

SYMPOSIUM

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

Jimmy A. McGuire¹ and Robert Dudley

Department of Integrative Biology and Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA

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¹E-mail: mcguirej@berkeley.edu

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, then 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 gecko* (Russell 1979), the agamids *Bronchocela cristatella* (Reid 1958; J. A. McGuire, personal observation), *Calotes versicolor* (Zug et al. 2009), and *C. ceylonensis* (Karunaratna et al. 2009), and the polychrotids *Anolis carolinensis* (Oliver 1951) and *A. pentaptrion* (A. Herrel, R. Boistel, R. Lebrun, G. Daghighfous, 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* (Schjötz 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 *Coelurosauravus* (Frey et al. 1997) by rib-like ossified dermal structures. These fossil species include the large-bodied Upper Permian fossil reptile *C. elivensis*, and the two Triassic lepidosauromorph 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*. *Coelurosauravus elivensis* was a similarly large (compared with *Draco*) reptile from the Upper Permian of Madagascar (Carroll 1978). The patagial structures of *Coelurosauravus* 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” plot was 40 g, the estimates based on regressions for *Draco* are 7.7 and 11.2 g based on males and females, respectively. The discrepancies between the published estimates of wing loading for *Kuehneosaurus* sp. and *C. elivensis* were similarly large. Revised wing loadings based on recalculated estimates of body mass for *Icarosaurus* are then 4.3 N/m² and 6.3 N/m², values that are substantially lower than those for the *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

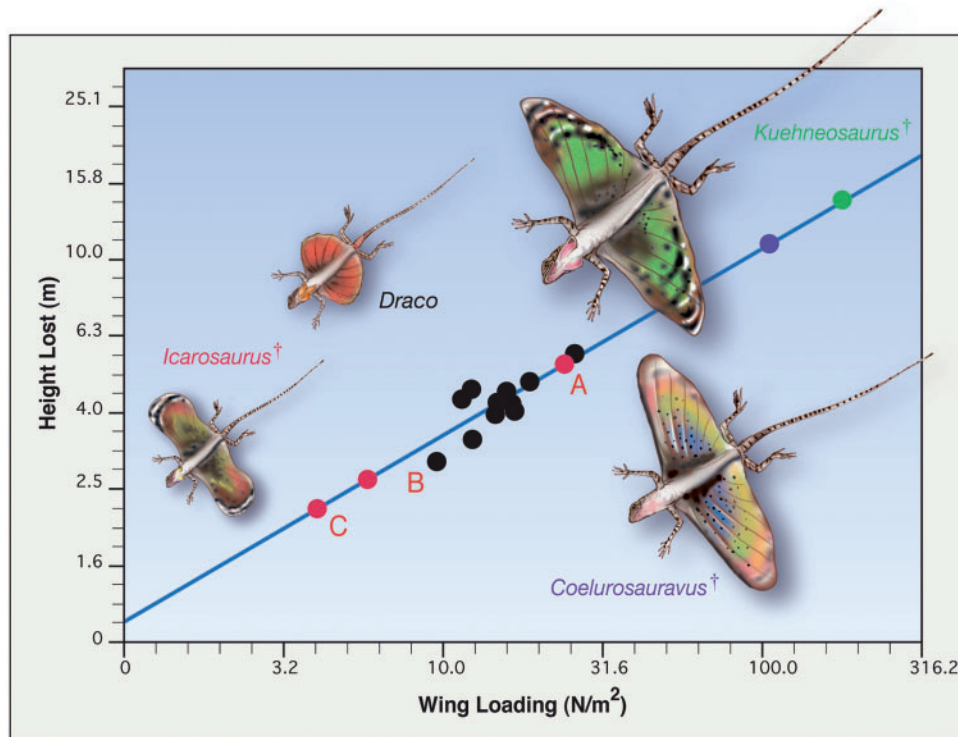


Fig. 1 The relationship between wing loading and height lost over the course of a standard glide length of 9.3 m (from McGuire and Dudley 2005). Black dots represent the original empirical observations of *Draco* on which the regression analysis was based. Green and purple dots represent the inferred points along the *Draco*-specific regression for *Kuehneosaurus* sp. and *C. elivensis*, respectively, based on published estimates of wing loading. Red dots represent three alternative positions along the regression for *I. seifkeri* depending on whether wing loading is based on estimates of body mass obtained from (A) a published regression of SVL on body mass across a diversity of lizard species, (B) a regression of SVL on body mass for female *Draco*, or (C) a regression for male *Draco*. The true colorations of the fossil taxa are unknown.

