

The Cost of Living Large: Comparative Gliding Performance in Flying Lizards (Agamidae: *Draco*)

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ABSTRACT: Despite exhibiting considerable interspecific variation in body mass, flying lizards of the genus *Draco* are isometric in their area-mass scaling relationships and exhibit no significant compensatory variation in wing aspect ratio. Thus, larger species are expected to be relatively poor gliders, in lieu of behavioral or physiological compensation, when compared with smaller congeners. Here we tested this hypothesis by conducting gliding performance trials for 11 *Draco* species spanning virtually the entire size range of the genus. We considered three primary performance variables: maximum velocity adjusted for wind conditions, height lost over a standard horizontal glide distance, and glide angle. Comparative analysis confirmed that larger species are relatively poor gliders and do not compensate substantially for their higher wing loadings via either behavioral or physiological mechanisms. Flying lizards were found to exhibit substantial context-dependent variation in glide performance, with smaller species often exhibiting extensive variation in height lost and glide angle between trials. Variation also was observed in empirically derived velocity profiles, with only a subset of individuals appearing to perform equilibrium glides. Such size-dependent variation in performance has important consequences for the ecology and evolution of flying lizards and other glissant taxa.

Keywords: allometry, biomechanics, independent contrasts, locomotion.

Because locomotion plays a key role in the lives of most animals, biologists have long been interested not only in

identifying the factors that influence maximal performance but also in understanding the role that evolution has played in shaping comparative performance capabilities. Much of the vast comparative locomotor performance literature has dealt with sprinting performance (e.g., Garland 1983, 1984, 1985; Huey and Bennett 1987; Losos 1990*a*, 1990*b*; Miles 1994; Bauwens et al. 1995; Bonine and Garland 1999; Irschick and Jayne 1999), although swimming (e.g., Gibson and Johnston 1995; Drucker and Jensen 1996), jumping (e.g., Emerson 1978, 1991; Losos et al. 1989; Katz and Gosline 1993; Bennett 2000; Wilson et al. 2000), and flight (e.g., Winter and von Helversen 1998; Altshuler and Dudley 2003; Altshuler et al. 2004) have also been investigated extensively. Each of these locomotor modes involves a complex interplay between morphological, physiological, and behavioral components, and it is therefore particularly challenging to identify the specific factors influencing maximal performance and the relative importance of each.

Compared to these other locomotor modes, gliding has been largely unstudied (but see Emerson and Koehl 1990; Emerson et al. 1990; McCay 2001). Gliding is a relatively simple mode of transport, as it is not expected to involve or require extensive physiological input—the power used to generate aerodynamic forces is derived exclusively from potential energy of the animal's body mass (i.e., gravity). This led McGuire (2003) to suggest that comparative studies of gliding performance offer the opportunity to evaluate the evolution of locomotor capabilities in a simplified framework requiring consideration of fewer variables than is otherwise necessary. This study attempts to understand the interaction between body size and locomotor performance evolution in an animal glider.

The flying lizards (*Draco*, Agamidae) of Southeast Asia are famous for their use of gliding as a locomotor behavior (fig. 1). Although less widely appreciated, it is no less remarkable that as many as seven species of *Draco* can occur sympatrically in various parts of the Sunda Shelf (i.e., peninsular Malaysia, Borneo, and Sumatra; Inger 1983; Musters 1983). In these zones of sympatry, adult body mass may vary by more than a factor of 10 (McGuire

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Figure 1: *Draco melanopogon* just after takeoff (*top*) and in midglide (*bottom*)

and Kiew 2001; McGuire 2003), and species that utilize the same microhabitats often differ most dramatically in size (J. A. McGuire, personal observation). It is accordingly natural to ask whether there is a relationship between multiple-species sympatry, body size variation among such species, and their use of gliding as a locomotor mode. We propose that simultaneous consideration of these three aspects of flying lizard biology will yield insights into *Draco*

evolution and ecology and can inform us about locomotor performance evolution in other glissant taxa. Here we present and analyze gliding performance data for 11 *Draco* species spanning essentially the entire size range of the genus. We then compare these data with earlier predictions of gliding performance based on allometric relationships of flight-related morphology and consider the implications of these data for flying lizard ecology and evolution. We

conclude by discussing implications of our empirical findings for gliding performance evolution in other glissant taxa.

