

1 Patterns of Development: The Altricial-Precocial Spectrum

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1.1. Introduction

Since the Late Triassic, the time of *Protoavis texensis* (Chatterjee 1991), over 200 million years of evolutionary diversification of birds have resulted in about 8900 living species. Rather than there being a gradual and continuous diversification of birds, recent paleontological perspectives suggest that most avian lineages produced during the Mesozoic did not survive the extinctions at the end of the Cretaceous period and that most recent lineages arose in a second, almost explosive phyletic radiation during a relatively short period of 10 million years in the early Tertiary (Chiappe 1995; Feduccia 1995).

Among other attributes of avian diversity, this radiation produced the broad spectrum of development patterns that we see in contemporary birds. The chicks of various species of bird differ markedly in the relative degree of maturation of many aspects of their behavior, physiology, and anatomy. The functional maturity of the chick at any point in its postnatal development is closely tied to the care it receives from its parents, and probably also to many aspects of its environment. Variation among taxa in the developmental trajectory of this suite of attributes has led ornithologists to separate birds into altricial and precocial developmental types. Designation of a species into one or the other category has been based largely on the condition of the hatchlings.

The attributions *nidifugous* and *nidicolous*¹ were introduced when Oken (1816) referred to *Nestflüchter* (nest-fleers, or nidifugous birds) and *Nesthocker* (nest-squatters, or nidicolous birds). The terms *Aves altrices* and *Aves precoces*² were introduced into ornithology by Sundeval (1836), who had based his classification of birds on the earlier study by Oken (1816). The original usages of *altricial* and *nidicolous* were synonymous, as were those of *precocial* and *nidifugous*. Today, these pairs of terms are used in slightly differing contexts, although their general meanings overlap in some aspects. *Altricial* and *precocial* primarily refer to the developmental stage of the chick, whereas *nidicolous* and *nidifugous* refer to nest attendance.

Additional terms have since been introduced to describe different syndromes of developmental maturity of hatchlings, parent-chick interactions, and chick-environment interactions (see Table 1.1 and the following discussion).

This chapter considers the altricial-precocial spectrum on several comparative levels. We discuss the various schemes by which developmental patterns, particularly the developmental state of the neonate, are classified at present. We then briefly review the history of avian systematics with special reference to the use of mode of development as a basis for classifying birds and the influence of classifications on thinking about the evolution of avian development. We consider evidence from the fossil record of neonates of birds and their phylogenetic outgroups to determine whether the altricial or the precocial state was ancestral in the evolution of avian ontogenies. We present a new analysis of the altricial-precocial spectrum based exclusively on physiological characters of the neonate, without consideration of such context-specific behaviors as locomotory activity and parent-offspring relations. We undertake this analysis to determine whether, in a developmental sense, the altricial-precocial "spectrum" has a single dimension or is multivariate and to see whether taxa are uniformly and continuously distributed along the spectrum or clustered in certain regions. The results of these analyses will influence our interpretation of the evolutionary diversification of developmental patterns. Finally, a glimpse of mammalian developmental patterns provides some comparative insights into the evolution of ontogenies in vertebrates and allows us to find out specific attributes of evolutionary diversification of ontogenies in both birds and mammals.

1.2. Classification of Hatchlings

The altricial-precocial spectrum extends from songbirds and parrots, whose chicks hatch in an almost embryolike state, on the one extreme, to the megapodes, whose hatchlings resemble adult birds and can fly from the first day after hatching, on the other extreme. Traditional classifications of development patterns recognize several categories arranged along an altricial-precocial gradient according to a combination of morphological and behavioral characteristics of the neonates. The basic differentiation and character de-

¹ *Nidi-*: from the Latin *nidus*, "nest"; *-fugous*: from the Latin *fugere*, "flee"; *-colous*: from the Latin *colere*, "inhabit."

² *Aves* (pl.): from the Latin *avis*, "bird"; *altrices*: from the Latin *altrix*, "wet nurse"; *precoces*: from the Latin *praecoquis*, "early maturing."

Table 1.1. Commonly used synonyms for precocial and altricial hatchlings

Portmann (1935)	Nice (1962)	Skutch (1976)	Most others	J.M.Starck (1993)	1	2	3	4	5	6	7	8	9	a	b	Some examples	
Gruppe 1	Precocial 1	Superprecocial	Precocial	Superprecocial												Megapodiidae	
Gruppe 2	Precocial 2	Precocial		Precocial 1													Anatidae, many charad
	Precocial 3			Precocial 2											Rheidae, Numididae, P Meleagrididae, Tetraon		
	Precocial 4	Subprecocial		Semi- precocial	Precocial 3											Cracidae, Turnicidae, F Gruidae	
Gruppe 3	Semiprecocial	Semialtricial	Semiprecocial													many Alcidae, Laridae, Stercorariidae	
Gruppe 4	Semialtricial 1	Altricial	Semialtricial	Semialtricial												Accipitridae, Ciconiida	
Gruppe 5	Semialtricial 2		Altricial	Altricial 1													Columbidae, Phaethont Phalacrocoracidae
Gruppe 6, 7	Altricial			Altricial 2													

1. Downy hatchling plumage
2. Motor activity
3. Locomotor activity
4. Follow parents
5. Search food and feed alone
6. Young fed by parents

7. Stay in nest
8. Eyes closed at hatching
9. Without external feathers at hatching
- a. No parent-chick interaction
- b. Contour feathers at hatching

scription goes back to Oken (1837), who said of altricial birds that “they come naked and blind into the world, needing to be fed in the nest.”³ Of precocial birds, Oken stated that “the young come from the egg with sight and feathered; not being fed, but soon running about and searching for their food by themselves.”⁴ This basic distinction between altricial and precocial has not changed to the present (Nice 1962; Ricklefs 1983; O’Connor 1984; J.M. Starck 1993).

“Superprecocial” megapodes (Fig. 1.1a) occupy the precocial extreme of the spectrum. The young are totally independent of their parents, and in some species the chicks can fly from the first day of postnatal life (Table 1.1). As already recognized by Stresemann (1927 – 1934), megapode superprecocity continuously grades into the precocity typical of galliform species, whose hatchlings seek their own food and depend on their parents only for protection and brooding. Thus, Nice (1962) distinguishes megapodes as precocial-1 and galliforms as precocial-2 or precocial-3. Ostriches, ducks (Fig. 1.1b), geese, jacanas, and many shorebirds exhibit a similar independence and usually are placed in the precocial-2 category of Nice. In some of the Galliformes (e.g., most Meleagrididae and Tetraonidae), parents find food items and point them out to their chicks on each foraging excursion. These taxa are placed in a lower category of precocity (precocial-3 of Nice). Chicks of cranes, rails, grebes, loons, bustards, and button quails (Fig. 1.1c) display a precocial development of mobility and sensory organs, but their parents offer them food for some time (often one to two weeks) after hatching (precocial-4 of Nice; see Table 1.1 for classification by different authors). The young of many alcids, gulls, and terns (Fig. 1.1d) are described as semiprecocial⁵ because of their relatively less developed locomotor activity, stronger nest attendance, and complete dependence on the parents for food. Within a few days after hatching semiprecocial chicks do undertake excursions around the nest to hide in vegetation, but they return to the nest to be fed by their parents.

Species whose chicks remain in the nest for much or all of their development are referred to as altricial or nidicolous. Among them, raptors (Fig. 1.1e), storks, herons, and many other families are designated as semialtricial-1 because neonates are densely covered by down and have open eyes; semialtricial chicks are relatively active soon after hatching. Fully altricial hatchlings hatch with closed eyes and exhibit little

motor activity other than begging. Some altricial chicks hatch with natal down (Fig. 1.1f; semialtricial-2 of Nice 1962), others hatch without externally visible feathers (Fig. 1.1g). The presence (ptilopaedic⁶) or absence of feathers (gymnopaedic⁷) has been used to further distinguish between altricial-1 and altricial-2 in J.M. Starck’s (1993) classification, which are equivalent to semialtricial-2 and altricial in Nice’s scheme. Whether the intermediate category is called semialtricial-2 or altricial-1 depends on the relative importance placed on feathering compared to vision (Table 1.1).

Traditionally, the altricial-precocial spectrum has been characterized by a heterogeneous set of characters including behavior (nest attendance; feeding behavior), parent-chick relationships, and purely anatomical traits (eyes open or closed; presence of natal down). These traits do not easily align themselves in a continuous sequence. Furthermore, because they include categorical traits that lack continuous distributions and have an uncertain relationship to the developmental state of the chick, they make comparisons among species and interpretations of evolutionary diversification difficult. Expression of some of the traits, particularly nest leaving and self-feeding, depend on nest site and food supply and may therefore be independent of development per se. Most classifications of neonates, including that of Nice (1962), are one-dimensional even though they are based on several characters: that is, developmental classes may be ordered so that the state of any one character predicts the state of all other characters preceding it in the progression. For example, all species that leave the nest at hatching have a downy plumage and open eyes; all species that are self-feeding leave the nest at hatching and have a downy plumage; and so on. Table 1.1 lists the characters frequently used in classifications of bird hatchlings. These include considerable redundancy (e.g., *locomotory activity* versus *stay in nest*), change in polarity (*eyes closed*, altricial; *follow parents*, precocial), and ambiguity about what is a character and what is a character state (e.g., *fed by parents*, *follow parents*, and *search for food alone* could be states of the single character *feeding*). Most classifications use up to nine different characters to describe the developmental mode of avian hatchlings. Here, we look more closely at how these characters have been applied to ascertain their consistency and utility. We use the terminology of Nice for reference.

The first character, *downy hatchling plumage*, dis-

³ “Sie kommen nackt und blind zur Welt; bedürfen der Aetzung im Nest” (p. 24).

⁴ “Die Jungen kommen sehend und mit Federn aus dem Ey, werden nicht geätzt, sondern laufen bald herum und suchen ihr Futter selbst” (p. 380).

⁵ “Platzhocker” of Peters and Müller (1951).

⁶ *Ptilo-*: from the Greek, πτελος, “feather”; *paedic*: from the Greek παις, “child.”

⁷ *Gymno-*: from the Greek (γυμνος, “naked”; *paedic*: from the Greek παις, “child.”





Fig. 1.1. (a) Precocial-1 hatchling of a brush turkey, *Alectura lathamii* (courtesy of E. Sutter, Basel). (b) Precocial-2 hatchling of Muscovy duck, *Cairina moschata*. (c) Precocial-4 hatchling of Japanese crane, *Grus japonica* in Frankfurt Zoo. (d) Semiprecocial hatchling of Forster's tern, *Sterna forsteri*. (e) Semialtricial-1 hatchling of Eurasian kestrel, *Falco tinnunculus*. (f) Semialtricial-2 hatchling of rock pigeon, *Columba livia* f. dom. (g) Altricial hatchling of rice finch, *Lonchura oryzivora* [All photos by J.M. Starck, except (a)].

tinguishes altricial (without down) from all other developmental categories. However, marked variability in the presence of down among close relatives (see the following) makes this an inconsistent and ambiguous trait. The second character, *motor activity*, is difficult to categorize because all neonates “move” to some extent, if only to beg for food. The third character, *locomotor activity*, referring to the ability to leave the nest at an early age, separates the two major developmental groups, altricial and precocial. We have already suggested that nest leaving is context-dependent, however, and may not correspond exactly to the developmental state of the neonate. In particular, many seabirds, especially Procellariiformes, remain in the nest and are classified by Nice (1962) as semialtricial, although they are physiologically advanced in heat production. The fourth character, *follow parents*, is also context-dependent according to the nature of the food resources and habitat. The fifth character, *search for food and feed alone*, is difficult to define precisely because chicks of many species find their own food but remain in family groups. Furthermore, other aspects of parental care, including protection and brooding, are not included in the precocial characters but may be equally indicative of developmental state.

Whereas precocial birds are characterized by patterns of behavior such as nest attendance, characters six through nine describe altricial hatchlings according to parent-chick interactions and developmental traits (eyes closed at hatching, lacking external feathers). Some of these are ambiguous and may even be misleading. Character six, *young fed by the parents*,

occurs both in altricial and in precocial groups and thus does not distinguish between them. The seventh character, *stay in the nest*, is the opposite of character three, *locomotor activity*, and therefore not an independent developmental character. It also refers to the nest attendance rather than to the developmental stage of the chick and in some groups, such as alcids, may reflect constraints of the nest site rather than the chick's ability to walk. The eighth character, *eyes closed at hatching*, is diagnostic for altricial hatchlings and may be indicative of the developmental stage of the nervous system. The ninth character, *hatch without externally visible feathers*, distinguishes a small subset of altricial hatchlings, but the character seems to be extremely variable and is probably not indicative of the state of development (see chapter 3).

