverence for avian flight:

. . . flight in birds was only a comparatively recent crowning feat in their evolution, and that for infinitely the greater part of the total time consumed since their first appearance birds may be regarded as having been flightless. . . . The flying, or the highest type of bird . . . seem[s] to have appeared . . . toward the end of the Cretaceous . . . But in some groups of birds, such as the Struthionids and the Penguins, may . . . have missed the evolutionary bus.

Lowe (1935, p. 412) concluded:

In the Struthiones the entire make-up of the adult is chick-like and reflects the beginning of the story of avian evolution instead of the end.

Lowe (1935, p. 414) considered the scapulocoracoid of ratites to be of "definitely reptilian" form.

Lowe (1942, p. 6) continued to make important anatomical observations on ratites, and cited the ". . . elementary simplicity of a high degree" of a wing muscle, the "Flexor carpi ulnaris" [M. expansor secundariorum] of *Rhea*, but interpreting the genus as:

. . . a simple, primitive, and blind-alley phase of a process of evolution which in other birds was eventually to end in the more complicated flying technique seen in the more highly placed Neognathæ.

Lowe (1942, pp. 6–7) also explicitly challenged the hypothesis of the "neoteny" of ratites:

. . . if their morphology could be properly ascribed to a process of Neoteny, . . . [this muscle] would have presented . . . the normal youthful conditions seen in the just hatched chick of an ordinary flying bird . . . and would have comparable in morphological details with those of the adult bird. But in *Rhea*, . . . the muscle bears little or no resemblance to that seen in the normal Neognathous chick, flying or non-flying . . . There is no indication in it of a possibility of flight in the ancestor or . . . owner of the wing, when the adult stage had been reached.

Lowe (1942, p. 9) noted that in *Rhea*:

. . . the stage of development in the wing . . . *considerably antedates in point of evolution any mere juvenile phase in the Neognathæ* [emphasis in original].

This view of primitive flightlessness of ratites led Lowe (1944: p. 518) to conclude that the feathers of *Archaeopteryx* were not strictly homologous with those of modern Aves. As for the theory of continental drift and the biogeography of ratites, Lowe (1944, pp. 521–2) preferred the scenario of the wide distribution and relictual persistence of primitively flightless "struthious stock" (either prior or subsequent to movement of continental plates) to the alternative of derived avian flightlessness, which he believed required that:

. . . at some time or other every family, genus or species, no matter how wide their geographical separation, all, without exception, *independently* lost the power of flight and became degenerate.

Contemporary opposition to Lowe's theory regarding the ratites was strong, although many of the "primitive" characters cited by Lowe were used by his critics to support the alternative hypothesis of heterochrony (e.g., McDowell, 1948). Murphy (*in* Gregory, 1935, p. 12) wrote:

Dr Lowe regards both of these characteristics [absence of apterylae and barbicels] as ancestral and primitive . . . that, in the case of the ostrich-like birds, feather evolution has not proceeded much beyond an embryonic or "early avian" stage . . . The result may rather have been attained through the actual dropping out or cutting off of the final stage of feather development somewhere along the line of the ostrich's phylogeny.

Tucker (1938, p. 224) submitted similar arguments:

Doubtless these ancestral forms were a good deal more primitive than present-day birds, and some of the Ratite characters, like the palaeognathous palate, may be a direct legacy from them. But . . . the conclusion seems that . . . [they] . . . are not in fact primitive in the phylogenetic sense, but are literally embryonic characters carried over into the adult, constituting a striking instance of neoteny or retarded development.

The hypothesis of the "primary flightlessness" of ratites championed by Lowe won support from several other anatomists (Holmgren, 1955; Glutz von Blotzheim, 1958). Although Lowe's hypothesis remained a minority view, it continued to have some influence on subsequent opinion. McGowan (1982, 1986) reconsidered the possible primitiveness of flightlessness in ratites based on an assessment of the evolutionary changes that would be necessary to transform a fully flighted bird into one possessing ratite-like characteristics. Also, McGowan (1984, p. 735) cited Lowe (1928a, 1935) in support of the conclusion that:

Indeed, most of the features that distinguish ratites from carinates are now considered to be primitive rather than derived.