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/m^2 , 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/m^2 , 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 $>45^\circ$) 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

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 *Coelurosauravus* 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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References

- Alcala AC. 1967. Population biology of the "flying" lizard, *Draco volans*, on Negros Island, Philippines. *Natural Appl Science Bull* 20:335–72.
- Arnold EN. 2002. *Holaspis*, a lizard that glided by accident: mosaics of cooption and adaptation in a tropical forest lacertid (Reptilia, Lacertidae). *Bull Nat Hist Mus Lond (Zool)* 68:155–63.
- Brasfield S. 2008. Innovations in air insertion (involving parachutes). [master's thesis]. [Monterey (CA)]: Naval Postgraduate School.
- Carrier DR. 1986. Lung ventilation during walking and running in four species of lizards. *Exp Biol* 47:33–42.
- Carrier DR. 1987. The evolution of locomotor stamina in tetrapods: circumventing a mechanical constraint. *Paleobiology* 13:326–41.
- Carroll RL. 1978. Permo-Triassic "lizards" from the Karoo System, part II, a gliding reptile from the upper Permian of Madagascar. *Palaeont Afr* 21:143–59.
- Colbert EH. 1967. Adaptations for gliding in the lizard *Draco*. *Am Mus Novitat* 2283:1–20.
- Colbert EH. 1970. The Triassic gliding reptile *Icarosaurus*. *Bull Amer Mus Nat Hist* 143:85–142.
- Dudley R, Byrnes G, Yanoviak SP, Borrell BJ, Brown R, McGuire JA. 2007. Gliding and the functional origins of flight: biomechanical novelty or necessity? *Ann Rev Ecol Evol Syst* 38:179–201.
- Dudley R, DeVries PJ. 1990. Tropical rain forest structure and the geographical distribution of gliding vertebrates. *Biotropica* 22:432–4.
- Evans SE. 1982. The gliding reptiles of the upper Permian. *Zool J Lin Soc* 76:97–123.
- Frey E, Sues H-D, Munk W. 1997. Gliding mechanism in the Late Permian reptile *Coelurosauravus*. *Science* 275:1450–2.
- Gray J. 1953. *How Animals Move*. Cambridge: University Press.
- Hairston NG. 1957. Observations on the behavior of *Draco volans* in the Philippines. *Copeia* 1957:262–5.
- Herre AW. 1958. On the gliding of flying lizards, genus *Draco*. *Copeia* 1958:338–9.
- Honda M, Hikida T, Araya K, Ota H, Nabjtabhata J, Hoi-Sen Y. 1997. *Cosymbotus craspedotus* (Frilly Gecko) and *C. platyurus* (Flat-tailed Gecko). Gliding behavior. *Herp Rev* 28:42–3.
- Inger RF. 1983. Morphological and ecological variation in the flying lizards (genus *Draco*). *Fieldiana Zool* 18:1–35.