The presence or absence of feathers at hatching may vary among related taxa or even within families. For example, within suboscine passerine birds the bearded bellbird (*Procnias averano*, Cotingidae) hatches with a dense cover of natal down (Snow 1970) and the eastern kingbird (*Tyrannus tyrannus*, Tyrannidae) is densely covered with natal down, whereas many others hatch naked (Skutch 1976). Within swallows (Hirundinidae), the barn swallow (*Hirundo rustica*) and the cliff swallow (*Petrochelidon pyrrhonota*) have natal down, but the purple martin (*Progne subis*) hatches naked (Wetherbee 1957). Within corvids, the yellow-billed cough (*Pyrrhocorax graculus*) hatches with a dense cover of natal down, but the red-billed cough (*Pyrrhocorax pyrrhocorax*) hatches almost naked. Clark's nutcracker (*Nucifraga columbiana*) and Ameri-

can crow (*Corvus brachyrhynchos*) chicks hatch with a dense cover of down, but black-billed magpie (*Pica pica*) and carrion crow (*Corvus corone*) hatch naked. Graded differences in the number of neoptiles, their length, and the presence and absence of feather tracts (pteryla) have been described for a large number of passeriform families (Wetherbee 1957; Collins 1963, 1965, 1968; Arnold et al. 1983). Within Psittaciformes, hatchlings of the Loriidae have a thick down cover but parrots (Psittacidae) have only very little down or are naked (Forshaw 1973). Such variability is not restricted to the time of hatching. Skutch (1976) reports that the blue-throated motmot (*Aspatha gularis*), a species of the high Guatemalan mountains, hatches naked but soon develops a thick coat of down. The closely related turquoise-browed motmot (*Eumomota superciliosa*), which lives in tropical lowlands, does not develop feathers until it is almost fully grown. Lack of feathers at hatching is not specific for altricial birds: in many altricial taxa, neonates have dense natal down, whose function is not well understood.

We have reformulated the nine characters to make the diagnostic features of each development class more evident and uniform (Table 1.2). Four basic characters are employed in classification systems, each with two or more states, as follows: plumage (none, natal down, or feathers), condition of eyes (closed or open), nest attendance (stay, remain in area, or leave), and parental care (parental feeding, parental food-guiding, brooding and protection only, or none). Even this arrangement clearly combines interdependent developmental, behavioral, and ecological traits. As with all such classification schemes, it is necessarily nonmetric and arbitrary and only loosely tied to the developmental state of the hatchling. Even the major split between the altricial and precocial groups hinges on whether young chicks spend time away from the nest site itself (semiprecocial) rather than remaining in the nest (semialtricial). This distinction may depend on the nest site as much as on development. For example, the chicks of cliff- and tree-nesting species tend not to wander from the nest, even though they may be fairly mobile. Some

ground-nesting species, such as penguins, tend not to leave the nest because of the dangers of wandering in dense colonies.

For the most part, the arrangement in Table 1.2 defines a one-dimensional ordering of developmental types. In part, this results from the particular characters included, which were chosen to represent a sequence of developmental types. As pointed out, the states of several of the characters are contingent on the states of others, as chicks cannot leave the nest unless their eyes are open and cannot be self-feeding until they leave the nest. Other characters might not be so consistently ordered. For example, thermal independence at an early age is well developed in some semialtricial Procellariiformes (Ricklefs et al. 1980) but relatively poorly developed in many precocial shorebirds such as Scolopacidae (Visser and Ricklefs 1993; see chapter 5).

There are few apparent exceptions to the order of characters in traditional classifications of the developmental state of the neonate. The South American hoatzin (*Opisthocomus hoazin*) is difficult to place because it hatches sparsely covered with down, but its eyes are wide open 24 hours after hatching. When two weeks old and before they are feathered, chicks start to clamber about on branches of their nesting trees (Dominguez-Bello, personal communication). Under normal conditions the chicks stay close to the nest, which is always built in trees over the open water of rivers. However, when predators approach they jump out of the nest into the water, hiding among emergent vegetation. Later, the chicks climb back into the nest. Storm petrels (Hydrobatidae) and many of the petrels (Procellariidae) provide another contrary example. These hatch after long incubation periods densely covered with down, with their eyes soon open, and they stay in the nest or burrow for long periods unattended by their parents. Their thermogenic capacity (Farner and Serventy 1959; Wheelwright and Boersma 1979; Bech et al. 1982) and aspects of their internal anatomy resemble those of many precocial species. Because of the vagueness of the traditional classification they have

Table 1.2 Reorganization of diagnostic features of Nice’s developmental classes

	Plumage	Eyes	Nest attendance	Parental care
Precocial-1	<u>Contour feathers</u>	Open	Leave	<u>None</u>
Precocial-2				<u>Brooding</u>
Precocial-3				<u>Food showing</u>
Precocial-4				
Semiprecocial	Down		<u>Nest area</u>	Parental feeding
Semialtricial-1				
Semialtricial-2	<u>Closed</u>		Stay	
Altricial	<u>None</u>			

been placed as semialtricial by Nice (1962) and O'Connor (1984) and as semiprecocial by Ricklefs et al. (1980) and J.M. Starck (1993). Hatchlings of loons and grebes (precocial-4) can swim ably but are often carried and fed by their parents. It is hard to believe, however, that they are less developed than waders (precocial-2) and phasianids (precocial-3). The difference in behavior seems to be related to food supply and habitat rather than to development. Among altricial birds, we find species that are similarly difficult to place in the traditional altricial-precocial classification. For example, many pigeons and doves (Columbidae), although highly altricial when hatching, leave the nest when only half grown (*Geopelia cuneata*; *Oena capensis*) and in the case of the purple-crowned fruit pigeon (*Ptilinopus superbus*) as little as one-quarter grown (Crome 1975).

Developmental patterns appear to be conservative and are generally uniform within large taxonomic groups. Auks (Alcidae) are probably the most diverse family in modes of development. Most species are classified as semiprecocial, but guillemots (*Cepphus* spp.), auklets (*Aethia* spp., *Cyclorhynchus* spp., and *Cerorhinca* spp.), and puffins (*Fratercula* spp.) leave the nest at 40 – 60 days of age, at 75% to 100% adult body mass, after which they are independent of their parents. Chicks of common murre (*Uria aalge*), thick-billed murre (*U. lomvia*), and razorbill (*Alca torda*) leave the nest after 20 – 30 days when they have reached about 25% adult size. Because the chicks are fed for some time after they leave the colony, they are described as intermediate between semiprecocial and precocial-4 (Sealy 1973; Gaston 1985). True precocity is found among the murrelets (*Synthliboramphus* spp.; *Brachyrhamphus* spp.) whose chicks leave the nest (Gaston 1992) soon after hatching and are cared for by their father during posthatching development (precocial-4). However, the distinction among semiprecocial, intermediate, and precocial-4 behavior in auks is exclusively based on the fledging time, nest attendance, and relative size of the fledglings. Such differences in time of fledging are related more to the feeding ecology (e.g., in-shore versus off-shore feeders) of the species (Ydenberg 1989) than to developmental differences. We discuss later a developmental scaling of avian neonates, which shows that auks are placed well within the precocial range.

The families within the order Charadriiformes, which includes the Alcidae, are the most diverse in development. Species range from the precocial-2 shorebirds (Scolopacidae and Charadriidae) to the semiprecocial Laridae and semialtricial Dromadidae. How much the neonates of these groups differ in physiological and developmental advancement is not well understood.

1.3. The Altricial-Precocial Spectrum and Avian Systematics

To study the evolutionary history of a clade, one would ideally like to place character states on a true phylogeny of the groups. This mapping would indicate ancestral and derived characters, reversals, and convergences. One of the ambiguities of this approach is that the distribution of character states among taxa provides the basis for estimating phylogenetic relationships by using both cladistic and phenetic methods. Thus, the character of interest may actually contribute to building the phylogeny that will be used to interpret its evolution. One way to circumvent this problem of circularity is to base the phylogeny on traits other than the one of concern.

Early classifications and systematic arrangements of birds used the developmental state of the hatchling as a basic character to distinguish groups at high taxonomic rank. Following von Baer (1828), most nineteenth-century avian biologists believed that development was evolutionarily conservative, and they used development as a taxonomic character for higher levels of classification. This resulted in placing species with similar developmental patterns together, reinforcing in our collective conscience the idea of evolutionary conservatism. This practice reflected certain presumptions about the evolution of developmental grade that persist to the present. Here we inquire about the distribution of the developmental mode with respect to more recent phylogenies based on molecular information or on the analysis of morphological data. When viewed in the light of these new phylogenetic classifications, is the developmental pattern evolutionarily conservative or flexible?

Lorenz Oken (1779 – 1851), who was professor of natural history at the University of Jena in Germany, introduced the terms *Nestflüchter* (“nidifugous”) and *Nesthocker* (“nidicolous”) into scientific discourse (Oken 1837). He based his classification of birds on the distinction between nidifugous and nidicolous development. His system was typically pre-Darwinian and attempted to arrange bird taxa according to a hierarchical rank in parallel to a classification of other classes of vertebrates.⁸ In his system, nidifugous birds, especially Galliformes, were ranked high because domesticated species are useful to humans; songbirds were ranked low because they are not. Although Oken's classification was soon replaced by others, the developmental state of the hatchling (that is, altricial ver-

⁸ For example, the taxon “nidifugous birds” was subdivided into four tribes, in parallel to the classes of vertebrates: (1) fishlike birds = all swimming and diving birds with short legs; (2) amphibianlike birds = wading birds with long bills; (3) perfect birds = Galliformes; (4) mammal-like birds = walking birds with strong legs but mostly missing the fourth toe.

sus precocial) remained an important character in the classification of birds. Sundeval (1836, 1872) also based his classification of birds on the ontogenetic mode. He introduced the terms *Altrices* and *Precoces*, which referred more to parental feeding versus self-feeding than to nest attendance by the chick. Sundeval's (1872) publication was translated into English by Nicholson (1889), whereby it gained some importance among English-speaking scientists. The English ornithologist Newman (1850) had previously used the terms *hestogenous* for precocial and *gymnogenous*⁹ for altricial and had split the class of birds into two subclasses characterized either by precocial or altricial development. Bonaparte (1853) distinguished two subclasses of birds, the *Precoces* (Grallatores)¹⁰ and the *Altrices* (Insessores).¹¹ Fitzinger (1856) established five equivalent groups ("rows" in his terminology) of birds, *Dickfußige Aetzvögel* (thick-footed birds that feed their young), *Dünnfußige Aetzvögel* (thin-footed birds that feed their young), *Scharrvögel* (scratching birds, i.e., terrestrial birds), *Wadvögel* (wading birds), and *Schwimmvögel* (swimming birds), thus contrasting two altricial classes with three classes of birds that were defined by their locomotion. Haeckel (1866) also retained a basic separation of birds on the supraordinal level into nidifuges (Autophagae,¹² Nidifugae, and Nestflüchter) and nidicoles (Paedotrophae,¹³ Insessores, and Nesthocker). Lilljeborg (1866) based his systematic review of the class of birds on Sundeval's classification. However, the distinction between altricial and precocial birds appears in his description of orders but is not used as a major character for classifying birds.

Shortly after the appearance of Darwin's *On the Origin of Species* in 1859, several classifications of birds were elaborated strictly on the basis of morphological similarities. The papers by Huxley (1867), Fürbringer (1888), and Gadow (1891, 1893) are outstanding examples of modern classifications of birds, based on morphological data acquisition and the principle of evolution. Fürbringer (1888) used a technique to reconstruct phylogeny that is similar to the cladistic approach developed by Willi Hennig (1950) 75 years later. It is important to note, however, that Gadow inclu-

ded developmental mode as a trait for the basic separation of avian orders: "Nestflüchter" (nidifugous birds, i.e., Galliformes, Charadriiformes, and Gruiformes), "niedere Nesthocker" (lower nidicolous birds, i.e., Sphenisciformes, Procellariiformes, and Ciconiiformes), and "höhere Nesthocker" (higher nidicolous birds, i.e., Columbiformes, Accipitriformes, Psittaciformes, Piciformes, and Passeriformes). Mode of development is listed as the first trait in his extensive character tables for classification of birds (pp. 69 – 92). Gadow described nidifugous development as ancestral, whereas nidicolous birds were separated into two equally ranking groups of "Niedere Nesthocker" and "Höhere Nesthocker." He thought the two groups of nidicolous birds had evolved independently.

Later, Wetmore (1930, 1934) adopted Gadow's (1893) arrangement of the nonpasseriform orders in his systematic classification of the birds of the world (Bock 1990), which ultimately provided the basis for the linear arrangement of birds in Peters's *Check-list of the Birds of the World* (1937 – 1987). Stresemann (1927 – 1934) also refers to Fürbringer, Gadow, and Wetmore in his attempt at a classification of birds. However, Stresemann's pessimistic view about knowing avian phylogeny led him to develop a classification with a larger series of orders of equal rank. Although his linear arrangement of orders implies some evolutionary development, he explicitly avoided statements about the phylogenetic relationships between the orders. His description of orders and families refers to the developmental stage of the hatchling, in a manner comparable to that of Lilljeborg (1866), but Stresemann did not use this trait as a diagnostic character. However, even without phylogenetic implications, he believed precocial development to be ancestral among birds and altricial chicks as derived. Mayr and Amadon (1951) in their classification of extant birds also retain Wetmore's original sequence of nonpasseriform birds.

