SYMPOSIUM

The Biology of Gliding in Flying Lizards (Genus Draco) and their Fossil and Extant Analogs

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Synopsis The flying lizards of the genus Draco are among the most remarkable and successful clades of gliding vertebrates. Here, we evaluate the evolution of gliding in Draco and other lizards, describe the suite of morphological innovations that characterize Draco, discuss the ecological context of gliding in this genus, describe functions of their patagial membranes that are not related to gliding, and summarize the interspecific allometry of the Draco gliding apparatus, as well as the corresponding consequences for their now empirically quantified gliding performance. Several fossil reptilian lineages had morphologies similar to that of modern Draco, with patagial membranes supported by elongated ribs or rib-like dermal structures. Using Draco’s snout-vent length/mass relationships, we provide improved estimates of wing loading for three of these fossil gliders (Icarosaurus seifkeri, Kuehneosaurus sp., Coelurosauravus elivensis) and then estimate absolute gliding performance for each taxon by extrapolating from Draco’s wing loading/glide performance relationship. We find that I. seifkeri likely represented the best nonflapping terrestrial vertebrate glider yet described, whereas the larger Kuehneosaurus and Coelurosauravus probably required high descent velocities to achieve sufficient lift for gliding, with commensurately greater height loss with each glide.

Introduction

The flying lizards of the genus Draco (family Agamidae) are widespread in Southeast Asia and southwest India. The genus is composed of approximately 45 species, with 39 currently recognized and several new species awaiting description. Flying lizards are famous for their gliding locomotor strategy, which they use to move between trees in their habitat of tall, dipterocarp-dominated, forests. All Draco lizards are strictly arboreal, and all share anatomical specializations that enhance aerodynamic lift during gliding, including a patagium supported by elongated thoracic ribs and expandable throat lappets supported by the hyoid apparatus. Together, the patagium and throat lappets serve as the primary airfoils and substantially reduce wing loadings relative to those of less specialized gliding or nongliding lizards. Here we review the evolutionary background of aerial performance in lizards generally, discuss morphological features and ecological contexts specific to gliding in Draco, evaluate the allometry of gliding performance in this taxon, and conclude with a functional interpretation of the morphologies of extinct reptilian gliders that show strong morphological parallels to flying lizards.

The origin of gliding in Draco and other lizards

The evolutionary origins of gliding in several lizard assemblages, including Draco (Agamidae), Ptychozoon (Gekkonidae), Hemidactylus (Gekkonidae), and Holaspis (Lacertidae), has received scant attention in the literature (but see Russell 1979; Arnold 2002; McGuire and Dudley 2005). We have recently proposed that aerial behaviors, including gliding, are natural extensions of arboreality and of the consequent selection for avoiding injury during falls (Dudley et al. 2007). The evolution of gliding can
be cast as a multistep process initiated with an aerial righting reflex, and then followed by behavioral adaptations such that the falling lizard assumes a characteristic splayed posture with the body and tail oriented in the horizontal plane while falling. This allows the lizard to maximize drag and thus to parachute to the ground at a reduced velocity relative to that of a tumbling lizard (Oliver 1951). Once a lineage has acquired these behavioral adaptations, any increase in relative surface area will improve parachuting. Gliding and associated lateral displacement of the body via lift forces, in turn, facilitate targeting of landing sites off the ground, where predatory pressure may otherwise be formidable.