Toward synthesis

Anatomical and embryological research on ratites (e.g., Owen, 1842; T.J. Parker, 1892; Lutz, 1942; Frank, 1954; Lang, 1956; Webb, 1957; Müller, 1963) complemented studies of development in other birds (e.g., W.K. Parker, 1888b; Steiner, 1922; Fell, 1939; Montagna, 1945; Klima, 1962; Sullivan, 1962), and led to broad support for the importance of heterochrony in the ratites. de Beer (1956, 1975) became a leading proponent of this hypothesis, citing (1956, p. 65):

. . . the presence in the Ratites of nestling-down, permanent sutures between the bones of the skull, and the dromaeognathous [paleognathous] structure of the palate . . . [as] demonstrably the result of neoteny or the secondary retention of features which were juvenile in the ancestors of the Ratites.

de Beer (1956, p. 66–7) concluded:

For those, if there be any, who still believe in the theory of recapitulation, it would no doubt be tempting to say that the neognathous palate "recapitulates" in its development the condition of the paleognathous palate which would therefore be ancestral. But in view of the overwhelming evidence that the Ratites are secondarily descended from flying birds . . . [and] the fact that the Ratites already show neoteny in two other features . . . it is impossible to believe that in their palates the Ratites are primitive.

Cracraft (1974, 1986) presented phylogenetic analyses of the ratites, in which the evolution of flightlessness was inferred (at least on the grounds of evolutionary parsimony) to have occurred only once (in the common ancestor of the group). Although differing in some topological findings, a phylogenetic analysis by Bledsoe (1988) also supported the monophyly of the ratites, and patterns of molecular (phenetic) similarity are consistent with this hypothesis (Prager *et al.*, 1976; Sibley and Ahlquist, 1990; Stapel *et al.*, 1984). Several other authors, however, questioned the monophyly of the ratites (Houde and Olson, 1981; McGowan, 1984; Feduccia, 1980, 1985; Olson, 1985; Bock and Bühler, 1990), raising doubts concerning the homology of the anatomical characters associated with flightlessness in the included families. None of the latter critics, however, proposed explicit phylogenetic alternatives to the hypothesis of monophyly.

Significant disagreement concerning the polarities and ontogeny of the distinctive characters of ratites remains. Unfortunately, some of the debate derives less from substantive differences in inference than from confusion concerning the concept of homology. Cracraft (1981, p. 689) correctly emphasized that:

. . . an argument of neoteny is a *prima facie* admission that the similarities in question are derived and not primitive, that is, the adult condition of the ancestor is "replaced" in the descendant by the juvenile condition.

This does not imply that any two *similar* "neotenic" states are necessarily synapomorphic, i.e., *shared* derived characters, but that both are derived and *possibly* homologous. In a discussion of the implications of recapitulation for the anatomy of ratites, however, Feduccia (1980, p. 135) confused truly primitive characters with derived, pseudo-primitive characters produced secondarily through heterochrony. Similarly, arguments by Olson (1985, p. 100) concerning "neotenic" characters of ratites indicate confusion on both the issues of homology and polarity.

Even where the derived nature of "neotenic" characters is appreciated, there is a tradition of assuming that such characters evolve "willy-nilly" in flightless birds, nullifying their utility in phylogenetic inference (e.g., Olson, 1973a,b, 1982). Feduccia (1980, p. 135) expressed an optimism concerning the evolutionary power of heterochrony by suggesting that the neognathous order ". . . Gruiformes would be the best candidates for some of the various forebears. . . ." of the "neotenic forms" of the ratites. Olson (1983) offered an extreme view of the potential of heterochrony when he implied that "neoteny" might have produced the kiwis and moas independently from different carinate groups (ibises and geese, respectively).

Impugning the phylogenetic informativeness of "neotenic" characters through overstatement is also typical. In a critique of the hypothesis of ratite monophyly, Feduccia (1985, p. 186) asserted:

Following Cracraft's use of neotenic characters as shared, derived features, we might logically include all flightless rails in the same genus as they all possess reduced wings, a keel-less sternum and an open ilioischiatic fenestra. . . .