1.3.1. Recent phylogenies

Two recent avian classifications have been constructed by using current phylogenetic methods. Cracraft (1981, 1986, 1988) applied cladistic methods to morphological (skeletal) characters in an analysis of avian orders, including extinct groups known only from fossils. Sibley and Ahlquist (1990) used phenetic (distance) analysis of DNA-DNA hybridization data to produce a phylogeny of all major taxa of the birds of the world, down to the taxonomic levels of genus and species in many cases. These classifications are based on totally different methods and data, and neither refers to developmental characters of hatchlings. Because all previous classifications at least implicitly refer to the mode of development, only Cracraft's and Sibley and Ahlquist's phylogenies are suitable for post hoc descriptions of the evolution of avian developmental patterns.

⁹ *Hesto-*: from the Greek εσθημα, "garment"; *gymno-*: from the Greek γυμνος, "naked"; *-genous*: from the Greek γεννομαι, "being born."

¹⁰ *Grallatores*: from the Latin *grallator*, "a person walking on stilts."

¹¹ *In-*: from the Latin *in*, "within"; *-sessores*: from the Latin *sedere*, "sit."

¹² *Auto-*: from the Greek αυτος, "self"; *-phagae*: from the Greek φάγειν, "feed."

¹³ *Paedo-*: from the Greek παις, "child"; *-trophae*: from the Greek τρεφω, "nourish."

We consider both phylogenies in parallel and discuss their contrasting implications. To determine whether altricial or precocial development was the ancestral state in birds, we also examine development in potential outgroups (i.e., crocodiles as an extant outgroup within archosaurs and dinosaurs as a fossil stem group).

Cracraft's (1981, 1988) phylogeny is based on morphological (skeletal) characters and attempts to resolve the major clades of birds. Although the phylogeny contains several unresolved polytomies (i.e., several clades branch off from the same node, resulting in a phylogenetic bush rather than a dichotomously branching tree), it presently is the only phylogenetic hypothesis of any consequence that concerns the relationships among orders of birds. Exclusively precocial development appears only in the Palaeognathae (Struthioniformes in other classifications), the Galliformes, the Anseriformes, the Podicipediformes, and the Gaviiformes (Fig. 1.2). Altricial development is found among many of the higher taxa. Cracraft's cladogram suggests that precocity is an ancestral character for birds. However, the unresolved polytomies do not allow for a single interpretation. We may assume that precocial development is ancestral for the higher taxa of birds and that altriciality, including semialtricial-2 and altricial in Nice's (1962) sense, evolved at least six times independently in different clades (Sphenisciformes; Pelecaniformes and Procellariiformes; Columbiformes; Passeriformes, Piciformes and Coraciiformes; Apodiformes and Caprimulgiformes; Strigiformes).¹⁴ Alternatively, we may assume that altriciality evolved in the stem group of all higher taxa of birds and that precocity in loons and grebes, as well as in cranes and waders, represents a reversal of that character. Also, semialtricial development in herons, storks, and raptors would be reversals from the altricial development toward more precocial development. Both alternatives assume six independent evolutionary events and are equally parsimonious. Cracraft's phylogeny suggests precocial development as the ancestral character for birds but does not clarify the evolution of the developmental mode in the higher taxa. Multiple evolutionary origins of altriciality, as well as reversal from altricial to precocial, may be inferred equally from his cladogram.

Sibley and Ahlquist's (1990) phylogeny of birds arranges all exclusively precocial orders in the infra-class Eoaves (Fig. 1.3). The button quails, which emerge from the first basal node as a sister group to the Neoaves, are also precocial.¹⁵ Button quails are assigned the rank of an (unnamed) infraclass with one order *incerte sedis*.¹⁶ All orders of the Neoaves except the Gruiformes and Ciconiiformes comprise taxa with

altricial development. Thus, Sibley and Ahlquist's phylogeny suggests that precocial development is ancestral for birds, provided that the button quails are placed correctly. When the button quails are not included in the phylogeny, it is not possible to decide whether the altricial or precocial development is the derived character state for birds, unless the presumed sauropsid stem group of birds was known to be precocial. Within the Neoaves, however, altriciality is almost certainly the ancestral character. Precocity evolved as a derived trait from altricial stem groups within the Gruiformes and the Ciconiiformes. The Ciconiiformes, according to Sibley and Ahlquist, are a most diverse group, embracing 29 families, and are hardly comparable to the Ciconiiformes of most traditional classifications (e.g., Morony et al. 1975). If we assume altriciality in the stem group of Ciconiiformes and Gruiformes, precocity must have independently evolved at least four times: in the order Gruiformes, in the suborder Charadrii, in grebes (Podicipedidae) within the parvorder Podicipedida, and in the loons (Gaviidae) within the parvorder Sulida. Altriciality, including semialtriciality, in all other taxa of the Ciconiiformes is considered a plesiomorphic (phylogenetically ancestral) character.

Both the Cracraft (1981, 1988) and the Sibley and Ahlquist (1990) phylogenies are somewhat ambiguous in what they tell us about the evolution of the altricial-precocial spectrum. Cracraft's cladogram indicates precocial development at the base of all birds and either several independent origins of altriciality or altriciality at the base of all higher taxa but several independent reversals back to precocial development. Sibley and Ahlquist's hypothesis is ambiguous about whether the altricial or precocial mode of development was ancestral in birds, depending on whether one considers the Turniciformes as correctly placed.¹⁷ How-

¹⁵ The taxon Eoaves in Sibley and Ahlquist's (1990) phylogeny embraces Craciformes, Galliformes, and Anseriformes together with the Tinamiformes and Struthioniformes in Fig. 353 (p. 838). The Eoaves are the sister taxon to Turnicimorphae and Neoaves (including all other birds). However, the DNA-DNA hybridization has a weak resolution at high taxonomic level, failing to produce 50% single-stranded DNA for any comparison of paleognathous birds with other birds. Therefore, the phylogenetic branching pattern is based on extrapolated ΔT_{50}^H values. The Sibley and Monroe (1990) classification deviates from the phylogeny and includes Galloanseres and Turniciformes into the Neoaves without further explanation. We use the original branching into Eoaves and Neoaves throughout our analyses. However, the poor resolution of the basal nodes in this study must be kept in mind for any interpretation that is based on this phylogeny.

¹⁶ *Incerte sedis* refers to an uncertain phylogenetic relationship.

¹⁷ Traditionally, Turnicidae were placed either as a family in the Galliformes or in the Gruiformes (Peters 1934). Recent evidence supports a phylogenetic relationship of Turnicidae and Rallidae, that is, Gruiformes (Starck and Rothow 1996).

¹⁴ Cracraft does not explain why he did not consider Psittaciformes, Cuculiformes, Trogoniformes, and Coliiformes in the analysis.

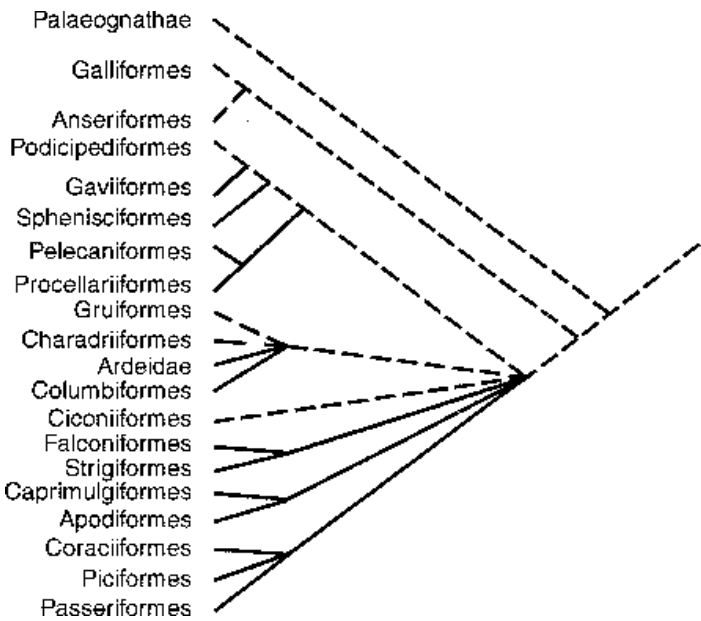


Fig. 1.2. Cladogram of the orders of birds (from Cracraft 1988). Slashed lines indicate precocial taxa; single-lined clades comprise altricial taxa.

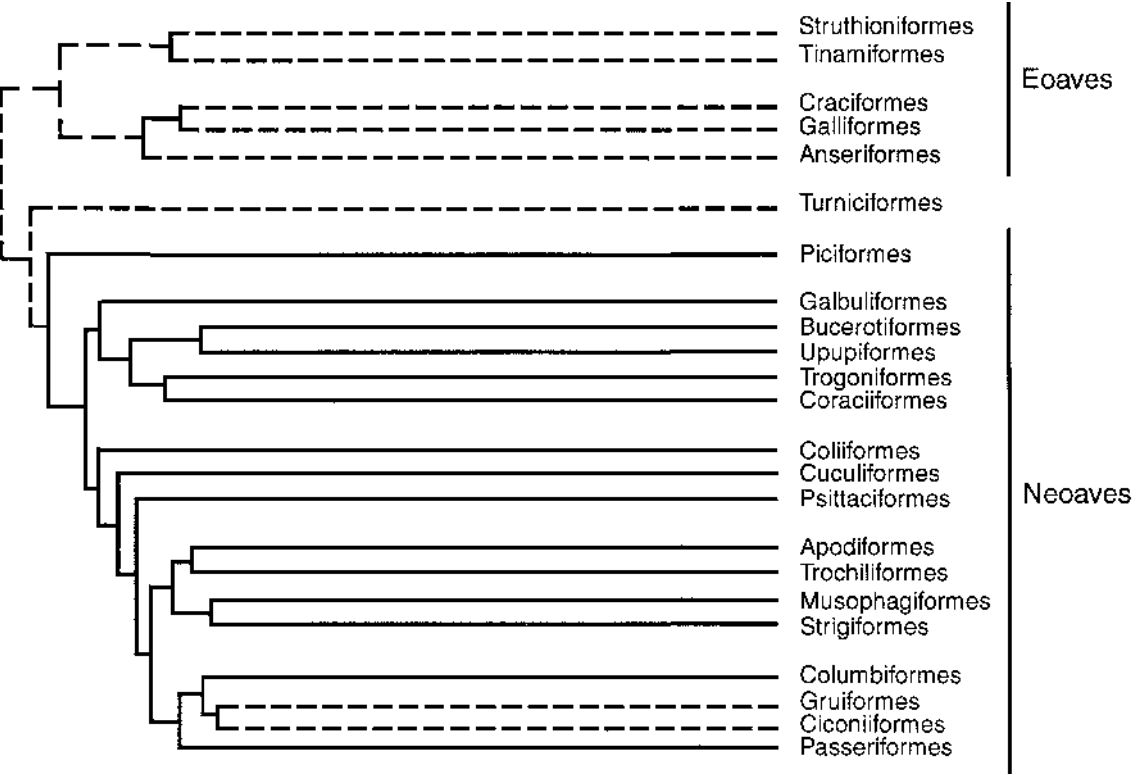


Fig. 1.3. Cladogram of the orders of birds (from Sibley and Ahlquist 1990). Slashed lines indicate precocial taxa; single-lined clades comprise altricial taxa.

ever, their phylogeny leaves little doubt that altriciality is a derived character of the Neoaves (or higher taxa of birds) and that precocity arose secondarily and independently in several taxa. One way to resolve uncertainty about the basal condition of birds and to help understand the phylogeny of developmental patterns is to study the living and fossil representatives of sauropsid outgroups and stem groups.

1.4. The Fossil Record of the Altricial-Precocial Spectrum

Rare findings of fossilized embryonic skeletons of birds have provided some insight into the ancestral state of the mode of avian development. Based on embryonic bird skeletons from the late Cretaceous of Mongolia, Elzanowski (1981, 1983, 1995) suggested that the young of *Gobipteryx minuta* were superprecocial. His ideas were based on the degree of ossification of the skeletal remains of embryonic *Gobipteryx*. He reasoned that the large extent of ossified areas in the appendicular skeleton indicated capability of flight, and thus superprecocity. In another paper, Elzanowski (1985) argued that hypothesized limitations on the ability of parent birds to feed their chicks supported his idea of superprecocity as the ancestral mode of development in birds. He also argued in circular fashion that superprecocity can be deduced from skeletal findings, from which he infers that the *Gobipteryx* laid extremely large eggs, suggesting extremely long laying intervals, which do not allow for parental care, thus suggesting superprecocity. Furthermore, the Enanthiornithes seem to represent an early Cretaceous radiation of birds, with *Gobipteryx* as a derived offshoot without close relationship to the stem group of modern birds (Feduccia 1995). Recently, Chatterjee et al. (n.d.) described embryonic skeletons of *Gobipipus reshetovi*, a ducklike bird from the Upper Cretaceous of the Gobi desert. Chatterjee et al. pursued arguments similar to those of Elzanowski in his earlier papers, but considered the degree of ossification of the skeletal remains of *Gobipipus* as indicating precocial rather than superprecocial development. As we see in chapter 3, however, the degree of ossification is a poor predictor of developmental mode. Thus, no indication of whether the stem group of birds was altricial or precocial comes from fossil embryonic birds.