Although only a few species of arboreal lizards have been observed to utilize the characteristic parachuting posture, including the gekkonid *Gekko cristatella* (Reid 1958; J. A. McGuire, personal observation), *Calotes versicolor* (Zug et al. 2009), and *C. ceylonensis* (Karunarathna et al. 2009), and the polychrotids *Anolis carolinensis* (Oliver 1951) and *A. pentaprion* (A. Herrel, R. Boistel, R. Lebrun, G. Daghfous, P. Tafforeau, J. B. Losos, B. Vanhooydonck, submitted for publication), we hypothesize that this is in fact a general feature of arboreal lizards. Interestingly, even lizards that lack obvious morphological adaptations for gliding, such as patagial structures and webbed appendages, may be capable of substantial horizontal displacements during descent, as has been observed in *Holaspis guentheri* (Schiøtz and Volsøe 1959; 13.5 m horizontal translation with 9 m loss of height), *A. carolinensis* (up to 4.6 m of horizontal translation when dropped from a height of 11.3 m; Oliver 1951), *B. cristatella* (Reid 1958; J. A. McGuire, personal observation), and *C. versicolor* (estimated 45° glide trajectory, Zug et al. 2009). These lizards are capitalizing on the well-known relationship between lift and the square of translational velocity (Norberg 1985); once gravitational acceleration acts on the body to yield a sufficiently high speed, both body drag and lateral lift forces can be substantial and ultimately yield a shallow glide angle given sufficient surface area. Taken to the extreme, even human beings are capable of generating substantial horizontal lift if falling fast enough and assuming an appropriate orientation of the body, as exemplified by BASE jumpers, both with or without wingsuits (Brasfield 2008) and ski jumpers (Schwameder 2008). In the specific case of flying lizards, we envision a rapid evolutionary transition from unspecialized parachutist to specialized glider in their common ancestor.

This conclusion is based on the absence of intermediate forms among the extant *Draco* assemblage—all the approximately 45 *Draco* species have the full suite of gliding specializations that typify this clade (see below).

**Morphology of the *Draco* gliding apparatus**

Lizards of the genus *Draco* have a number of morphological adaptations, including the familiar patagium or gliding membrane, that are either unique or unusual among extant lizards. The *Draco* patagium is unique among living animals in that it is an actively controlled structure supported by elongated thoracic ribs and a specialized musculature (Colbert 1967; John 1970a; Russell and Dijkstra 2001). The musculature that controls the patagium is composed of highly modified external and internal intercostal muscles, external oblique muscles, and a system of ligaments spanning the individual elongated thoracic ribs. The recruitment of intercostal muscles for patagial control resulted in a profound reorganization of the respiratory apparatus (John 1970b, 1971). Whereas all other lizards ventilate their lungs primarily through expansion and contraction of the rib cage via the intercostal muscles (Carrier 1986, 1987), the provisioning of power for ventilation by *Draco* has been shifted to the pectoralis muscles. John (1970b, 1971) studied the histochemistry of the pectoralis muscles of *Draco dussumieri*, and argued that the muscle fibers of this (and presumably all other) *Draco* species are highly specialized for the greater level of activity required by this functional shift. The patagial morphology is generally conserved across all species of *Draco* and, indeed, McGuire and Dudley (2005) argued that the patagium was subject to a constraint in morphological design deriving from its posterior attachment at the base of the hind limbs, thereby limiting the maximum possible length of the supporting ribs. However, although the general shape of the patagium is relatively invariant across species, there is variation in the number of ribs supporting the structure, with some species displaying a strong statistical mode of five ribs supporting the patagium and others with a strong statistical mode of six (Inger 1983; Musters 1983). Indeed, it appears that there have been multiple transitions between these alternative states (McGuire and Kiew 2001).

Among lizards, patagial structures are not unique to *Draco*. For example, a patagium is also present in at least two other extant lizard assemblages, the flying geckos of the genus *Ptychozoon* (Russell 1979), and
the geckos Hemidactylus craspedotus and H. platyurus (Honda et al. 1997). However, the patagium in Ptychozoon and Hemidactylus is relatively small and is unsupported by an underlying skeleton or by sophisticated musculature, and thus must open passively as it catches air during controlled aerial descent (Marcellini and Keefer 1976; Honda et al. 1997; Russell et al. 2001; Young et al. 2002). Although unique to modern reptiles, structures similar to the patagium of Draco evolved repeatedly and convergently in other extinct gliding reptiles, including Kuehneosaurus, Icarosaurus, and Coelurosauravus. (Robinson 1962; Colbert 1970; Carroll 1978; Evans 1982; Frey et al. 1997; see below).