Setting aside the inaccuracies of the anatomical generalizations (adult flightless rails are neither strictly acarinate nor possess open ilioischiatic fenestrae) and the unsupported suggestion that monophyly would necessarily imply membership in the same *genus*, this statement implies that either one must consider *all* "neotenic" characters as homologous or consider them *all* to be convergent. The truth, however, probably lies somewhere between these two extremes. Even the harshest critics of "neotenic" characters in phylogenetic reconstruction would admit the homology of the many flightlessness-related characters of subgroups of ratites, e.g., those uniting the kiwis (T.J. Parker, 1892; Pycraft, 1900; McGowan, 1982).

For those characters generally acknowledged to have been the result of heterochrony, imprecision prevails regarding the mechanisms and organ systems involved. Related to the tradition of synonymizing paedomorphosis (perhaps heterochrony) with neoteny in regard to paleognathous birds, differential diagnoses among the three ontogenetic mechanisms producing paedomorphosis (neoteny, postdisplacement and progenesis) and the three counter-mechanisms resulting in peramorphosis (acceleration, predisplacement and hypermorphosis) are all but lacking in the ornithological literature. The diminutive pectoral apparatus and delay in closure of cranial sutures of ratites may, in fact, involve neoteny, especially in light of the retarded progress of the latter until several years after hatching (Elzanowski, 1988; Beale, 1991). Also, the obtuse scapulo-coracoid angle shared by adult ratites and embryonic carinates also suggests neoteny *sensu stricto* (Nauck, 1930; Kaelin, 1941), but postdisplacement has not been empirically excluded. The radically derived anatomy of ratites, however, defies the proposal of any single heterochronic mechanism as completely explanatory (Table 9.2). Levinton (1988) rightly emphasized the potentially complex interactions of diverse heterochronic perturbations in different organ systems within lineages, and it is evident that most or all ratites manifest (at least) peramorphosis of the pelvic limb as well as paedomorphosis of the pectoral limb (McKinney and McNamara, 1991). Elzanowski (1988) critiqued many supposed examples of "neoteny" in ratites, including several features of the skull, pectoral limb, pelvis, and integument, and proposed that some of these instead may be the result of peramorphosis or may simply be plesiomorphous. Critical data for the diagnosis of the ontogenetic basis of the unique morphology of ratites are lacking; however, it is clear that several developmental mechanisms are involved, producing a complex constellation of variably localized heterochronic changes in skull, pectoral and pelvic appendages, and integument (Table 9.2).

Table 9.2 Changes in body size, plumage, skull, appendages, and underlying heterochronic mechanisms hypothesized in selected flightless birds.

Species	Body size	Plumage	Skull	Girdle and appendage: Pectoral	Girdle and appendage: Pelvic	Hypothesized heterochronic mechanism(s)
Ratites	Increase[a]	Paedomorphosis, peramorphosis	Paedomorphosis, peramorphosis	Paedomorphosis, peramorphosis	Paedomorphosis, peramorphosis	Neoteny of feather structure, hypermorphosis of pterylosis; possible localized paedomorphosis of palate and cranial sutures, possible generalized cephalic hypermorphosis; neoteny or hypermorphosis of pectoral girdle, neoteny of pectoral limb; neoteny and/or hypermorphosis of pelvic girdle, hypermorphosis of pelvic limb
New Zealand geese	Increase	—[b]	Peramorphosis	Paedomorphosis	Peramorphosis	—[b]
Flightless steamer-ducks	Increase	No change	No change	Paedomorphosis	No change	Pectoral postdisplacement[c]
Auckland Islands teal	Decrease	Paedomorphosis	No change	Paedomorphosis	No change	Generalized progenesis
Auckland Islands merganser	No change	Paedomorphosis	Peramorphosis	Paedomorphosis	No change	Neoteny of plumage pattern and pectoral apparatus
Titicaca grebe	Increase	No change	Peramorphosis	Paedomorphosis	Peramorphosis	Pectoral postdisplacement,[c] cranial and pelvic hypermorphosis
Galápagos cormorant	Increase[a]	Paedomorphosis	Peramorphosis	Paedomorphosis	Peramorphosis	Neoteony of plumage pattern and pectoral apparatus, cranial and pelvic hypermorphosis
Adzebills	Increase	—[b]	Peramorphosis	Paedomorphosis	Peramorphosis	—[b]
Weka[d]	Increase	Negligible change	Negligible change	Paedomorphosis	Peramorphosis	Pectoral neoteny, pelvic hypermorphosis
Inaccessible Island rail[d]	Decrease	Paedomorphosis	No change	Paedomorphosis	Peramorphosis	Plumage and pectoral progenesis, pelvic hypermorphosis
Kakapo	Increase	Indeterminate	No change	Paedomorphosis	Peramorphosis	Pectoral neoteny, pelvic hypermorphosis
Dodo	Increase	Paedomorphosis	Peramorphosis	Paedomorphosis	Peramorphosis	Plumage and pectoral neoteny, cranial and pelvic hypermorphosis