Horner and Weishampel (1988) briefly reported on embryonic skeletons of an ornithischian and a theropod dinosaur. On the basis of fine-structural analyses of the epiphyses of leg bones, they claimed that the theropod dinosaur *Troodon cf. formosus*¹⁸ developed

precocially while the ornithischian *Maiasaura peeblesorum* developed altricially. They thought that *Maiasaura* might have stayed in the nest until one-quarter grown. Weishampel and Horner (1994) used a cladogram to analyze the evolution of life histories of dinosaurs, with special reference to the mode of development. The admittedly incomplete data suggest altriciality in Hadrosauridae (*Telmatosaurus*, *Maiasaura*, and an undescribed *Hypacrosaurus*). Jacobs et al. (1994) described the young of nodosaurids (Ornithischia) and suggested that they exhibited altricial development based on the incomplete development of the epiphyses of their long bones. Altricial development also was assigned to an embryo or hatchling of *Camptosaurus*, which had not yet ossified epiphyses (Chure et al. 1994). Winkler and Murry (1989) described accumulations of juvenile hypsilophodontid dinosaur bones (species not determined) of different size classes, which they interpreted as representing nests with young of different ages. Similar dinosaur nests were also described by Horner and Makela (1979) and Horner (1982, 1988, 1996), suggesting that altriciality, extended nestling periods, and possibly parental care may have been characteristic of some dinosaur species. This view has recently been challenged by Geist and Jones (1996), who found that the state of fossilization of long bone epiphyses is not indicative of mode of development.

The closest extant relatives of birds among the archosaurs are crocodiles, even though crocodiles and birds have evolved on separate phylogenetic lineages for at least 200 million years. Parent crocodiles care intensely for their brood in various ways, but the hatchlings are clearly precocial. Because precocity is found in both crocodiles and basal avian taxa (Eoaves), we cannot determine whether precocial development is ancestral or secondarily and independently derived. In conclusion, neither the fossil record of embryonic archosaurs nor the closest living relatives of birds tell us much about the ancestral developmental mode in birds. There is some evidence, however scarce and ambiguous, that altriciality might have evolved in dinosaurs, but the developmental mode of the stem group of birds is still unknown. Regardless of whether precocity or altriciality was the ancestral state, the other would have to have evolved independently in at least two lineages.

1.5. A New Metric for Avian Hatchlings?

In most classifications of avian development, many intermediate forms, or grades, are spread between the two extremes of the altricial and precocial conditions. To understand better the evolution of the developmental pattern, it would be helpful to know whether developmental grades are distributed along one or more dimensions of variation, whether species tend to be

¹⁸ The original publication erroneously described that specimen as *Oreodromeus makelai*. Its true identity has just recently been described after further preparation (Horner and Weishampel 1996).

clumped into distinct groups or are continuously distributed along the developmental gradient(s), or whether gaps separate the distributions of major developmental grades. The presence of clusters of species would suggest discrete developmental strategies that rest on adaptive peaks, particularly if each cluster included species from more than one lineage. The presence of gaps in an otherwise continuous distribution would suggest that intermediates are not viable developmental possibilities: neither precocial enough to function independently nor altricial enough to reap fully the benefits of intensive parental care.

Any new scaling of a neonatal condition, of course, can be compared to the classical altricial-precocial spectrum. However, whether a new scaling can, or should, replace an older classification system is a difficult question. The answer to this question depends on why we wish to classify developmental patterns and on the particular context and goals we have for clarifying strategies of growth and development. For example, Portmann's (1935–1962) studies on the evolution of development in birds and mammals were guided by the idea of a graded hierarchy of increasing integration of morphology, physiology, and behavioral traits. His goal was to establish a hierarchical system of "morphogrades," with the most complex forms on top of the hierarchy. In contrast to that approach, Nice (1962) attempted to develop a classification system of bird hatchlings suitable for comparative behavioral studies. For example, the distinction between semi-altricial and semiprecocial, basically whether the chick leaves the nest site or remains at the nest, may have less to do with the developmental state of the neonate than it does with the structure and placement of the nest and with the chick's behavior in the nest-site context. Thus, depending on the purpose of the classification, this distinction may be useful or confusing. Our goal is to understand the evolutionary pathways of ontogenetic development. For this purpose, a system that distinguishes development patterns by functional (physiological) measures that are strictly comparable across taxa will be most useful.

Here we develop a continuous metric to describe the state of maturation of the neonate. We use this metric to examine the relationship of traditional classifications to a scale of development with clear functional meaning, and we apply this scale to understand the evolutionary diversification of patterns of development among the clades of birds. We chose a measure of functional capacity at the tissue level, rather than an organism-level criterion, to focus on maturation of function and avoid the complication of environment-dependent behavior. The functional maturity of tissues can be compared directly across species independently of the chick's surroundings. Furthermore, functional maturity may determine the potential capacity of the neonate for a wide variety of different behaviors re-

quired by different environmental settings and levels of parental care.

We use the dry matter content of a tissue as an index to its functional maturity. Dry matter content appears to be generally associated with the working machinery of cells and connective tissues. We assume that this is a general phenomenon among birds, if not vertebrates, which makes dry matter content directly comparable among all species. It increases with age in virtually all tissues and all species, both before and after hatching (Ricklefs 1983). Other measures of functional maturity, such as the activities of certain enzymes, are often age- and tissue-specific and may vary widely among species, as in the case of aerobic versus glycolytic pathways of energy metabolism in species with sustained versus burst-type activity. In addition, changes in dry matter content of particular tissues usually are well correlated with changes in other measures of function, such as the activities of enzymes in skeletal muscles over the course of maturation of those tissues (Marsh and Wickler 1982; Choi et al. 1993). Finally, dry matter content of tissues is inversely correlated with growth rates, reflecting the generally inverse relationship between embryonic activity and functional maturity (Choi et al. 1993; Ricklefs et al. 1994). Thus, dry matter content links the functional capacity of the neonate to other aspects of growth that have a direct bearing on evolutionary fitness.

Tissues that begin to function at different times during development might exhibit different rates of maturation. For example, the neonatal gut must digest food and assimilate nutrients in all species, the stomach and liver are probably equally employed in both altricial and precocial neonates, and cardiac muscle also is functional in all species prior to hatching; thus, one would not expect to find consistent differences in the water contents of these tissues at hatching (O'Connor 1977, 1978a, 1978b). In contrast, skeletal muscles used for flight and pedal locomotion develop at different times and come into use at different times in different species, depending on when the chick leaves the nest and when it begins to fly. For example, ducks walk and swim virtually from hatching but do not fly until the end of the growth period; galliform chicks achieve flight when they are still smaller than adults. Some parts of the brain must function in all species from an early age to accomplish certain simple behaviors. Even altricial neonates respond to stimuli that indicate the presence of adults, and they can solicit food; altricial neonates also can sense brain temperature and engage behavioral mechanisms to dissipate heat to regulate body temperature even if they cannot generate heat metabolically for this purpose. However, more complex behaviors and locomotion develop at different times in different species and place different requirements on the development of function in the higher centers of the brain.

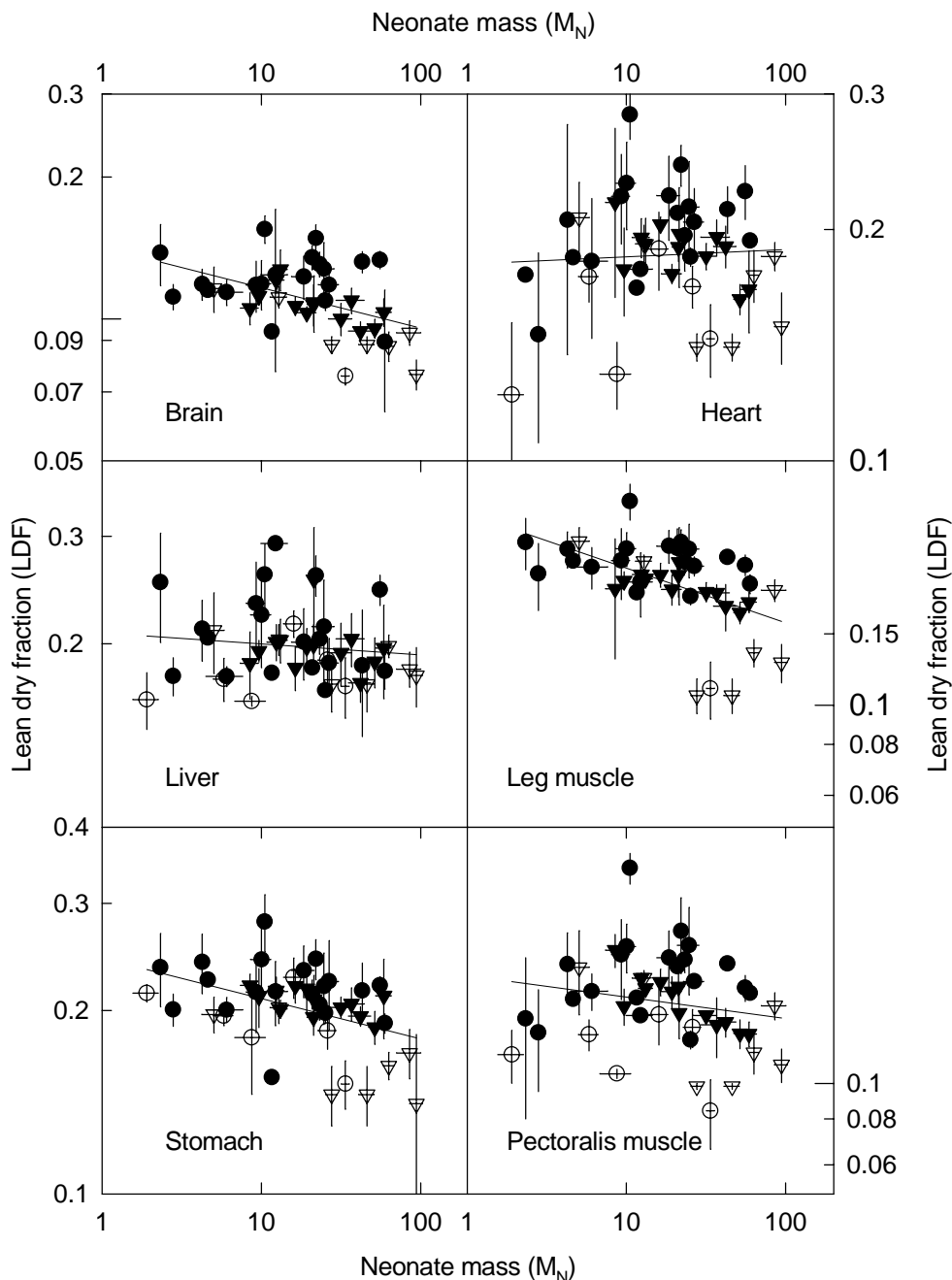


Fig. 1.4. Relationship of lean dry fraction of tissues and neonate mass for six different organs (brain, heart, liver, leg muscle, stomach, and pectoralis muscle). Mode of development is indicated by the following labels: open circles, altricial neonates; open triangle, semialtricial neonates; solid triangle, semiprecocial; solid circle, precocial. The same labels for mode of development are used in all figures of this chapter.

Analysis of the dry matter contents of several tissues across species will reveal one or more dimensions of variation, depending on the degree to which the dry matter contents of the different tissues vary independently among species. If variation is multidimensional, one could conjecture that the course of

maturation of each tissue responded independently of others, depending on the particular requirement of the chick. In contrast, if the dry matter contents of different tissues vary in parallel, each tissue would appear to gain its functional maturity on the same developmental schedule, whether its functional capacity is used or

not. Hypothetically, such unidimensional variation in development might be dictated by some internal constraint of the developmental program, for example, the response of tissue maturation to a common hormonal environment. A single dominant dimension to variation in development also could reflect the similar timing of the functional development of each tissue as a way of regulating the growth rates of tissues at about the same level at a particular stage of development.

With a continuous scale of functional maturity (e.g., dry matter content) entered into a multivariate analysis, we can address four issues: (a) the dimensionality of variation in the development pattern, (b) the pattern of distribution of species along axes of variation in development, (c) the relationship of functional capacity to traditional classifications of the developmental state of the neonate, and (d) the evolutionary diversification of the developmental pattern.

We assembled a data set for this analysis made up of lean dry fractions (LDF, lipid-free dry mass/lipid-free wet mass) of six tissues of the neonates of 46 species of birds: the tissues were heart, pectoral muscle, leg muscle, brain, stomach, and liver (Fig. 1.4). We placed the 46 species in 14 taxonomic groups, following Sibley and Ahlquist (1990), for further analysis of between-group and within-group variation. These groups are quail (Galliformes, 2 species); ducks (Anatidae, 9); geese (Anseridae, 1); coots (Rallidae, 1); sandpipers (Scolopacidae, 5); plovers (Charadriidae, 2); gulls, terns, and skuas (Laridae, 12); alcids (Alcidae, 4); grebes (Podicipedidae, 1); tropic birds (Phaethontidae, 1); penguins (Spheniscidae, 1); petrels (Procellariiformes, 5); and songbirds (Passeriformes, 2).