In addition to the patagium, lizards of the genus Draco are characterized by additional and less familiar features associated with their gliding. For example, all flying lizards possess elongated and mobile ceratohyal cartilages in their hyoid apparatus that support laterally extensible throat lappets; these structures function as a smaller and secondary anterior airfoil. The lappets have been hypothesized to function in much the same manner as a canard wing on some fixed-wing aircraft, generating additional lift and enhancing balance and stability (Thomas and Taylor 2001). All species of Draco also have modified hind limbs that, in cross-section, form a general streamlined and contoured airfoil, suggesting that they are also involved in the generation of lift (McGuire 2003). The posterior margins of the hind limbs and the base of the tail are also bordered by elongated fringing scales that serve to further increase the effective aerodynamic surface area.

The ecological context of gliding in flying lizards

Although there was some early controversy regarding whether Draco glided at all [e.g., Pope in Schmidt (1927) and Gray (1953) argued that Draco lizards probably utilized the patagia strictly for display], it is now clear that gliding is a fundamental feature of Draco biology. Gliding is not simply an effective escape mechanism, but is also the primary means of moving within their three-dimensional arboreal environment (Hairston 1957; Herre 1958). Flying lizards are highly territorial and their home ranges generally encompass one to several trees (Alcala 1967; Mori and Hikida 1993, 1994). These trees are actively patrolled by males, with females moving freely among territories (Alcala 1967). Furthermore, it is apparent that males lacking territories move about the landscape in search of unoccupied territories; Mori and Hikida (1993) found that suitable territories were claimed soon (i.e., within a few hours) after a dominant male was removed. These horizontal movements through the landscape are almost entirely accomplished via gliding, as males only rarely come to the ground on their own volition. Indeed, based on hundreds of hours of observation made during the past 16 years of fieldwork, JAM has never found a male Draco on the ground. Females, on the other hand, must come to the ground to deposit eggs. Alcala (1967) found that female D. spilopterus at his field site in the Philippines experienced higher annual mortality than did males, an outcome that is unusual among territorial lizards (Stamps 1983). Alcala (1967) hypothesized that this elevated rate of mortality in females was a consequence of female-specific terrestrial activity.

The role of the patagium in Draco mating

Although there is no doubt that the patagium of Draco serves as an airfoil, it also plays an important role as a display structure. During courtship, as well as in territorial disputes between rival males, the patagium is opened and its dorsal surface oriented toward the observer, usually in conjunction with extension of the dewlap and throat lappets (Hairston 1957; John 1967; Mori and Hikida 1994; J. A. McGuire, personal observation). In all but a few lineages of Draco, patagial coloration is species-specific, with most species also exhibiting sexual dichromatism (Musters 1983; McGuire and Alcala 2000; McGuire et al. 2007). Whereas most species exhibit “male-biased” dichromatism (males with more vividly-colored patagia), there are a few species in which males and females have similar or identical patagial coloration (i.e., D. maximus, D. cristatellus, and D. fimbriatus) and two species (D. ornatus and D. quinquefasciatus) in which females have more colorful patagia than do males. The switch from male-biased to female-biased dichromatism in these two species has not been investigated, although one intriguing possible explanation is a reversal in mating system, with females being the more territorial sex. The ventral surface of the patagium also is pigmented, often with a yellow, orange, or bluish wash, and in several species the ventral surface is covered with black blotching or even completely suffused with black pigments (i.e., in some insular populations of D. boschmai and D. timoriensis). As is the case for the dorsal patagium, the ventral patagial coloration often is sexually dichromatic. However, since the ventral surface of the patagium is not typically
presented during display, Mori and Hikida (1994) hypothesized that the coloration might serve as an indicator of gender during flight.