Draco lizards exhibit substantial interspecific body size variation, with adult body mass ranging between 3 and 35 g. Although much of this variation is concentrated within one of the three primary *Draco* clades, large body size (i.e., snout-vent length > 125 mm) appears to have evolved independently at least four times in this genus (Inger 1983; McGuire and Kiew 2001; McGuire 2003). Each of these evolutionary transitions has occurred in lineages found in sympatry with other *Draco* species. Furthermore, of the approximately 60 insular and mainland populations composed of single species, not one is large-bodied (McGuire 2003). Evolution of large body size may therefore be selectively advantageous only when other *Draco* species occur in sympatry. In such cases, gliding performance may be adversely influenced if aerodynamic surface areas change isometrically with increases in body mass. Glide angles during equilibrium gliding vary in inverse proportion to the wing aspect ratio (i.e., the ratio of wing span to wing chord), whereas glide velocity increases in proportion to the wing loading (i.e., the ratio of body weight to wing area; see Norberg 1990). Larger gliders with relatively less wing area relative to body weight must ballistically descend greater distances and attain higher air velocities to reach equilibrium gliding at the corresponding minimum glide angle (McGuire 2003). On the other hand, if *Draco* lizards do change shape with body size in such a way that the interspecific relationship between area and mass remains constant (e.g., if larger species have proportionally larger patagial membranes) or if aspect ratio exhibits positive allometry, then the evolution of large body size might have little or no effect on gliding performance. Such an outcome is sometimes referred to as functional equivalence or functional similarity in the scaling literature (e.g., Sweet 1980; LaBarbera 1989).

For 29 species of flying lizards, McGuire (2003) tested the alternative hypotheses of isometry and functional similarity of aerodynamic surface area and found that functional similarity was strongly rejected by the data, whereas isometry could not be rejected. Indeed, the observed slopes when two alternative area measurements were regressed on body mass were very close to the exact value predicted under isometry (0.67), and the expected slope under isometry fell well within the 95% confidence intervals in all cases. Given an isometric relationship between aerodynamic surface area and mass, larger species must be characterized by higher wing loadings relative to smaller species. McGuire (2003) also investigated the relationship between aspect ratio and body mass and found no compensatory increase by larger species in wing aspect ratio. These anatomical results strongly suggest size-dependent

gliding performance limitations in flying lizards, unless heretofore unidentified morphological or behavioral compensatory mechanisms are at play (see Emerson and Koehl 1990). This study accordingly investigates the comparative gliding performance of *Draco* species over a large range of body sizes in order to test our primary hypothesis that smaller *Draco* species are more capable gliders than larger *Draco* species. We predict that larger species glide more rapidly, lose more height over a standard horizontal glide distance, and exhibit steeper glide angles than do smaller species. We further hypothesize that larger species will exhibit less individual and intraspecific performance variation in gliding trials than will smaller species, because larger species are expected to be under greater pressure to perform maximal or near-maximal glides in order to cover a standard horizontal glide distance from a common take-off height.

Material and Methods

Gliding Trials

Gliding trials were conducted at three sites in Malaysia, two on the Malay Peninsula (Ulu Gombak Field Studies Centre, Selangor; Wang Kelian, Perlis) and one on the island of Borneo (Poring Hot Springs, Sabah). Flying lizards were captured alive and maintained in captivity for 2–5 days, during which period gliding trials were conducted. Lizards were not fed during this period. The gliding trials required a relatively large and open flight arena such that the study animals could not easily escape into nearby vegetation. At each of our gliding arenas (large, level fields), we erected two large poles, one as a takeoff pole and the other as a landing pole. We matched the dimensions of our arenas at each of the three sites as closely as possible. Each takeoff pole was approximately 6 m in height, and the landing pole was 4–5 m in height. The poles were placed 9.3 m apart, a spacing comparable to the typical spacing of adult trees in the forests in which we collected the lizards used in the study. A video camera (Sony Video8 Handycam) on a tripod was oriented orthogonally to the axis between the landing and takeoff poles at a fixed distance (and corresponding image magnification) to allow for the recording of complete glides between the two poles. With this camera arrangement, a known filming speed (60 fields/s), and the known distance between the takeoff and landing poles, positional data as a function of time could be obtained for the entire glide trajectory. Only adult *Draco* were included in this study, using a criterion of snout-vent length within 10% of the observed maximum for the species.

Lizards were placed individually at the base of the take-off pole and were then encouraged (when necessary) to

climb to the top either by tapping on the pole or by prodding the lizard with a long bamboo rod. Following a 1–2-min acclimation period, the lizard was then motivated by small movements of the bamboo rod to jump from the top of the takeoff pole and glide toward the landing pole, upon which it usually landed (see video 1 in the online edition of the *American Naturalist*). Immediately after each glide, horizontal wind speed at a height of 3 m was measured in the plane of the glide trajectory with a digital anemometer (TSI VelociCalc Plus); wind direction was recorded with a compass. Because high wind could adversely affect our results, we generally did not attempt gliding trials when wind velocity consistently exceeded 2 m/s. Vertical components of ambient wind were assumed to be zero but were not perceptible in filmed trials. Lizards usually jumped and glided directly from the takeoff pole to the landing pole. If the lizard performed an approximately planar (straight-line) glide to either side of the landing pole such that the trajectory deviated by 30° or less from the line segment connecting takeoff and landing poles, the linear deviation from the landing pole was measured and the glide was retained for further analysis. Although these glides were not orthogonal to the video camera, the known angular deviation from orthogonality allowed for cosine correction of raw velocity estimates. Glides in which the lizard banked curvilinearly to the left or right relative to the takeoff pole were excluded from consideration. All study lizards were killed for morphological measurements and subsequent deposition in museum collections either after they had provided five suitable glides or after 5 days had passed since initial capture. Body mass was measured using a 10-, 20-, 30-, or 50-g spring-loaded Pesola scale immediately before preservation in