In five of the six tissues, lean dry fraction decreased with increasing mass of the neonate (M_N) (Fig. 1.4). Therefore, we calculated the residual of each value from the equation relating lean dry fraction of tissue to the logarithm of neonate mass. This was done by analysis of covariance, in which taxonomic groups were effects and the $\log_{10}(M_N)$ was the covariate. Thus, the slope of the line relating lean dry fraction to $\log_{10}(M_N)$ was the within-group regression. Both taxonomic group and neonate mass had significant effects on lean dry fraction for all tissues except liver, for which neither group nor neonatal mass was significant. For each tissue, a single regression line having the within-group slope was established and forced through the mean of the lean dry fraction of the tissue and the $\log_{10}(M_N)$ of the entire sample. The slope of the relationship between the LDF and $\log_{10}(M_N)$ was highest for the leg muscle (-0.064 ± 0.001 SE, that is, a decrease of 6.4% for each tenfold increase in neonate mass); the slope varied between -0.020 and -0.034 for the pectoral muscle, stomach, and brain (Fig. 1.4).

The functional maturity of the neonate presents two phenomena: a general decrease in dry matter content of each tissue with increasing neonatal mass (Fig. 1.5)

and significant differences in the lean dry mass between taxonomic groups. The residuals of lean dry fraction of each tissue with respect to body mass were subjected to a principal components analysis based on the correlation matrix, which normalizes the variation of each of the variables (tissues) to the same standard deviation (Fig. 1.6). The first principal component explained 70% of the total variance in the data set (Table 1.3). Variation in five of the six tissues (heart, pectoral and leg muscles, brain, and stomach) contributed nearly equally to the first component, reflecting the strong correlations of the dry fractions of these tissues among themselves ($r = 0.66$ to 0.87). The second principal component uniquely comprises variation in the lean dry fraction of the liver (Table 1.3).

The prominence of the first principal component suggests that functional maturity might be conveniently scaled on a single dimension. The high correlation of the LDF values among most of the tissues further suggests that the lean dry fraction of the entire neonate might be a suitable measure of developmental grade. Total lean dry fraction of the neonate is strongly correlated with the lean dry fraction of each tissue ($r = 0.80$ to 0.93) except liver ($r = 0.61$), and it is also related to the first principal component from the tissue-level analysis ($r = 0.85$). Furthermore, differences between taxonomic groups explain more of the variation in whole-body lean dry fraction ($R^2 = 0.77$; $F_{13,32} = 8.2$; $P < 0.0001$) than in the first principal component ($R^2 = 0.68$; $F_{11,29} = 5.7$; $P < 0.0001$). The values of LDF of the neonate for individual species range from a low value of 0.113 for the blue-eyed shag (*Phalacrocorax auritus*), which is altricial in Nice's (1962) classification, to a high of 0.340 for the blue-winged teal (*Anas discors*), which is precocial-2. The LDF appears to increase with the functional maturity (precocity) of the neonate.

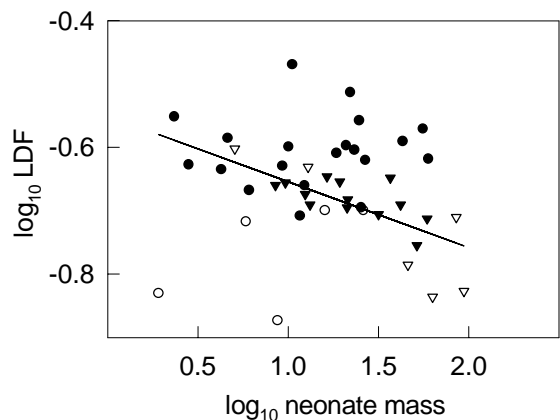


Fig. 1.5. Relationship of \log_{10} -transformed lean dry fraction of neonates and \log_{10} -transformed neonate mass. Regression line was forced through the mean of M_N .

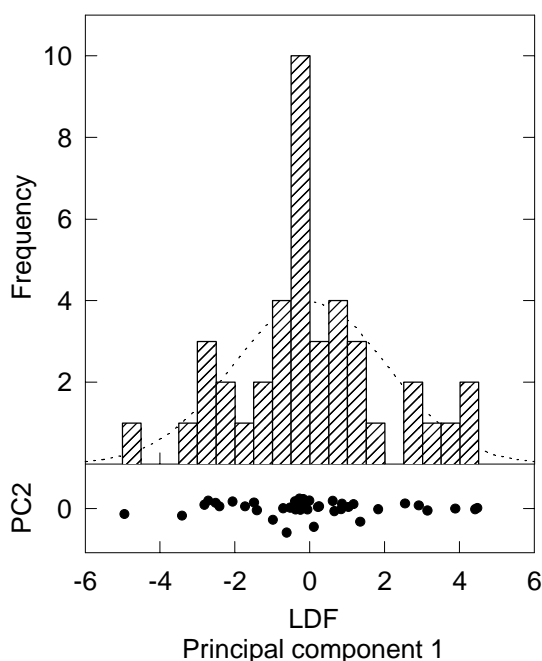


Fig. 1.6. Principal component analysis of lean dry fractions of neonates. For details of the analysis see text and Table 1.4.

The lean dry fraction of the neonate decreases with the increasing mass of the neonate. An analysis of covariance shows that the within-group regression of the $\log_{10}(\text{LDF})$ on $\log_{10}(M_N)$ has a slope of -0.104 (0.019 SE; $R^2 = 0.91$; $F_{14,31} = 22$; $P < 0.0001$). Accordingly, we define a normalized index of lean dry fraction (I_p) as the deviation from the allometric (log-log) relationship of the lean dry fraction on neonate mass. We suggest the equation

$$I_p = \log_{10}(\text{LDF}) - \text{predicted } \log_{10}(\text{LDF}) \quad (1.1)$$

or

$$I_p = \log_{10}(\text{LDF}) + 0.1 * \log_{10}(M_N) + 0.8 \quad (1.2)$$

for this index; -0.8 is approximately the intercept (at neonate mass = 1g) for altricial species (e.g., Passeriformes). Thus, I_p is generally close to zero or positive, with higher values indicating a higher dry matter content of a neonate of a given size (Figs. 1.6 and 1.7; Table 1.4). The value of I_p in our sample varies from -0.18 for the house martin (*Delichon urbica*) to 0.44 for the brush turkeys (*Alectura lathamii*), indicating the range among the species in our analysis. The 14 taxonomic groups account for 91% (R^2) of the total variation in I_p ($F_{13,32} = 24$; $P < 0.0001$).

The distribution of species on the index I_p reveals a mixed pattern. On the one hand, the nonaltricial species (semialtricial, semiprecocial, and precocial) are spread out broadly along the upper part of the range of values. If we consider only groups that are self-feeding at hatching (precocials), these range from ducks ($I_p = 0.37$) to sandpipers (0.25), plovers (0.24), and one galliform (0.16). Neonates of petrels (Procellariidae, $I_p = 0.24$), alcids (Alcidae, 0.27), gulls, and terns (Laridae, 0.24), which are downy but fed by their parents (semialtricial or semiprecocial), fall within the distribution of precocial species. The eared grebe (0.27) and American coot (0.30), whose chicks are fed by the parents during the early part of the postnatal period but leave the nest soon after hatching (Nice's precocial-4), are also well within the distribution of fully precocial groups.

The second feature of the distribution of I_p is a substantial gap between most fully altricial species (-0.18 – 0.04) and the semialtricial-2 Adelie penguin (*Pygoscelis adeliae*, 0.14); a concentration of species, both precocial and semiprecocial, in the range between 0.21 and 0.28 ; and the distribution of all the ducks and the Canada goose (*Branta canadensis*) above 0.32 . Among the Procellariiformes, two species have an $I_p < 0.20$, the southern giant fulmar (*Macronectes giganteus*, 0.17) and the white-chinned petrel (*Procellaria aequinoctialis*, 0.196), whereas the other species cluster between 0.26 and 0.29 . The red-tailed tropic bird (*Phaethon rubicaudis*) is at the low end of the

Table 1.3. Principal component scores of lean dry fraction of different organs (compare Fig. 1.6)

	Eigenvectors					
	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
Brain	0.41	0.26	0.74	0.12	0.39	0.24
Leg	0.46	-0.11	-0.19	0.04	-0.85	-0.12
Heart	0.44	-0.24	0.51	0.06	0.25	-0.66
Liver	0.27	0.83	0.38	0.24	-0.06	0.17
Pectoralis	0.42	-0.41	0.07	0.49	0.20	0.61
Stomach	0.44	0.01	0.08	-0.83	0.13	0.32
Eigenvalue	4.18	0.91	0.39	0.27	0.15	0.10
Proportion	0.697	0.152	0.065	0.045	0.024	0.017
Cumulative	0.697	0.849	0.914	0.959	0.983	1.000

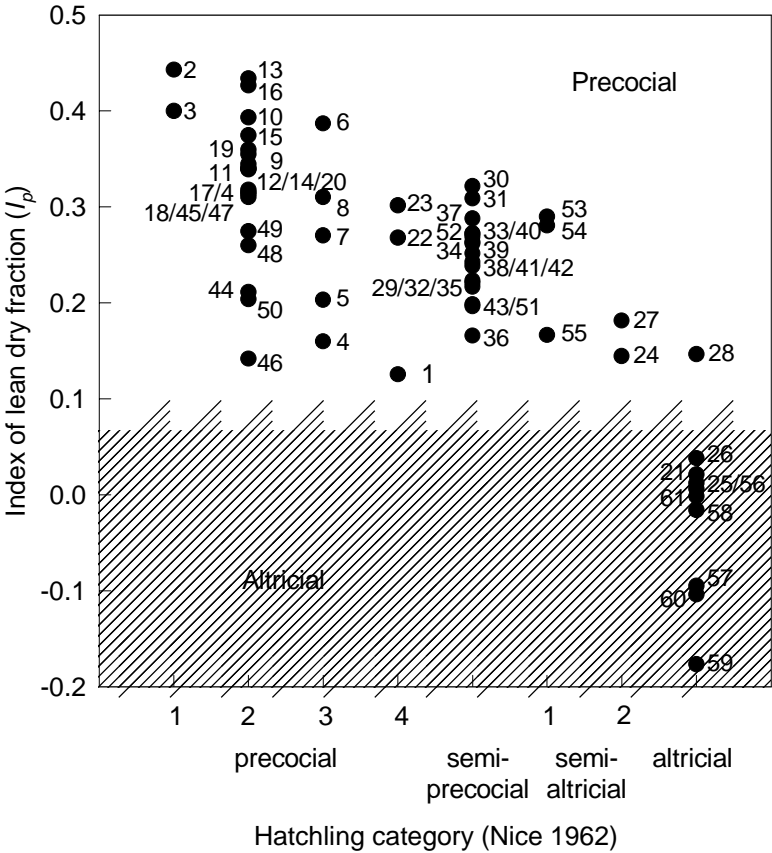


Fig. 1.7. Correspondence between the index of lean dry fraction (I_p) of neonates and the hatchling categories of Nice (1962). Numbers refer to species column in Table 1.4.

semiprecocial group (0.18), and the Japanese quail (*Coturnix coturnix japonica*) resides at $I_p = 0.16$. Additional values for dry fraction have been reported in the literature for neonates or term embryos of several species, but the dry matter contents include lipids (but not yolk) and are therefore somewhat inflated. These data nonetheless yield additional values of I_p that reinforce the pattern presented previously. At the precocial end of the spectrum, two species of megapodes exhibit high values (based on lipid-free masses) of I_p : mallee fowl (*Leipoa ocellata*) 0.40, and brush turkey (*Alectura lathami*), 0.44 (Vleck et al. 1984). Domesticated duck (0.31) and goose (0.34) also have high I_p values but perhaps lower than nondomesticated species (Romanoff 1960). Additional data for galliforms, also from Romanoff, range between bobwhite (*Colinus virginianus*, 0.20), ring-necked pheasant (*Phasianus colchicus*, 0.39), domestic fowl (0.27), and domestic turkey (0.31). Neonates of barred button quail (*Turnix suscitator*) have surprisingly low values of I_p , averaging 0.125, possibly related to their extremely small hatchling size. Values for altricial species include indices of 0.01 for the altricial lovebird (*Agapornis roseicollis*, Psittaciformes), -0.10 for zebra finch

(*Poephila guttata*, Passeriformes), -0.016 for the blue tit (*Parus caruleus*), -0.18 for the house martin (*Delichon urbica*), and -0.10 for the house sparrow (*Passer domesticus*). The brown pelican (*Pelecanus occidentalis*, Pelecaniformes) is surprising at $I_p = 0.15$, considering that other Pelecaniformes, a booby and a shag, have values of 0.04 and 0.01, respectively. In several cases, variation in I_p within groups appears to be related to differences in functional maturity. For example, among the Procellariiformes, diving petrels and fulmarine petrels ($I_p = 0.20, 0.17$) are brooded for several weeks after hatching and have a weaker thermogenic response to cooling than do other petrels ($I_p = 0.26 - 0.29$), which typically are not brooded after hatching (Roby and Ricklefs 1983). Values of I_p for several species of “reptiles”¹⁹ were at the lower end of the precocial range for birds or even intermediate between altricial and precocial birds (Ricklefs and Cullen, unpublished data): agamid liz-

¹⁹ Reptiles are a paraphyletic taxon of evolutionary classification of vertebrates. For simplicity of reading we use “reptiles” (in quotation marks), which is synonymous to the phylogenetically correct term *nonavian sauropsids*.