- John KO. 1967. Observations on the mating behaviour and copulation in *Draco dussumieri* Dum. & Bib. (Reptilia: Sauria). J Bombay Nat Hist Soc 64:112–5.
- John KO. 1970a. On the 'patagial musculature' of the South Indian flying lizard *Draco dussumieri*, Dum & Bib. British J Herpetol 4:161–8.
- John KO. 1970b. Studies on the histophysiology of the muscles of the South Indian flying lizard, *Draco dussumieri* (Dum. & Bib.). J Anim Morphol Physiol 17:44–55.
- John KO. 1971. A histochemical study of the pectoralis muscle of the South Indian flying lizard. Experientia 27:517–9.
- Karunaratna S, Amarasinghe S, Stöckli E. 2009. Taxonomic and biological study on *Calotes ceylonensis* Müller, 1887 (Reptilia: Agamidae) of Sri Lanka. Bonn Zool Beiträge 56:229–38.
- Marcellini DL, Keefer TE. 1976. Analysis of the gliding behavior of *Ptychozoon lionatum* (Reptilia: Gekkonidae). Herpetologica 32:362–6.
- McGuire JA. 2003. Allometric prediction of locomotor performance: an example from Southeast Asian flying lizards. Am Nat 161:337–49.
- McGuire JA, Alcalá A. 2000. A taxonomic revision of the flying lizards (Iguania: Agamidae: *Draco*) of the Philippine Islands, with a description of a new species. Herpetol Monogr 14:81–138.
- McGuire JA, Brown RM, Mumpuni Riyanto A, Andayani N. 2007. The flying lizards of the *Draco lineatus* group (Squamata: Iguania: Agamidae): a taxonomic revision with descriptions of two new species. Herpetol Monogr 21:179–212.
- McGuire JA, Dudley R. 2005. The cost of living large: comparative gliding performance in flying lizards (Agamidae: *Draco*). Am Nat 166:93–106.
- McGuire JA, Kiew BH. 2001. Phylogenetic systematics of Southeast Asian flying lizards (Iguania: Agamidae: *Draco*) as inferred from mitochondrial DNA sequence data. Biol J Linn Soc 73:203–29.
- Mori A, Hikida T. 1993. Natural history observations of the flying lizard, *Draco volans sumatranus* (Agamidae, Squamata) from Sarawak, Malaysia. Raffles Bull Zool 41:83–94.
- Mori A, Hikida T. 1994. Field observations on the social behavior of the flying lizard, *Draco volans sumatranus*, in Borneo. Copeia 1994:124–30.
- Musters CJM. 1983. Taxonomy of the genus *Draco* L. (Agamidae, Lacertilia, Reptilia). Zool Verhand 199:1–120.
- Norberg U. 1985. Evolution of vertebrate flight: an aerodynamic model for the transition from gliding to active flight. Am Nat 126:303–27.
- Norberg U. 1990. Vertebrate Flight: Mechanics, Physiology, Morphology, Ecology and Evolution. Berlin: Springer-Verlag.
- Oliver JA. 1951. "Gliding" in amphibians and reptiles, with a remark on an arboreal adaptation in the lizard, *Anolis carolinensis carolinensis* Voigt. Am Nat 85:171–6.
- Pough FH. 1973. Lizard energetics and diet. Ecology 54:837–44.
- Reid JA. 1958. Gliding by the green crested lizard. Malayan Nat J 12:119.
- Russell AP, Dijkstra LD. 2001. Patagial morphology of *Draco volans* (Reptilia: Agamidae) and the origin of glissant locomotion in flying dragons. J Zool 253:457–71.
- Robinson PL. 1962. Gliding lizards of the upper Keuper of Great Britain. Proc Geol Soc Lond 160:137–46.
- Russell AP. 1979. The origin of parachuting locomotion in gekkonid lizards (Reptilia: Gekkonidae). Zool J Linn Soc 65:233–49.
- Russell AP, Dijkstra LD, Powell GL. 2001. Structural characteristics of the patagium of *Ptychozoon kuhli* (Reptilia: Gekkonidae) in relation to parachuting locomotion. J Morph 247:252–63.
- Schiøtz A, Volsøe H. 1959. The gliding flight of *Holaspis guentheri* Gray, a west-African lacertid. Copeia 1959:259–60.
- Schmidt KP. 1927. The reptiles of Hainan. Bull Amer Mus Nat Hist 54:395–465.
- Schwameder H. 2008. Biomechanics research in ski jumping, 1991–2006. Sports Biomech 7:114–36.
- Stamps JA. 1983. Sexual selection, sexual dimorphism, and territoriality. In: Huey RB, Pianka ER, Schoener TW, editors. Lizard Ecology: Studies of a Model Organism. Cambridge: Harvard University Press. p. 169–204.
- Thomas ALR, Taylor GK. 2001. Animal flight dynamics I. Stability in gliding flight. J Theor Biol 212:399–424.
- Young BA, Lee CE, Daley KM. 2002. On a flap and a foot: aerial locomotion in the 'flying' gecko, *Ptychozoon kuhli*. J Herpetol 36:412–8.
- Zug GR, Vindum JV, Jacobs JF, Lwin KS, Win YM. 2009. *Calotes "versicolor"* (Burmese Garden Lizard). Gliding. Herpetol Rev 40:340–1.