[a] Evolutionary size increases inferred for most ratites may not apply to kiwis; small size of Apterygidae may be primitive or represent a derived reversal.
[b] Subfossil remains only, characters of integument unknown, heterochronic mechanisms not diagnosable.
[c] Inference tentative, based on static morphometric analysis.
[d] Currently under study, inferences preliminary.

HETEROCHRONY AND THE EVOLUTION OF FLIGHTLESS CARINATES

Historical perspective

Penguins and Lowe's "primary" flightlessness

The anatomical peculiarities of penguins were widely appreciated by the early twentieth century, but early research on the ontogeny of penguins produced diverse interpretations. For example, Wray (1887, p. 353) found that:

> The embryo of the Penguin shows in its wings no signs of being a degeneration or modification of the specialized flight-wing of other Carinates.

In contrast, Pycraft (1907, p. 18) concluded:

> The wing of the embryo penguin . . . will be found to differ remarkably from that of the adult, and entirely confirms the contention that the paddle of the modern Penguin has been derived from a functional flying wing . . . It agrees in all essentials with that of the adult flying bird more closely than at any other later stage of development.

True to his recapitulationist perspective, Lowe (1933, p. 522) interpreted the ontogeny of penguins differently:

> We find nothing . . . resembling an approach to the morphological details to be noted in a similar series proper to the embryo of a flying bird.

Lowe (1933, p. 534) concluded:

> . . . while the Penguin seems to have specialized *directly* from the primitive non-flying generalized ancestor, all other swimming and diving birds are neither more nor less than flying Carinate types, and are, in fact, what one might term only pseudo-aquatic [emphasis in original].

As with Lowe's interpretation of the ratites, criticism of his analysis of flightlessness in the penguins was forthcoming. Murphy (*in* Gregory, 1935, pp. 14–15) wrote:

> Dr Lowe . . . sees through his study of the penguin feather the outcome, not of a process of degeneration, but one of failure to develop. . . . The arrangement of the wing feathers in the penguins may be said to be larval in character, with specialities superimposed . . . Many penguin characters, including those of feathers, are doubtless to a certain extent larval, but this by no means precludes the likelihood that in earlier stages this same feather structure may have been succeeded by others which have since dropped away.

Wiman and Hessland (1942) and Simpson (1946) rejected Lowe's (1933) recapitulationist view of the flightlessness of penguins, arguing instead that the Sphenisciformes were derived from an ancestor capable of aerial flight. Also, Simpson (1946) described a partial reversal in tarsometatarsal fusion in modern penguins (compared with Miocene penguins), a shift that McDowell (1948, p. 540) credited to "neoteny".

Other flightless carinates and Lowe's "secondary" flightlessness

Between the 19th century series of publications treating the anatomy of the extinct dodo and solitaire (e.g., Strickland and Melville, 1848; quoted above) and the early part of the twentieth century, possible ontogenetic mechanisms of flightless carinates exclusive of the penguins received relatively little attention. Typical of the period were the references by Newton (1896) to "disuse" leading to an "aborted condition" of carina sterni of the flightless parrot, the kakapo. Similar observations were made for the takahe (Rallidae: *Porphyrio mantelli*) by T.J. Parker (1882) and the Galápagos cormorant by Gadow (1902). A notable exception was the study of the diminutive, flightless Inaccessible Island rail (Rallidae: *Atlantisia rogersi*) by Lowe (1928b). Lowe (1928b, pp. 105–6) explicitly considered ontogenetic mechanisms, and wrote:

> . . . the almost wholly black coloration characteristic of the chicks of the Ralline family is apparently retained for a much longer time than is usual in immature examples, would seem to suggest that *Atlantisia* is a generalised and so presumably a near representative of some more primitive type. In the most adult example . . . there is still a very evident air of immaturity . . . borne out by the discovery that the remiges or wing-feathers, as regards the development of the rami and radii, exhibit microscopically a stage of evolution which has not advanced beyond that seen in the body or contour feathers of such a volant form as *Rallus aquaticus*.

Lowe (1928b, pp. 108–9) continued:

> The view might be taken that such a condition is an indication of an arrest or a retardation of development . . . At any rate, the almost invariable explanation of the morphological changes present in flightless rails or other birds is that they are simple manifestations of degeneration or retrogression resulting from mere disuse of the wing . . . merely secondary changes practically akin to atrophy.

Lowe (1928b) reserved "secondary" flightlessness among Rallidae to those in which he found no qualitative anatomical changes, especially in feather structure (e.g., *Dryolimnas*, *Porphyriornis* and *Porzana*), and noted the relationship between flightlessness and the generally slow pectoral development of rails. Thus Lowe (1928b) resurrected Fürbringer's (1888) distinction between flightless birds having no flighted ancestors (*Prot-Apterornithes*) and those having secondarily lost flight (*Deuter-Apterornithes*). Fürbringer (1888), however, had reserved the former for ancient, largely hypothetical proto-birds (*Protorthornithes*) and included the ratites (which he believed to be polyphyletic) in the latter group (Newton, 1896).

Subsequently, Lowe (1934) included the flightless steamer-ducks in the "secondary" group, inferring (p. 482):

> . . . that the rate of growth of the wing of the non-flying embryo has either been already relatively retarded before hatching or the rate of general body growth relatively accelerated.

Lowe (1935, pp. 411–12) contrasted the condition of flightless carinates with that of ratites:

> . . . when a carinate flying bird becomes flightless it still remains . . . essentially similar in anatomical details to the generality of flying birds. Even its wings do not undergo essential change, except as regards a simple atrophy relative to the rest of the body. A diminution or want of development in size may, of course, occur in the sternum, fore-arm, and muscles, but in such flightless birds such as the ocydromine Rails of New Zealand the various component parts of the remigial and body-feathers—barbs, barbules, and barbicels—all reflect the essential structure and disposition of the normal carinate flying and body feathers, except that their development may have been inhibited, and so caused to lag behind in a juvenile phase.

Lowe (1935, pp. 424–8) extended "secondary flightlessness" to some rallids (now evidently including *Gallirallus*, *Diaphorapteryx* and *Atlantisia*), the dodo and solitaire, and the Galápagos cormorant, but his discussion of "temporary" and "permanent" retardation of growth indicates a misunderstanding of the physiological causes of paedomorphosis. Lowe (1935, p. 430) reaffirmed that although neoteny may have contributed to the pectoral retardation of flightless steamer-ducks and rails:

> . . . the inhibiting factor has not converted them from a neognathous to a palæognathous condition. They present nothing approaching to the larval make-up of the Ostrich.

In one of his last papers on avian flightlessness, Lowe (1942, p. 7) revealed a reluctance to credit even "secondary flightlessness" to neoteny (narrowly conceptualized), writing:

> It may be that some would explain these cases of secondary flightlessness in Neognathous birds by the phenomenon of Neoteny, but by whatever name we may choose to designate them, I am driven to believe that they will ultimately be proved to be due either to the action of some *permanent* inhibitory growth-factor or hormone, such as acts *temporarily* as a normal occurrence in the chicks of Ducks and Rails, or, on the other hand, to the absence of some normal stimulating growth-factor [emphasis in original].