Table 1.4. Neonatal mass (gram), dry matter fraction of the neonate based on lipid-free dry masses, index I_p of dry matter fraction of neonate mass as derived by the equation $I_p = \log_{10}(\text{LDF}) + 0.1 * \log_{10}(M_N) + 0.8$, and hatchling category according to Nice (1962). Numbers in species column refer to labels in Fig. 1.7.

	Species	Neonate mass (std.)	LDF	I_p	Nice
1	<i>Turnix suscitator</i> ^a	3.8 (0.439)	0.185	0.125	Precocial-4
2	<i>Alectura lathamii</i> ^b	87.2	0.281	0.443	Precocial-1
3	<i>Leipoa ocellata</i> ^b	89.4	0.254	0.400	Precocial-1
4	<i>Coturnix coturnix</i>	5.8 (0.82)	0.192	0.160	Precocial-2
5	<i>Colinus virginianus</i> ^c	6.12	0.211	0.203	Precocial-2
6	<i>Phasianus colchicus</i> ^c	17.5	0.290	0.387	Precocial-2
7	<i>Gallus gallus</i> f. dom.			0.27	Precocial-2
8	<i>Meleagris gallipavo</i> f. dom.			0.31	Precocial-3
9	<i>Aythya valisineria</i>	55.7 (5.69)	0.240	0.355	Precocial-2
10	<i>Somateria molissima</i> ^d	43.1 (0.86)	0.269	0.393	Precocial-2
11	<i>Somateria molissima</i> ^e	22.0 (0.76)	0.257	0.344	Precocial-2
12	<i>Clangula hyemalis</i>	26.6 (3.84)	0.249	0.339	Precocial-2
13	<i>Anas discors</i>	10.5 (0.75)	0.340	0.434	Precocial-2
14	<i>Anas acuta</i>	23.3 (1.03)	0.253	0.340	Precocial-2
15	<i>Aythya americana</i>	20.9	0.277	0.375	Precocial-2
16	<i>Mergus cucullatus</i>	24.7 (3.84)	0.307	0.426	Precocial-2
17	<i>Anas platyrhynchos</i>	18.5 (2.99)	0.246	0.318	Precocial-2
18	domestic duck			0.31	Precocial-2
19	<i>Branta canadensis</i>	59.6 (4.64)	0.241	0.360	Precocial-2
20	domestic goose			0.34	Precocial-2
21	<i>Agapornis roseicollis</i> ^f	2.6	0.148	0.012	Altricial
22	<i>Podiceps nigricollis</i>	9.3 (1.23)	0.235	0.268	Precocial-4
23	<i>Fulica atra</i>	10.0 (1.44)	0.252	0.301	Precocial-4
24	<i>Pygoscelis adeliae</i>	63.1 (4.58)	0.146	0.144	Semialtricial-2
25	<i>Phalacrocorax auritus</i>	33.7 (1.99)	0.113	0.006	Altricial
26	<i>Sula sula</i>	27.7 (2.34)	0.124	0.038	Altricial
27	<i>Phaethon rubricauda</i>	46.1 (5.15)	0.164	0.181	Semialtricial-2
28	<i>Pelecanus occidentalis</i> ^g	61.7	0.147	0.146	Altricial
29	<i>Cephus grylle</i>	9.7 (0.19)	0.208	0.217	Semiprecocial
30	<i>Aethia pusilla</i>	58.9 (6.61)	0.221	0.321	Semiprecocial
31	<i>Fratercula arctica</i>	36.8 (7.41)	0.225	0.309	Semiprecocial
32	<i>Uria aalge</i>	21.4 (0.60)	0.194	0.221	Semiprecocial
33	<i>Larus atricilla</i>	51.5 (4.32)	0.200	0.272	Semiprecocial
34	<i>Sterna hirundo</i>	31.7 (5.24)	0.200	0.251	Semiprecocial
35	<i>Rissa tridactyla</i>	19.3 (2.76)	0.197	0.223	Semiprecocial
36	<i>Catharacta skua</i>	15.9 (2.19)	0.176	0.166	Semiprecocial
37	<i>Sterna fuscata</i>	26.0 (3.35)	0.222	0.288	Semiprecocial
38	<i>Gygis alba</i>	13.2 (1.31)	0.212	0.238	Semiprecocial
39	<i>Larus philadelphia</i>	12.4 (1.52)	0.226	0.264	Semiprecocial
40	<i>Larus argentatus</i>	41.9 (6.70)	0.204	0.272	Semiprecocial
41	<i>Sterna paradisaea</i>	16.4 (1.11)	0.219	0.262	Semiprecocial
42	<i>Anous tenuirostris</i>	21.3 (1.87)	0.204	0.243	Semiprecocial
43	<i>Anous stolidus</i>	8.5 (1.09)	0.202	0.198	Semiprecocial
44	<i>Micropalma himantopus</i>	6.1 (1.57)	0.215	0.211	Semiprecocial
45	<i>Calidris minutilla</i>	25.3 (1.37)	0.236	0.313	Precocial-2

continued

Table 1.4 (continued)

	Species	Neonate mass (std.)	LDF	I_p	Nice
46	<i>Numenius phaeopus</i>	2.3 (0.20)	0.202	0.142	Precocial-2
47	<i>Phalaropus lobatus</i>	4.6 (0.13)	0.281	0.315	Precocial-2
48	<i>Calidris alpina</i>	2.8 (0.07)	0.260	0.260	Precocial-2
49	<i>Charadrius semipalmatus</i>	12.3 (2.32)	0.232	0.275	Precocial-2
50	<i>Pluvialis dominica</i>	4.3 (0.28)	0.219	0.204	Precocial-2
51	<i>Procellaria aequinoctialis</i>	11.6	0.195	0.196	Semiprecocial
52	<i>Oceanodroma leucorhoa</i>	5.1 (0.81)	0.250	0.269	Semiprecocial
53	<i>Pelecanoides urinatrix</i>	94.0 (8.82)	0.196	0.290	Semialtricial-1
54	<i>Pelecanoides georgicus</i>	12.9 (1.53)	0.234	0.280	Semialtricial-1
55	<i>Macronectes giganteus</i>	85.3 (14.87)	0.149	0.166	Semialtricial-1
56	<i>Aimophila carpalis</i>	1.9 (0.35)	0.148	0.002	Altricial
57	<i>Poephila guttata</i> ^f	0.6	0.134	0.095	Altricial
58	<i>Parus caeruleus</i> ^h	1.2 (0.2)	0.150	0.016	Altricial
59	<i>Delichon urbica</i> ^h	1.7 (0.2)	0.100	0.177	Altricial
60	<i>Passer domesticus</i> ^h	3.5 (1.1)	0.110	0.104	Altricial
61	<i>Sturnus vulgaris</i>	8.7 (1.90)	0.134	0.021	Altricial

Data from ^a J.M. Starck (unpublished); ^b Vleck et al. 1984; ^c Romanoff (1960); ^d Greenland, probably *S. m. borealis*; ^e Atlantic NE North America, probably *S. m. dresseri*; ^f Bucher et al. 1984; ^g Bartholomew and Goldstein (1984).

ard (*Amphibolurus barbatus*, 0.09), snake (*Coluber constrictor*, 0.20), turtle (*Chrysemys picta*, 0.21), and iguana (*Iguana iguana*, 0.11).

One point of correspondence between the scale of functional maturity developed here and Nice's (1962) classification of neonates is the restriction of I_p values below 0.1 to the altricial species (Fig. 1.7). The precocial ducks and megapodes occupy the extreme opposite end of the scale, but other precocial groups, such as the Galliformes and waders (Charadriidae and Scolopacidae), are situated in the middle of the spectrum, along with the semialtricial petrels and penguins. We find continuous variation in I_p with values for species in several of Nice's categories overlapping broadly.

Although variation in development mode within orders and families is small compared to that between orders and other higher taxa, the relationship between functional maturity and phylogeny appears to be complex (Fig. 1.8). One may summarize the relationships among the taxonomic groups by contrasting Sibley and Ahlquist's (1990) phylogeny, which is based on DNA-DNA hybridization, with Cracraft's (1986) phylogeny, which is based on morphological characters. The earliest major node, or branch point, separates the Eoaves, which are all precocial in Nice's (1962) terminology, and the Neoaves, which encompass the whole range of developmental types from precocial to altricial. Even among the precocial Eoaves, I_p appears to vary over almost the full range of nonaltricial species, from the

ducks to the Galliformes. The basal taxa of the Neoaves are altricial (Picae, Coraciae, Coliae, Cuculimorphae, Psittacimorphae, and Apodimorphae). However, the more derived taxa of the Gruiformes and Ciconiiformes in our sample range from coots and grebes, which lie close to the precocial end of the scale (0.30 and 0.27), to shags and boobies (0.01 and 0.04), which cluster at the altricial end. Thus, precocial (including semiprecocial) development has also been derived independently, at least in the Strigiformes (Caprimulgidae, nighthawks with semiprecocial young) and in the gruiform-ciconiiform lines. According to Sibley and Ahlquist's phylogeny, the evolution of secondarily altricial development from nonaltricial ciconiiform stem groups must have occurred in the Pelecanidae, Sulidae, Anhingidae, and Phalacrocoracidae. In contrast, Cracraft's phylogeny places all precocial forms among the lower nodes of the cladogram. The results of such comparisons are as conflicting as are the underlying phylogenetic hypotheses, and it is difficult to draw convincing conclusions based either on Sibley and Ahlquist's or Cracraft's hypothesis.

Finally, we ask whether the level of functional maturity (dry matter content) is related to other attributes of the neonate associated with its functional capacity. Natal down reduces the thermal conductance of the neonate and is associated with endothermy. Down is essentially absent in many altricial species, and so there is a connection between natal down and I_p at a large

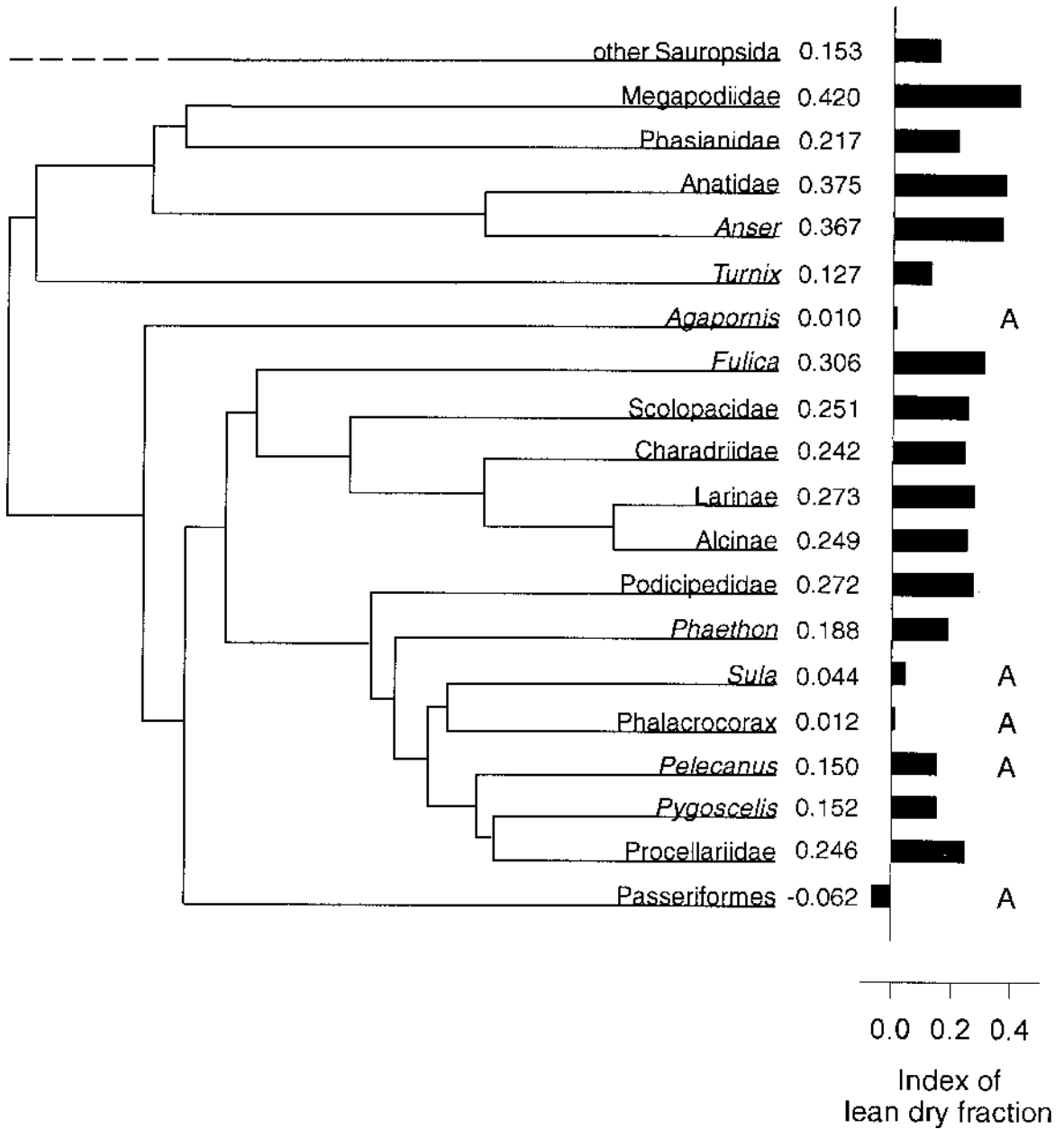


Fig. 1.8. Phylogenetic relationship of the species analyzed for index of lean dry fraction.