**Scaling relationships and gliding performance in flying lizards**

Flying lizards exhibit a roughly 10-fold interspecific variation in adult’s body mass, and the associated scaling relationships between body size and aerodynamic surface area may have important consequences for the evolution of gliding performance in this group. McGuire (2003) used reduced major-axis regression analysis of phylogenetically corrected area, mass, and wing span data for 29 species of *Draco* to assess how wing loading (the ratio of body weight to wing area) and wing aspect ratio vary with overall body size. Surprisingly, flying lizards exhibit isometry (i.e., geometrical similarity) in their wing area—body mass relationships (as opposed to functional similarity). Wing loadings of larger species are consequently substantially higher than those of smaller species, suggesting higher equilibrium glide speeds. Wing aspect ratio, on the other hand, is not correlated with either body mass or wing loading, indicating that larger species do not compensate for their higher wing loadings by having wings with higher aspect ratios. These findings strongly imply that larger species should be relatively poor gliders relative to smaller species because individuals with higher wing loadings will require greater glide velocities, and thus longer ballistic falls under gravity, in order to generate wing lift sufficient to offset their greater body mass.

McGuire and Dudley (2005) tested the hypothesis that larger species should be relatively poor fliers by quantifying gliding performance for 11 species of *Draco* spanning nearly the entire size range exhibited by the genus. Gliding performance was measured at three outdoor gliding “arenas” in Peninsular and Bornean Malaysia, whereby individual lizards were captured in the field and transported to a nearby gliding arena, which consisted of an open field within which a takeoff pole (6 m in height) and a landing pole (4–5 m in height) were erected 9.3 m apart. A video camera with known filming speed was placed orthogonal to the expected glide trajectories between the two poles. Individual lizards were placed on the takeoff pole, prompted to run to the top of the pole, allowed to acclimate for a few minutes, and then were coerced to jump from the takeoff pole and glide to the landing pole. A total of 249 such glides was obtained. By digitizing and plotting glide profiles from the raw video footage, multiple performance variables were measured including total height lost, glide angle, and glide velocity over the course of a standardized glide distance for each event. These data also allowed McGuire and Dudley (2005) to evaluate the occurrence of equilibrium glides versus non-steady-state behavior. The primary finding was a significant positive correlation between height lost over a standardized glide distance and the wing loading. This finding matched the predictions derived from a study of allometric scaling (McGuire 2003), and confirmed that larger species have not evolved compensatory biomechanical or morphological mechanisms that might have allowed them to overcome their substantially greater wing loadings. Gliding performance thus derives from a relatively straightforward interaction between the total area of the flight membranes, body mass, and the force of gravity. Relative to the more complicated mode of flapping flight, with variable physiological inputs, gliding performance is accordingly much more predictable on the basis of morphological features alone.

**Predicted performance of fossil gliders**

The observation that dimensions and shape of the lift-generating structures in *Draco*, together with body mass, largely determine performance capabilities can be generalized to other glissant lineages, allowing locomotor capabilities to be predicted using morphological considerations alone. Several fossil lineages share similar morphological features for gliding with modern flying lizards, including patagial membranes supported either by elongated ribs or, in the case of *Coelurosaursus* (Frey et al. 1997) by rib-like ossified dermal structures. These fossil species include the large-bodied Upper Permian fossil reptile *C. elizensis*, and the two Triassic lepidosaur-morph reptiles *Kuehneosaurus* sp. and *Icarosaurus siefkeri* (Colbert 1970; Carroll 1978; Evans 1982). Some of these fossil gliders were substantially heavier than *Draco* and have been inferred to have had much greater wing loadings, leading us to investigate the relative gliding performance of these individuals that represent early evolutionary experiments in vertebrate flight. Because the aerodynamic structures of these taxa were similar to those of *Draco*, we used associated regression analysis to predict the gliding performance of these extinct taxa. However, the fossil lineages differed from *Draco* in having higher aspect ratio wings (i.e., their wings were proportionally longer relative to the mean wing chord). We therefore employed wind tunnel experiments to determine the relative compensatory value that wings with high
aspect ratio might have provided for the fossil gliders, and to evaluate whether prediction of gliding performance using wing loading alone is justified for these fossil lineages.

