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S27-4 Patterns among avian flight style, nesting biology, development, body size, and locomotor modularity

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Abstract Morphological investment emphasizing either the hind limb or forelimb module varies predictably with trends in: (1) parental care, as in nest construction and placement, feeding and protection of young, (2) developmental hatchling stage, as in the precocial-altricial spectrum, (3) body size, and (4) flight style, as in weak, one-paced or maneuverable. Simultaneous comparison of these life history variables within a five-parameter model is presented here to better understand the evolutionary history of avian diversity, focusing on locomotor biology.

Key words Locomotor modules, Flight styles, Parental care, Precocial-altricial spectrum

1 Introduction

Aspects of avian biology such as nesting strategy, flight style, body form, and hatchling type are usually studied as separate topics, but rarely addressed as integrated and mutually dependent variables. Herein, I suggest that it is also particularly insightful to compare range and expression among each of these variables together, within an integrated matrix. Consistent trends are then observed among suites of traits for locomotor and life history features when surveying primitive and derived avian taxa, for which predation pressure appears to be the primary selective force triggering and molding the changes. To begin, I briefly review the five model parameters involved.

2 The five parameters

Avian body plans can be viewed as a composite of three discrete locomotor modules — forelimbs, hind limbs, and tail — which are differentially elaborated according to specializations in life-style (Gatesy and Dial, 1996). Unique among vertebrates, these three avian locomotor modules are operated by separate muscle groups, thus permitting each module to function without necessarily impinging on the other. A differential investment in the hind limb or forelimb module results in predictably distinct flight styles and behaviors.

Nest building varies from a simple accumulation of materials on the ground to elaborately built structures placed in secluded and elevated positions (Collias and Collias, 1984). The progression from simple to complex nest construction appears to correlate with an increasing effort to protect young from predators (Nice, 1962; Skutch, 1985; Martin, 1988). An increase in the complexity of nest building, as well as in the feeding and protection of young, correlates with morphological emphasis on the anatomy of the forelimb and, to a lesser degree, tail.

The precocial-altricial spectrum ranges from the megapodes, whose advanced well-feathered hatchlings are virtually flight-capable from day one, to the Passeriformes, the chicks of which are nearly embryonic, hatching naked, blind, thermally dependent, and essentially incapable of movement (Ricklefs, 1983; Starck and Ricklefs, 1998). The spectrum is unevenly distributed, altricial developmental stages predominating in the great majority of birds today (Starck, 1993). Precocial development may be considered a primitive condition while altricial development correlates with advances in parental care.

Most altricial species are small in body size while precocial taxa are relatively large. Birds span over five orders of magnitude in body size, extant species ranging from the 5 g Cuban bee hummingbird to the ostrich, exceeding 150 kg (Peters, 1983; Calder, 1984). The relationship between body size and power output means that smaller birds can make more of their environment on the wing. While many small species within an order are capable of vertical flight, the larger members can only rise at shallower angles, as in the Psittaciformes.

The range and diversity of flying abilities among birds is extraordinary (Savile, 1957; Norberg, 1990; Warrick, 1998). Specific morphological attributes facilitate high maneuverability and linear acceleration. Generally, species that are intrinsically maneuverable possess larger wings relative to body mass; and species that are facultatively maneuverable have the ability to generate high mass-specific power at slow speeds by creating large force asymmetries between the two wings (Warrick, *l.c.*).

3 Five-way comparison of the parameters

Inspection of the trends among primitive and derived taxa in the above five variables provides insights into a fairly straightforward evolutionary trajectory (Fig. 1). The more primitive groups possess the following characters: large body size, superprecocial to precocial young, locomotor morphology dominated by the hind limb module, minimal parental care, flightlessness or capacity for only brief, episodic flight, and simple ground nesting (e.g., megapodes, most other Galliformes, some Anseriformes. The next taxonomic cluster exhibits relatively large body size, precocial young, constricted flight styles, ground or platform nests, and increased propensity for parental care (e.g., Podicipediformes, Gruiformes, Gaviiformes, and some Anseriformes). The next level of complexity comprises taxa with medium-to-large body size, a more evenly balanced locomotor arrangement involving tail, hind limb and forelimb, simple elevated nests, altricial young with increased parental care, and increased flight machinery with more diverse flight styles (e.g., Columbiformes, Ciconiiformes, Falconiformes).