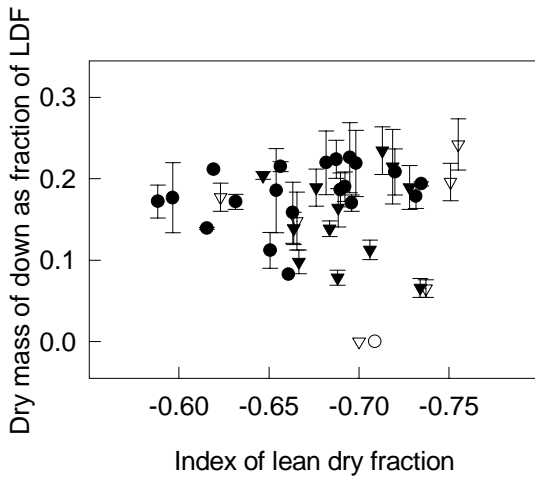


Fig. 1.9. Relationship between index of lean dry fraction (I_p) and dry mass of down as a fraction of LDF.

scale. Among nonaltricial species, however, the dry mass of the down, shown in Fig. 1.9 as a fraction of the total dry mass of the chick, bears no particular relationship to I_p . Down mass varies among these species from as little as 6.5% of the dry mass in the Adelie penguin to 21% in the ducks and 26% in the alcid.

The functional maturity of the neonate has often been related to the size of its brain. We calculated residuals from the regression of $\log_{10}(\text{brain mass})$ and $\log_{10}(\text{body mass})$ for the 46 species. Again, no relationship exists between residuals of the regression of brain size on body mass and the dry matter content of the neonate tissue, including the brain. The pronounced differences in the relative sizes of the brain between the groups included in this study presumably reflect other aspects of development and ecology than the actual functional maturity of the neonate.

From this analysis, we draw the following general, albeit tentative, conclusions. (a) The functional maturities of five tissues that have different patterns of use during development appear to vary in parallel, defining a single axis of variation in the functional maturity of the neonate. (b) The lean dry fraction of the whole neonate provides a useful scale of the developmental grade. (c) Because lean dry fraction decreases with increasing neonate mass, we have calculated an index (I_p) that takes the mass of the neonate into account. The index I_p is the deviation of the observed lean dry fraction from the allometric regression of the lean dry fraction on the neonate mass. (d) On this functional maturity scale, altricial species are distributed at low values of I_p and seem to be separated from nonaltricial species that show a wide range of variation in functional maturity in a higher range of I_p . The results of our analysis suggest variation along a unidimensional and continuous spectrum of functional maturity that contrasts with Nice's (1962) categorical classification

of hatchlings. (e) Although species classified by Nice as "altricial" fall within the first group, there seems to be no clear distinction in functional maturity between semialtricial, semiprecocial, and especially precocial birds. Nice's groups overlap considerably in functional maturity (Fig. 1.7). (f) Putting the scale of functional maturity next to Sibley and Alquist's (1990) avian phylogeny suggests that although developmental maturity exhibits taxonomic conservatism on the level of families and orders, it appears to have shifted at several evolutionary branch points that separate larger taxonomic groups. Because the basal taxa of the Neoaves are altricial, semiprecocial and precocial modes of development in the Gruiformes and Ciconiiformes are secondarily derived. Furthermore, the development of boobies, shags, pelicans, and frigate birds may be secondarily altricial, having been derived from ancestral taxa with nonaltricial development. Cracraft's (1988) phylogeny suggests even more independent evolutionary origins of altriciality. However, our general impression is that the mode of development is primarily a quantitative variable, which may evolve rapidly across the precocial to semialtricial range under suitable selective pressures. It is apparently tied to circumstances of ecology, as discussed later. Thus, the relative conservatism of the developmental mode within taxa of familial and ordinal rank may reflect evolutionary conservatism of ecology rather than that of development.

1.6. A Mammalian Perspective

As in birds, mammalian neonates exhibit a varying degree of independence, ranging from extremely altricial marsupials and monotremes to the relatively independent young of ungulates. Compared to birds, the mammalian embryo develops under fundamentally different physiological and structural conditions that place it in a different framework of selection and internal constraints. The most striking differences in reproductive strategies of birds and mammals are as follows. (a) Birds are oviparous, whereas mammals are viviparous (except for the oviparous monotremes). (b) Nutrient supply to the mammalian embryo through the placenta is continuous and almost unlimited as compared to the energy-limited egg compartment in birds. (c) The intrauterine development of the mammalian embryo allows the mother a relative independence of movement during almost all phases of its reproductive status, whereas birds incubate their eggs through the whole embryonic period and are bound to the nest. (d) Lactation allows the nourishment of neonates and growing young mammals to be relatively independent of the actual environmental conditions (e.g., immediate food abundance and weather conditions, which have important effects on avian postnatal growth; see chapter 16). (e) The costs of reproduction are almost exclusively borne by the female in mammals, whereas

they are more equally partitioned among sexes in many birds. The evolution of altricial and precocial neonates under such different reproductive strategies makes an interesting contrast between birds and mammals. Here, we briefly outline similarities and differences in avian and mammalian ontogenies to determine whether altriciality and precocity refer to the same phenomenon in birds and mammals and to gain some insight into the major selective conditions that drive the diversification of mammalian ontogenies. We review current ideas and provide a perspective on mammals, but we cannot give a comprehensive treatment in limited space.

1.6.1. The mammalian altricial-precocial spectrum

The mammalian neonates show considerable differences in their developmental stage. For example, many insectivores (Insectivora), all rabbits (Lagomorpha), many rodents (Rodentia and Muridae), and most carnivores (Carnivora) give birth to small neonates that have closed eyes and ears, and no hair, are generally poorly developed, and are dependent on maternal care for a long lactation period. Newborn marsupials and monotremes are extremes, resembling early embryos, even compared to other altricial mammals. Precocial neonates are found among the ungulates (Cetacea, Sirenia, Proboscidea, Hyracoidea, Perissodactyla, and Artiodactyla), the Pinnipedia, and several rodent taxa (Rodentia). Precocial mammals, especially ungulates, may run swiftly and for long distances shortly after birth, and some begin to feed on solid food within a few days. The neonates of some taxa are intermediate

between altricial and precocial development; for example, nonhuman primates are born with well-developed fur and open sensory organs but depend to a much higher degree on parental care than do precocial neonates. Different intermediate stages may be found within orders. For example, within the rodents, mice and rats (Muridae) produce highly altricial young, whereas spiny mice (*Acomys inous*) and guinea pigs (*Cavia* sp.) have highly precocial young (Fig. 1.10). Bats (Chiroptera) show a similar diversity of neonates, ranging from altricial young (Megachiroptera), which are born naked, to more precocial taxa (Phyllosomatoidea), which are born with open eyes and are covered with fur (Eisenberg 1981). Derrickson (1992) developed a classification scheme for mammalian neonates that employs developmental categories for neonatal independence in four areas: thermoregulation, sensory organs, locomotion, and nutrition (Table 1.5). Mammalian orders clearly exhibit greater flexibility of developmental mode than do avian orders, with Carnivora and Rodentia exhibiting the full range from altricial to precocial.

1.6.2. Portmann's view

The general perception of the evolution of altricial and precocial mammals has for a long period been dominated by the ideas of Adolf Portmann and his student Fabiola Müller. Although these ideas are difficult to accept in the light of modern evolutionary biology, the data and basic information provided with their publications are most valuable. Portmann's concept encompasses four paradigms. (a) The evolution of avian ontogenies proceeds from independent development toward

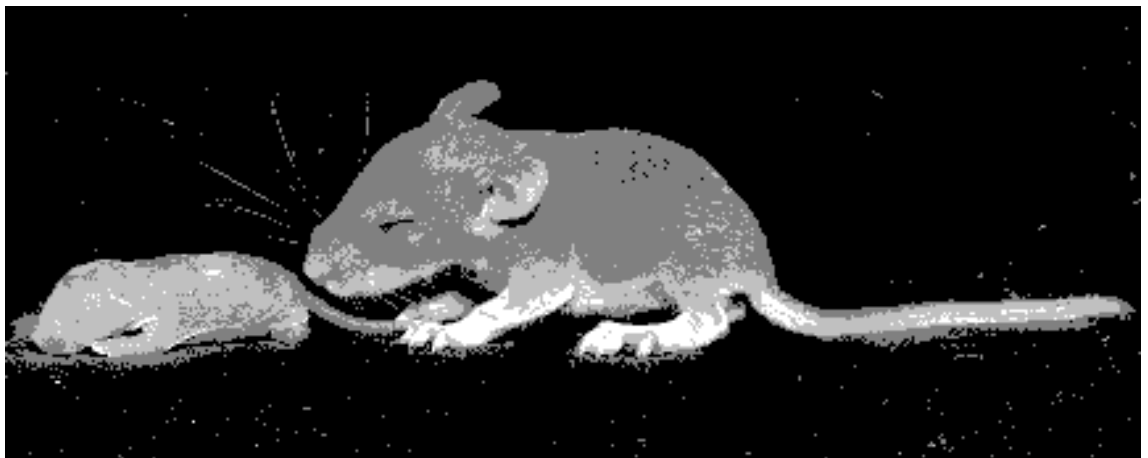


Fig. 1.10. Neonate of an altricial house mouse (*Mus musculus*, Muridae) and a precocial spiny mouse (*Acomys minous*, Muridae) to demonstrate the diversity of neonates within Muridae, Rodentia (with kind permission of D. Starck).

Table 1.5. Developmental categories of neonates in mammalian orders (after Derrickson 1992). Black fields indicate the major mode of development for that order; striped fields indicate that the specific mode of development occurs in few species only.

Order	Altricial	Intermediate	Precocial
Insectivora			
Macroscelididae			
Chiroptera			
Scandentia			
Primates			
Edentata			
Pholidota			
Lagomorpha			
Rodentia			
Cetacea			
Carnivora			
Pinnipedia			
Tubulidentata			
Proboscidea			
Hyracoidea			
Artiodactyla			

increasing dependence of the embryo and neonate on its parents. In contrast, mammalian ontogenies evolved from altricial to precocial. (b) Ontogenies evolve in categorical units (macroevolutionary changes) and may be recognized by specific syndromes of altriciality or precocity (Geigy and Portmann 1941), “morphologische Wertigkeit” in his terminology (Portmann 1938a, 1938b). (c) The evolution of ontogenies proceeds as the correlated evolution of organ systems and, therefore, must be considered in relation to taxonomic (phylogenetic) position rather than in the context of the environment of the neonate. (d) Central to Portmann’s ideas is the “rule of precedence,” which assumes that changes in the ontogenetic mode (e.g., the conversion from nidicolous to nidifugous) must precede the evolution of specific structural characters of precocity. For example, in mammals, the neonate must become precocial before it can evolve a large neonate brain size, thus resulting in an ordered evolution from altricial to primitive precocial, which precedes the derived precocial condition.