_Icarosaurus siefkeri_ was a small lizard-like kuehneosaurid reptile that occurred in the late Triassic of what is now northern New Jersey (Colbert 1970; Carroll 1978). It was morphologically similar to _Draco_ in that it had patagia supported by elongated ribs. The snout-vent-length (SVL) of _I. siefkeri_ has been estimated to be 95 mm (Colbert 1970), comparable to moderate-sized species of _Draco_ (SVL of adult _Draco_ ranges between 60 and 150 mm; McGuire 2003). Because the ribs of _I. siefkeri_ were much longer than those of _Draco_, its wings were correspondingly larger, and its patagial area has been estimated as 173.9 cm² (Colbert 1970). However, the estimate of body mass for _I. siefkeri_ of 40 g (based on regression of SVL on body mass for a diversity of lizard species; Pough 1973) was substantially greater than would be expected for _Draco_ of comparable size, resulting in an estimated wing loading of 22.6 N/m², which is comparable with that of the largest species of _Draco_ (see McGuire and Dudley 2005).

_Kuehneosaurus_ sp. from the Upper Keuper (Triassic) of Great Britain was a much larger relative of _I. siefkeri_ (Robinson 1962). This reptile exceeded the size of even the largest species of _Draco_, with a SVL of ~240 mm. Wing loading for this species was estimated to lie between 156.9 and 215.7 N/m² (Evans 1982), values which are 6.5-fold to 9-fold greater than that of the largest species of _Draco_. _Coelurosaurus elivensis_ was a similarly large (compared with _Draco_) reptile from the Upper Permian of Madagascar (Carroll 1978). The patagial structures of _Coelurosaurus_ may have been supported by rib-like ossified dermal structures rather than by true ribs (Frey et al. 1997), and these support structures differed from those of _Draco_, _Icarosaurus_, and _Kuehneosaurus_ in that they appear to have originated from a single point in the axillary region. However, the aerodynamic function of the patagium was inferred by Frey et al. (1997) to have been similar to that of _Draco_ and the kuehneosaurids. The estimated wing loading of _C. elivensis_ is 107.9 N/m² (Evans 1982), a value roughly 4.5 times greater than that of the largest species of _Draco_.

We expect that all three of these fossil taxa weighed less per unit SVL than do typical lizards because of aerodynamic constraints imposed by gliding, as is the case for _Draco_. Thus, estimates of body mass based on the regression by Pough et al. (1973) for a diversity of lizards likely resulted in inflated values. To correct for this effect, we employed ordinary least-squares (OLS) regression of SVL on body mass for 28 species of _Draco_, and used the resultant regression equation to re-estimate the body mass of the fossil gliders. Separate analyses were conducted using data for males (n = 517) and females (n = 360), because the sexes differ substantially in body mass per unit aerodynamic surface area in _Draco_ (McGuire 2003). Whereas the published estimate of body mass for _I. siefkeri_ based on the “general lizard” performance-limited species of _Draco_ species (_D. melanopogon_) with the lowest observed wing loadings (7.3–12.8 N/m²), as cited in McGuire and Dudley (2005).

With the published and recalculated estimates of wing loadings for the fossil reptiles, we used the reduced major axis (RMA) regression equation derived from the empirical study of gliding performance of flying lizards (McGuire and Dudley 2005) to estimate aerodynamics of the fossil taxa. This exercise entailed plotting-inferred wing loadings for the fossil taxa onto the regression line generated from data on the empirical gliding performance data of extant flying lizards (Fig. 1). The smaller _I. siefkeri_ is then clearly estimated to be a much better glider than either its larger relative _Kuehneosaurus_ sp. or _C. elivensis_. This holds true regardless of whether the body mass of _I. siefkeri_ is assumed to be the previously published estimate (40 g) or the recalculated estimates based on the body proportions of _Draco_. If we predict the performance of _I. siefkeri_ in the context of the published wing loading (22.6 N/m²), it would lose 5.0 m in height during a 9.3-m horizontal glide (Fig. 1). This estimate is comparable to that of the most performance-limited species of _Draco_ (_D. fimbriatus_), which is a canopy-specialist (McGuire and Dudley 2005). However, _I. siefkeri_ had a skeleton of light construction similar to that of _Draco_ (Colbert 1970), and the mass of this species was probably similar to that of _Draco_ species with comparable SVL. Given the wing loading estimates for _I. siefkeri_ (4.3 and 6.3 N/m²) based on _Draco_’s proportions, we then infer a loss of only 2.3–2.8 m in height over the course of a standard 9.3-m horizontal glide. This estimate does not include the potential benefits of its two-fold greater wing aspect ratio than that of typical _Draco_, and suggests that loss of height...
would have been minimal over the horizontal range in question. If we assume the minimum wing loading estimate for Kuehneosaurus sp. of 156.9 N/m², we then infer a loss of 12.1 m in height when traversing a horizontal distance of 9.3 m. Coelurosauravus elivensis, with a wing loading of 107.9 N/m², is predicted to have lost 10.2 m over the course of a 9.3-m glide. In other words, considering wing loadings alone, Kuehneosaurus and Coelurosauravus may only have been capable of a steep descent (i.e., a steep glide angle >45°) when traversing horizontal distances of ~10 m.