Toward synthesis

Descriptive support for a "neotenic" basis of flightlessness in rails and other flightless land birds continued (e.g., Olson, 1973a,b; Feduccia, 1980; James and Olson, 1983), and resemblances between adult flightless birds and subadult flighted species provided new insights into the ontogeny of flightlessness. These correspondences include: reduction of the carina and incomplete development of the caudal margin of the sternum (T.J. Parker, 1882; Lowe, 1928b, 1934; Fell, 1939; Klima, 1962); obtuse scapulocoracoid angles (Nauck, 1930; Kaelin, 1941); and disproportionate reduction of the distal wing elements relative to proximal elements (Gadow, 1902; Steiner, 1922; Montagna, 1945; Sullivan, 1962; Levinton, 1988).

Contrary to the prominence accorded penguins in early studies of the ontogeny of flightlessness, the possible role of heterochrony in the evolution of flightlessness in wing-propelled diving birds (by any name) has received minimal attention in recent decades. Some of this disinterest reflected an assumption that "neoteny" necessarily produces an underdeveloped wing. Olson (1977, p. 690), in a discussion of flightless auks, stated:

> The great modifications seen in the wing . . . are not the result of neoteny, as seen in many other flightless birds . . . Instead, these modifications represent highly derived specializations for wing-propelled diving.

However, it is now appreciated that neoteny and other heterochronic mechanisms leading to paedomorphosis are not limited in effect to simple underdevelopment, but can generate important innovations (McKinney and McNamara, 1991). Some of the morphological specializations of flightless wing-propelled diving birds that have obscured possible paedomorphosis (e.g., proportions within the wing skeleton) may themselves be the result of heterochrony (Livezey 1988, 1989a).

An overly narrow view of "neoteny" also influenced expectations concerning the timing and generality of the resultant morphological effects and this led to speculations concerning likely candidates for "neotenic" flightlessness based on general developmental differences among taxonomic groups. Feduccia (1980, p. 112) assumed that "neoteny" necessarily affects all organ systems equally. The possibility of localized paedomorphosis of the pectoral apparatus seems not to have been considered, although this appears to characterize several other flightless carinates (Livezey and Humphrey, 1986; Livezey, 1992a,b, 1993a). Moreover, the discovery by Poplin and Mourer-Chauviré (1985) of a large, extinct flightless megapode from New Caledonia indicates that paedomorphosis targeting specific organ systems also occurs in the Galliformes.

Further study of flightless carinates has indicated a substantial diversity of underlying heterochronic change, although diagnostic examination of ontogeny has yet to be accomplished for any taxonomic group (Table 9.2). In addition to neoteny, preliminary assessments indicate that pectoral paedomorphosis in several groups evidently may involve postdisplacement or progenesis (Livezey and Humphrey, 1986; Livezey, 1989b,c, 1990, 1992a,b, 1993a,b,c, 1994). Most instances of avian flightlessness are associated with increased body size (Table 9.2), and this in part reflects peramorphosis of regions other than the pectoral limb. Peramorphosis of the pelvic limb is especially conspicuous in some groups (McKinney and McNamara, 1991; Livezey, 1992a,b, 1993a,b, 1994), associated with a "compensatory" shift in appendicular specialization recognized by Gadow (1902) for the Galápagos cormorant. Andors (1988) proposed that the primary heterochronic mechanism that produced the extraordinary body form of the giant, flightless "terror cranes" (Diatrymidae) may have been hypermorphosis. Probably the most extreme pectoral paedomorphosis among carinates is that of the extinct gruiform *Apterornis* (Livezey, 1994). A diversity of heterochronic mechanisms and evolutionary trends in body size and sexual dimorphism is evident in flightless rails (Table 9.2; Livezey, in prep.).

Increased sexual size dimorphism also is associated with loss of flight in a number of species, and is especially marked in those lineages in which non-pectoral peramorphosis is indicated (Livezey and Humphrey, 1986; Livezey, 1989b, 1990, 1992a,b, 1993b). Furthermore, in the flying steamer-duck (Anatidae: *Tachyeres patachonicus*), a species with negative allometry between wing area and body mass, sexual differences in body size produce flightlessness in a minority of males in some marine populations, whereas the smaller females remain capable of flight (Humphrey and Livezey, 1982).