The most morphologically, ecologically, and versatile fliers are the highly derived and speciose Passeriformes, characterized by small body size, well-balanced investment in hind limb, tail, and forelimb modules with diverse wing and tail designs, a wide range of feeding and nesting habits, intense parental care, and altricial-to-superaltricial young. Positioned at the terminus in this schema are the aerial cursors (e.g., Apodidae, Trochilidae, Hirudinidae), endowed with extraordinary flight capabilities. This group exhibits small body size, atrophic hind limb modules and pronounced forelimb musculoskeletal investment, elaborately constructed and secluded nests, (or simple nests placed within predator-free environments), intense parental care, and superaltricial young.

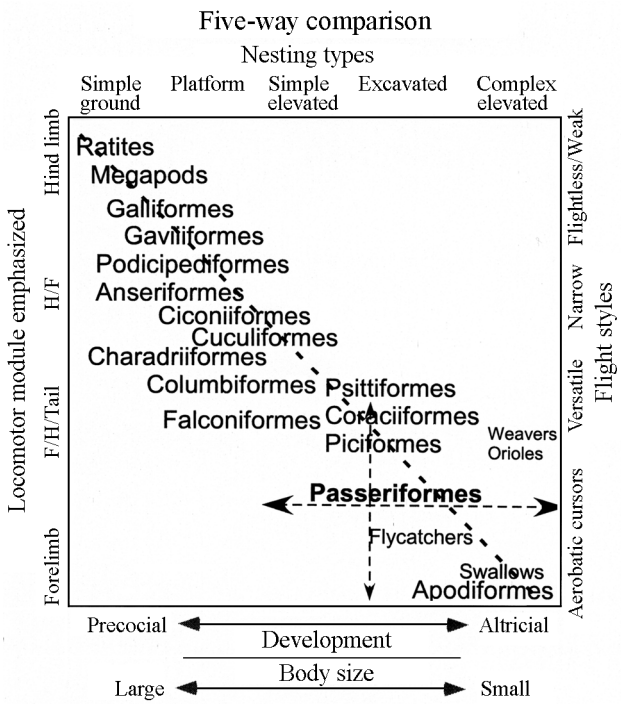

Fig. 1 Five-way comparison of variables associated with avian locomotion and the evolution of life-history traits
Note the nearly linear progression in the suite of traits associated with primitive bipedal cursors towards aerial cursors. Passerines exhibit the greatest diversity in form and flight styles by attaining small body size, substantial forelimb and tail modular investment, and complex nesting biology (H=hind limb-, F=forelimb-, Tail=tail-modules).

Taken together, the trends in the five variables are coherently linear and unidirectional, the more derived species sequestering young in a secured nest and providing significant parental care, thus permitting a morphological trajectory towards reduced hind limb and increased forelimb investment for increased flight capacity (Fig. 1). These observations suggest that bipedal, hind limb-dominated proto-avian theropods were relatively large, hatched precocial young, provided rudimentary parental care, and had forelimbs to assist incline running as they escaped to elevated refugia (Dial, 2003). This interpretation is consistent with most, if not all, of the recently discovered proto- avian paleontological material in China and Asia (e.g., *Caudipteryx*), as these fossils represent long-legged, cursorial bipeds with partial wings (Norell et al., 2002; Ji et al., 1998).

4 Conclusions

Among vertebrates, birds possess a unique modular anatomical arrangement permitting different modes of locomotion from regionally specific musculoskeletal modules (forelimbs, hind limbs, and tail). Body size, developmental stage at hatching, flight style, nesting biology and locomotor modularity appear to be intimately correlated. Simultaneous inspection of trends among these attributes suggests that primitive taxa are relatively large, cursorial, hind limb-dominated species building crude ground nests and providing relatively unsophisticated parental care. In contrast, derived taxa possess complex flight capabilities in which forelimb and tail dominate, are physically small, and exhibit complex parental care in order to sequester helpless young within a complexly engineered, elevated nest. The evolution of birds may thus be viewed as a morphological shift from hind limb locomotor machinery, consistent with primitive extant species as well as proto-avian theropods, to forelimb-powered flight stimulated primarily by predation pressure and motivated secondarily by filling niches to exploit diverse food resources.

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