This result then begs the aerodynamic question—how much benefit would these fossil reptiles have obtained from their higher aspect ratio wings? Variation in aspect ratio as well as wing loading may influence gliding performance, with relatively longer wings expected to increase the lift:drag ratio and consequently improve glide performance during the equilibrium phase of a glide (Norberg 1990). Evangelista et al. (unpublished data) performed wind tunnel experiments with a full-scale model of D. maximus. In their experiments, the model was manipulated such that it had no wing, a normal-sized wing, or a double-sized wing (i.e., twice the length and corresponding wing aspect ratio). These analyses indicated that D. maximus with normal and double-sized wings in fact have very similar (slightly higher) lift:drag ratios across a variety of Reynolds numbers and angles of attack. Thus, for gliders in the size range of Draco and their fossil analogs, we hypothesize that wing loading will have substantially greater influence on relative performance than would aspect ratio, especially given that we are concerned with the total height lost over a standard glide. Total loss of height includes the combination of height lost during the ballistic component of the glide, which is dependent primarily on wing loading, as well as the (more limited) height lost during the equilibrium phase of the glide, which is influenced primarily by the lift:drag ratio. As a result, we conclude that our use of associated regression to estimate the performance of the fossil gliders based on our empirically derived relationship between wing loading and height lost by Draco is justified, at least over the horizontal range.
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distances under consideration. We note that the performance variable considered here, total height lost over a standard horizontal glide distance, also is ecologically more relevant than is height lost during the relatively flat equilibrium phase of a glide (McGuire and Dudley 2005).

Our analysis suggests that the small-bodied fossil reptilian reptile I. seifkeri was the best nonflapping (i.e., nonavian, nonchiropteran, and nonpterosaur) terrestrial vertebrate glider yet discovered. In contrast, the large-bodied Kuehneosaurus and C. elivensis must have been relatively poor gliders relative to Icarosaurus and modern Draco lizards. Even moderately sized gliders pay a substantial penalty relative to smaller species given their increased wing loadings. The large-bodied Kuehneosaurus and Coelurosaurusaurus would have performed shallow-trajectory glides at high velocities, consequently requiring an extended ballistic dive and a loss of substantial height with each gliding event. This finding suggests that these species must have occurred in very tall forests such as those occupied today by Draco and a preponderance of other gliding lineages (Dudley and DeVries 1990). Our findings further suggest that powered flapping flight, if indeed derived from gliding behaviour, likely originated in smaller species that later evolved larger body size in conjunction with biomechanical innovations that overcame the physical constraints of body mass relative to wing area.

Conclusions and future directions

Although we now have a solid understanding of allometric scaling relationships in Draco, and of the impact that body size evolution has played in determining two aspects of gliding performance (i.e., height lost over a standardized glide distance and glide angle), many questions remain. For example, we do not even have rudimentary information regarding maneuverability, either in terms of relative rotational capacities among species or how a single individual executes changes in direction. Furthermore, we lack a detailed aerodynamic model of Draco’s gliding biomechanics based on wind-tunnel experiments and model-based simulations. Although challenging at the spatial scales over which these animals fly, we anticipate future research exploring each of these aspects of the gliding biology of Draco.

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