HETEROCHRONY AND AVIAN FLIGHTLESSNESS: FUTURE DIRECTIONS

Morphometric and embryological approaches

A revolution in the mathematical description of relative (allometric) growth was begun by Huxley (1932), and the quantitative nature of the ontogenetic processes involved in heterochrony was recognized soon thereafter (de Beer, 1940). The mechanisms underlying heterochrony and its morphological products are well summarized graphically (Tissot, 1988; McKinney and McNamara, 1991). Most studies of avian heterochrony, however, remain descriptive, non-quantitative, and based on static analyses of adults. A number of bivariate and multivariate approaches can provide useful numerical summaries of ontogenetic change and its relationship to interspecific differences among adults (Livezey, 1989b, 1990, 1992a, 1993c). Critical ornithological studies based on known-age developmental series of flighted and flightless relatives, including pre-hatch embryos and detailed records of ossification, muscle primordia, and pterylosis, have yet to be performed. Such research would be particularly powerful for an analysis of heterochrony in the ratites, for which the ontogeny of ostriches (currently the subject of an expanding commercial aviculture) would be most appropriate. Where possible, the physiological and behavioral corollaries of ontogeny should be examined as well.

James and Olson (1983, p. 31) envisioned a streamlined ontogeny of avian flightlessness:

> The genetic mechanism for the evolution of a flightless bird from a flying one is actually quite simple. All birds are flightless when they are small chicks, and the young of flying birds have the same features that characterize the adults of flightless birds . . . Merely by retaining the skeletomuscular structure of infancy into adulthood—probably by the alteration of a few regulatory genes—almost any bird species could become flightless.

The supposed role of regulatory genes in producing paedomorphosis, however, remains largely hypothetical and probably is overly simplistic. An understanding of the genetic bases of heterochrony in birds is crucial to an assessment of the evolutionary "ease" with which the resultant conditions (e.g., paedomorphic flightlessness) arise.

Recent work by Dawson *et al.* (1994) revealed that thyroidectomized starlings (Sturnidae: *Sturnus vulgaris*) attained sexual maturity but displayed several "juvenile" characters judged to be comparable to those found in *adult* ratites, including long contour feathers lacking barbicels, aborted palatal and rostral development, and incomplete closure of cranial sutures (although presence of the latter in adult ratites was contested by Elzanowski (1988)). Decades earlier, Edinger (1942) suggested that the giantism and plumage structure of ratites might be related to hyperactivity of the pituitary. Although the speculations by Edinger (1942) and Dawson *et al.* (1994) concerning the role of endocrinology in the evolution of modern ratites are less than convincing, these reports indicate the considerable promise that experimental embryology may hold for the elucidation of the ontogenetic processes underlying avian heterochrony. Combined with a new appreciation for the physiological implications of avian flightlessness (Calder and Dawson, 1978; Vleck *et al.*, 1980; Livezey, 1992b, 1993b), the extension of the study of heterochrony beyond simple anatomical comparison and into embryological and physiological dimensions is the next logical step (McNab, 1994).

Phylogenetic perspective on avian heterochrony

An understanding of phylogenetic relationships is critical for comparative studies and the detection of evolutionary change. From the ontogenetic standpoint, avian transitions to flightlessness provide multiple (hierarchically nested) evolutionary "replicates", in that loss of flight results from a variety of subtly and (in some cases) distinctly different perturbations in ontogeny. Late development of the pectoral appendage in birds makes paedomorphosis the most obvious ontogenetic inference in flightless birds, but as more detailed studies of avian flightlessness are made it is likely that several heterochronic mechanisms will be documented. For example, the direction of changes in body size and plumage dichromatism that accompanied paedomorphosis in the flightless Auckland Islands teal (Livezey, 1990, 1991) and Auckland Islands merganser (Livezey 1989c) were determinable only within the context of corroborated phylogenetic hypotheses (Livezey, 1990, 1991). Even if a phylogenetic hypothesis remains controversial, it permits the placement of the associated evolutionary inferences within an explicit historical context.