Briefly, the egg-laying monotremes, with very short gestation periods, and small “embryonic” neonates were considered the most ancestral condition. Their ontogenetic mode was thought to represent a “missing link” between “reptiles” and mammals (Müller 1968a). Marsupialia were considered to be an intermediate link to eutherian mammals because of their poorly evolved parental (maternal) care for the young, and embryonic and postnatal closure of eyes, ears, and

lips (Müller 1968b, 1969, 1972a, 1972b, 1972c, 1972d). Within the eutherian mammals, insectivores, rodents, and carnivores were thought to represent the ancestral syndrome of altriciality as inherited from marsupials, with a high number of young, a short gestation period, and naked neonates whose eyes and ears are closed and who cannot thermoregulate appropriately. Portmann and Müller suggested that the diversity of neonates in the “lower ranking orders of mammals” — for example, within the rodents neonates may be altricial (*Rattus norvegicus*, Muridae) or precocial (*Cavia cobaya*, Caviidae) — represents evolutionary trials toward the “next higher category.” Besides prolongation and abbreviation (shortening) of the gestation period, heterochrony in many organ systems (especially in the skeleton of the skull and legs) was recognized as an important mechanism of evolutionary change of ontogenies (Schinz 1937; Müller 1972a, 1972b, 1972c, 1972d). Precocial eutherian mammals comprise all marine mammals, primates, and ungulates. The highest grade of ontogeny was suggested for humans, who were thought to represent a secondarily nidicolous species passing through the nidifugous stage in utero (Portmann 1941, 1945, 1952, 1957, 1962). Although Portmann published extensively about this topic, his ideas remained notably ambiguous concerning retardation and acceleration of human embryonic development and how secondarily altricial young could be precocial while embryos. An important generalization from Portmann’s studies is that the timing

of birth in mammals is much more flexible than the timing of hatching in birds. Also, heterochrony was recognized in the development of specific organ systems (e.g., the forelimbs, mouth, intestinal tract, and lungs of marsupials), resulting in the considerable diversity of mammalian neonates.

Reproductive strategies in monotremes, marsupials, and eutherian mammals are not simply a sequence of evolutionary grades but rather represent independently derived specializations in each group. For example, this can be seen on the structural level by the derived structure of mammary glands and in the physiology of lactation. Most marsupials develop a choriovitelline placenta (yolk-sac placenta), whereas the eutherian mammals rely on a chorioallantoic placenta (allantois placenta); only the bandicoots (*Perameles* spp.) have both (Renfree 1983; Tyndale-Biscoe and Renfree 1987). A phylogenetic analysis of amniotic fetal membranes suggests that the reduction of an extensive chorioallantoic placenta should be considered a derived character (Luckett 1977). Further specializations of the neonate marsupial, for example, the highly functional tongue musculature and the functionality of the mesonephros (embryonic kidneys), are described by Hughes and Hall (1988). It has been pointed out by Renfree (1983) that mammalian reproduction evolved along two alternative avenues, one favoring the lactation strategy, as in marsupials, the other favoring gestation, as in eutherian mammals. For marsupials, extended lactation apparently was the more successful reproductive strategy, allowing for very small young, which had unlimited potential for growth when conditions were good but could be easily jettisoned under adverse conditions.

1.6.3. Heterochrony and mammalian development

Gould (1977, p. 349; 1988) presents a general hypothesis of heterochrony in mammalian ontogeny, mostly based on Portmann's work and relating it to patterns of selection. He attempts to understand macroevolutionary changes by relating progenesis²⁰ and altricial development (early maturation) to r -selection, and prolongation of development (hypermorphosis,²¹ with extended periods of differentiation) and precocity to K -selection. However, even if we would adopt the view relating diversification of ontogenies to patterns of selection, it is difficult to recognize any straightfor-

ward relationship between mode of development and r or K strategy. Altricial development is found among insectivores and rodents, usually thought of as r -selected taxa, as well as edentates (anteaters and sloths), which represent typically K -selected taxa. Monotremes have extremely altricial neonates but a low reproductive rate, intensive parental care, and slow postnatal development; platypus (*Ornithorhynchus anatinus*) and echidna (*Tachyglossus aculeatus*) would be characterized as typical K -strategists. Precocial species, however, are found among large ungulates and aquatic mammals (cetaceans and manatees), which are seemingly K -selected, as well as rodents (*Cavia*) and hyracoids (*Hyrax*), which typically are r -selected (Fischer 1992). Gould (1977) considers heterochrony to be a driving force in the evolutionary diversification of ontogenetic modes in mammals and extended this idea to hypothesize a pedomorphic origin of humans from other primate genera (for reviews, see Bolk 1926; D. Starck 1962, 1974, 1975; Gould 1977; Shea 1988).

1.6.4. Life history approach

Eisenberg (1981) placed mammalian ontogenies in the context of life history evolution. He described two major trends in the diversification of ontogenies. On the one hand, large adult body size favors the production of large, precocious young, which develop during a long gestation period and thus, to some degree, depend on the reliable availability of food for their mothers. Large neonates are thought to correlate with a long life-span, an extended period of reproduction, and reduced litter size. On the other hand, Eisenberg suggested that altricial mammals were selected for the ability to "recycle" their young (that is, the mother may resorb the embryo at any stage of its development), thus regaining invested energy at any point of the reproductive cycle, when adverse environmental conditions would prohibit the successful rearing of young. This conceptual framework has been supported anecdotally by observational evidence but certainly should be examined more closely, particularly to determine whether development is associated closely enough with ecology for an explanation of the within-order diversity of neonates (e.g., Rodentia and Carnivora). Recent studies of neonate brain size, mode of development, and life history traits (Martin 1981, 1984; Bennett and Harvey 1985; Grand 1992) have supported Portmann's view of a strong relationship between precocial development and large neonatal brain size. However, these studies rely on a basically dichotomous perception of development and cannot explain the obvious variation within taxonomic groups.

Derrickson (1992) used four categorical traits (thermoregulatory, sensory, locomotory, and nutritional) to characterize mammalian neonates (Table 1.5). Independence in all four traits was assigned to precocial

²⁰ Progenesis: pedomorphosis (retention of formerly juvenile characters by adult descendants) produced by precocious sexual maturation of an organism still in a morphologically juvenile stage (Gould 1977).

²¹ Hypermorphosis: the phyletic extension of ontogeny beyond its ancestral termination (usually to a larger body size).

development, and dependence in all four to altricial, with intermediate stages exhibited by a variety of taxa. Neonates were then compared in nine life-history traits. The results of her analysis show that (a) the length of the gestation period is extended in precocial primates but shortened in precocial rodents; (b) the neonate mass varies according to developmental category, (c) the litter size and growth rate vary dichotomously along the altricial-precocial spectrum; (d) litter mass and age of first parturition show no significant variation among developmental categories. Derrickson's analysis shows clearly that mammalian neonatal patterns have not evolved along a single continuous axis of diversification and that altricial and precocial development probably arose independently in response to more than one kind of selection pressure. According to Derrickson's analysis, the concept of an altricial-precocial spectrum in mammals differs strikingly from that in birds. In mammals, the developmental mode is highly corre-

lated with the neonate size and gestation period, suggesting that the developmental advancement of precocial species reflects a prolongation of the embryonic developmental period but perhaps not an increase in maturation with respect to growth, as is apparent in birds (Fig. 1.11).

1.7. Conclusions

The analysis of lean dry fraction suggests that the developmental mode in birds varies continuously along a single dimension. If this reflects evolution correctly, one may conclude that evolutionary diversification of ontogenies has followed gradual rather than categorical changes. The only clear contrast in the index of lean dry fraction I_p appears between altricial birds and all other birds, including semialtricials. At present, we cannot resolve whether this is a true gap or whether additional data might fill the space between altricials

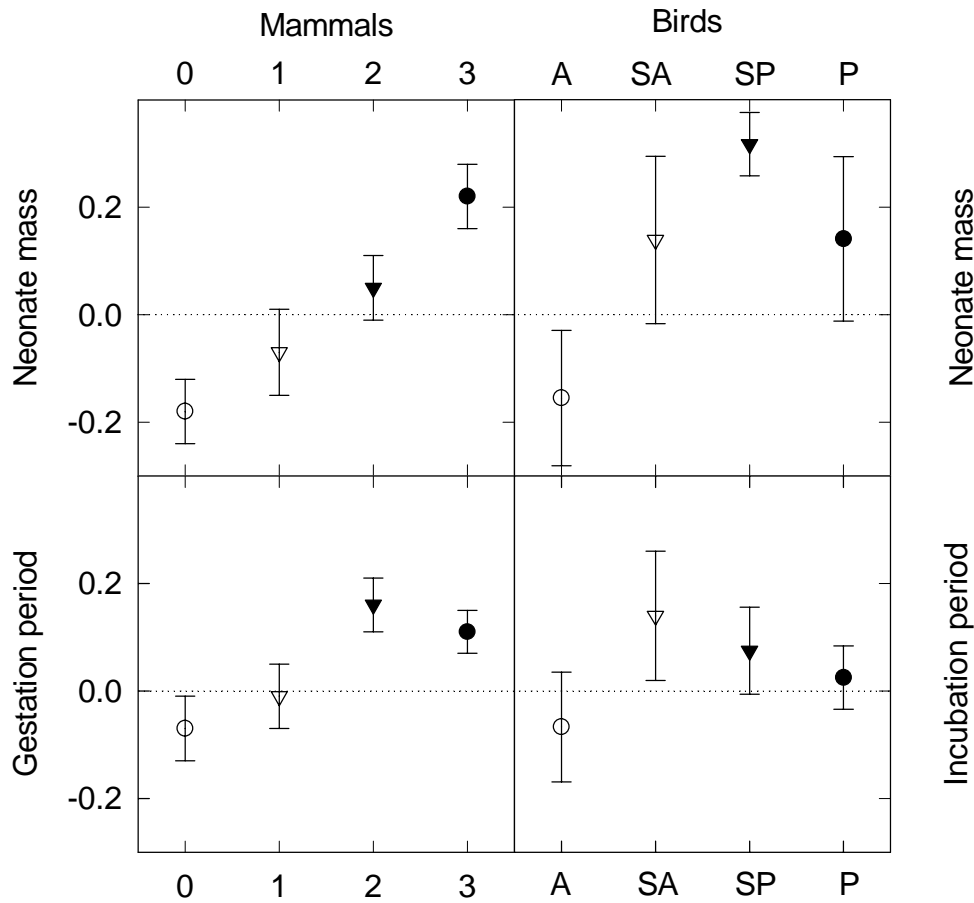


Fig. 1.11. Comparison of the (a) mammalian and (b) avian altricial-precocial spectrum. The upper panels show averages and standard deviation of residuals from an allometry of the neonate mass on body mass for four developmental categories; the lower panels show residuals from an allometry of gestation period (incubation period) on adult body mass. The developmental categories for mammals follow Derrickson (1992); 0, altricial; 1 and 2 intermediate forms; 3, precocial. For birds; A, altricial; SA, semialtricial; SP, semiprecocial; P, precocial.

and other groups. Regardless, values of I_p in altricial birds appear only to extend the range of variation exhibited by all other birds along a single dimension. Thus, we recognize a continuous gradient of functional maturity comprising all developmental modes, in which altricial birds exhibit values of I_p beyond the ranges of all other developmental modes. It is important to note that except for altricial birds, traditional categories of development (e.g., Nice 1962) cannot be distinguished by unique ranges of I_p values. For example, precocial and semiprecocial birds (in Nice's category) occupy a wide range of I_p values, overlapping at the lower end of the range with semialtricial birds. Thus, realizing that continuous and overlapping variation of functional maturity underlies most categories of development, we might be wiser to recognize only altricial development as a quantitatively distinct category. Attention should focus on understanding the basis for variation in functional maturity among all other birds as well as the uniqueness of altricial development.

The analysis leaves us with a set of questions that are difficult to answer. What actually causes evolutionary change in lean dry fraction or I_p ? Is the schedule of development changed so that I_p represents distance along the developmental progress of maturation? Several lines of evidence discussed in the next chapter (see also J.M. Starck 1989, 1993) suggest that this is not the case and that the time patterns of development are rather unchanged in birds.

Another puzzling question concerns why the apparent functional levels of all tissues except liver change together. Why is variation in avian development organized along a single dimension? Our data support earlier studies by O'Connor (1977, 1978a, 1978b) which suggest that developmental processes are tied together in such a way that changes in any one tissue must be accompanied by changes in all others. That is, development is a phenomenon of the whole organism rather than independent phenomena of individual tissues, in spite of the fact that the onset of function in different tissues seems to vary independently of their developmental schedules.

Finally, what is the meaning of the relation between neonate mass and lean dry fraction? Why should larger species tend to have lower function and capacity, particularly as they seem to show greater independence as neonates?

Phylogenetic analyses of mode of the development could not clearly resolve whether altricial or precocial development was the ancestral trait in birds. Multiple independent origins of altriciality and precocity are highly probable from the phylogenetic comparisons. The probability of an independent evolutionary origin of altriciality in dinosaurs indicates that the mode of development might have changed frequently during evolution. The high integration of development of dif-

ferent organ systems and its variation in only a single dimension suggests that the overall similarity of altricial or precocial chicks of different taxa represents parallel evolution rather than similarity based on common ancestry.

When it is difficult to reconstruct the ancestral character state of developmental modes through phylogenetic analyses, we might proceed by investigating ecological characteristics of extinct ancestral avian taxa that are predictive of developmental mode. For example, precocial chicks always have to search for food on the ground, have a wide spectrum of food items, and gather easily accessible prey. Altricial young however, may rely on the prey capture skills of their parents and thus may be fed a food that is inaccessible for precocials. We return to this question in chapter 16.

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