Unfortunately, progress in the study of heterochrony in flightless birds has been hampered significantly by inadequately known phylogenetic relationships within the taxonomic groups concerned. Some of the difficulties arise from poor understanding of phylogenetic methodology. For example, McGowan (1984, p. 734) reported that carinates, unlike theropod dinosaurs and ratites, possess a (presumably derived) pretibial bone, and therefore concluded that ". . . they [carinates] could not have given rise to the ratites . . ." If correct, this conclusion has important implications for the evolution of flightlessness and inferences

concerning heterochrony in the group. Phylogenetic inferences based on single characters carry little weight, however, and can only be assessed credibly with other characters under the criterion of global parsimony of evolutionary change (wherein a reversal or loss of a specific character is a possibility). Also, there is a misleading ornithological tradition of treating diversity of form, regardless of the polarities of the characters involved, as evidence of distant relationship or polyphyly (Feduccia, 1980; Olson, 1985; Bock and Bühler, 1990), whereas such differences may simply reflect phylogenetically uninformative, autapomorphic differentiation (Cracraft, 1974). Some anatomical diversity in ratites (e.g., within the pelvis) may be the result of minor perturbations of shared ontogenetic trajectories within lineages (Elzanowski, 1988).

The dearth of explicit phylogenetic hypotheses has led to misunderstandings concerning evolutionary patterns and rates of change. For example, McGowan (1986, pp. 342–3) noted that pectoral changes evident in a flightless carinate, the weka (Rallidae: *Gallirallus australis*), were comparatively minor compared with those of ratites, and stated on questionable biogeographical grounds that: ". . . the Weka could have a genealogy dating back as long as that of ratites." Although the meaning of this statement is unclear, it would be precluded by a phylogenetic hypothesis for rails within which the capacity for flight could be mapped. Assumption of the polyphyly of ratites and the multiple losses of flight in rails has led to a widespread belief that "neoteny" can produce flightlessness rapidly (Olson, 1973a,b, 1982, 1985; James and Olson, 1983), although only the estimated ages of oceanic islands inhabited by endemic flightless birds are germane to questions of absolute rates of change, and these only provide upper limits.

Interpretations of individual characters, taken together, form the basis for understanding morphological evolution and phylogeny, and each character must be considered on its own merits. In this context, the assumption by de Beer (1956) that the palate of ratites is "neotenic" simply because there is evidence of neoteny in cranial sutures and feather structure is questionable, given the potential for different ontogenetic perturbations among different anatomical structures (McKinney and McNamara, 1991). Also, most ornithological citations of recapitulation remain vague. For example, Houde and Olson (1981, p. 1237) cited ". . . the existence of at least some of the features of the paleognathous palate in the early ontogeny of some neognathous birds" in support of the primitiveness of the paleognathous palate in ratites. The theory of recapitulation suffered, in part, from its early, uncritical popularity (Churchill, 1980), and the importance of the relationship between ontogenetic and phylogenetic transformation to evolutionary study is far from resolved (Løvtrup, 1978, 1989; Rieppel, 1990; Patterson, 1983; Mayr, 1994). There is evidence for limited recapitulation in ontogenetic sequences showing terminal additions (McKinney and McNamara, 1991) and this may facilitate the determination of character polarities (Nelson, 1978; de Quieroz, 1985).

The history of study of avian flightlessness, especially that of the ratites, underscores the reciprocal relationship between the study of ontogeny and phylogenetic reconstruction. Heterochrony is by definition an evolutionary problem and therefore is interpretable only within an historical context. A phylogenetic approach to heterochrony also reveals the hierarchy of ontogenetic evolution, which for Aves may range from the class-level neoteny hypothesized by Thulborn (1985) to heterochrony of morphology, physiology, and behaviour through progressively exclusive taxonomic groups. A phylogenetic approach may indicate that the "intermediate" metabolic rates of ratites (Calder and Dawson, 1978; Vleck *et al.*, 1980) are explainable by the basal phylogenetic position of the group (see Duncker, 1989). This possible plesiomorphy contrasts with the partial, possibly heterochronically produced reversals in metabolic parameters suggested in some flightless carinates, e.g., the kakapo and dodo (Livezey, 1992b, 1993b). Moreover, it may be that the best corroborated phylogenetic hypothesis would vindicate to varying extents each of the seemingly competing (but not mutually exclusive) theories for the evolution of ratites and their flightlessness, including primitiveness or intermediacy of some characters, reversals through paedomorphosis, and genuine novelties (perhaps shared by entire clades) associated with heterochrony.

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