10% formalin. Lizards were preserved with patagia fully expanded in order to facilitate areal measurements once the specimens were returned to the lab. Measurement protocols are described in detail by McGuire (2003).

Video Analysis and Gliding Parameters

Raw video footage was processed in the lab with a Panasonic VCR (AG–1750) linked to a desktop computer via a frame grabber. Glides were analyzed by viewing video footage field-by-field with QuickImage (a modification of NIH-Image available at <http://www.usm.maine.edu/~walker/software/QuickImage/Quickimage.b15.hqx>) to capture desired fields from which (x , y) coordinates were subsequently obtained. We typically recorded coordinates of the lizard for every fifth video field (i.e., at intervals of 1/12 of a second). When the lizard could not be detected on the fifth field, we obtained the appropriate coordinates on a nearby frame. The coordinates were recorded in a spreadsheet into which appropriate formulas were entered for calculations of horizontal, vertical, and absolute velocities as well as glide duration. Because *Draco* lizards are small relative to the camera's visual field, digitization errors contributed to nonsystematic variation in the raw positional data. We accordingly reduced this noise by applying a three-point smoothing algorithm to velocity estimates (see Lanczos 1956). Angular deviations of the camera from horizontal were incorporated on the basis of a known horizon filmed for each camera configuration. Velocity corrections for glides in which the lizard deviated at a constant angle either away from or toward the camera were incorporated at this time. A scatter plot depicting the



Video 1: Still photograph from video clip (available in the online edition of the *American Naturalist*) illustrating arrangement of takeoff and landing poles during gliding trials. Note the adult male *Draco maculatus* (wing loading = 12.5 N/m²) that has just launched itself from the takeoff pole.

two-dimensional trajectory was produced for each glide (see fig. 2 for two representative glides).

Performance parameters estimated in this study were adjusted for maximum observed velocity during a glide (and corrected for wind speed measured immediately following the glide), height lost over a standard horizontal distance of flight, and total glide angle. These parameters were chosen because of clear predictions that could be made for each, given known interspecific scaling relationships among flying lizards. We did not attempt to evaluate maneuverability, primarily because of difficulties in establishing an experimentally tractable protocol, although our field observations suggest that smaller species are more maneuverable than are larger species.

Maximum velocity during a glide and the corresponding adjusted maximum velocity differed only in that the latter included a correction for ambient wind speed. We generally arranged the takeoff and landing poles relative to the prevailing wind direction so that glides to the landing pole would be accompanied by a tailwind, as this seemed to increase the likelihood that the lizard would glide in the desired direction. Thus, many of our glides were accompanied by a slight tailwind. In such cases, the wind speed was subtracted from the lizard's calculated horizontal components of velocity to yield the adjusted maximum velocity. In cases in which a headwind was detected, the recorded wind speed was added to the lizard's unadjusted horizontal velocity component. Total height lost during gliding was determined for the standard horizontal distance of 9.3 m, equal to the linear distance between the takeoff and landing poles. In addition to size-related pre-

dictions for total height lost, we expected differences between glides to the landing pole and glides beyond the landing pole to the ground, because the former are typically characterized by a braking maneuver with a terminal upswing.

Total glide angle is simply the angle relative to horizontal between the lizard's initial takeoff point and its landing point. In the case of a glide beyond the landing pole, the projected intersection of the lizard with the landing pole was taken as the effective landing point. Because we could not see the lizard's exact position on the landing pole for many glides but could nevertheless interpolate this point from the lizard's final position in the air, we obtained the glide angle from the glide plot using a protractor rather than calculating a more precise glide angle from the actual coordinate data on the spreadsheet. As with total height lost, we expected that the total glide angle would differ between glides to the landing pole and glides that extended beyond the landing pole because of the terminal upswing that typically concluded glides directly to the pole.

Statistical Analysis

Because we hypothesized that body size evolution constrains gliding performance primarily through effects on wing loading, our statistical tests involved regression of the three performance parameters on this derived morphological variable. Before conducting regression analyses, we first corrected for phylogenetic autocorrelation, as it is now generally accepted that species values cannot be treated as independent data points for statistical analysis.

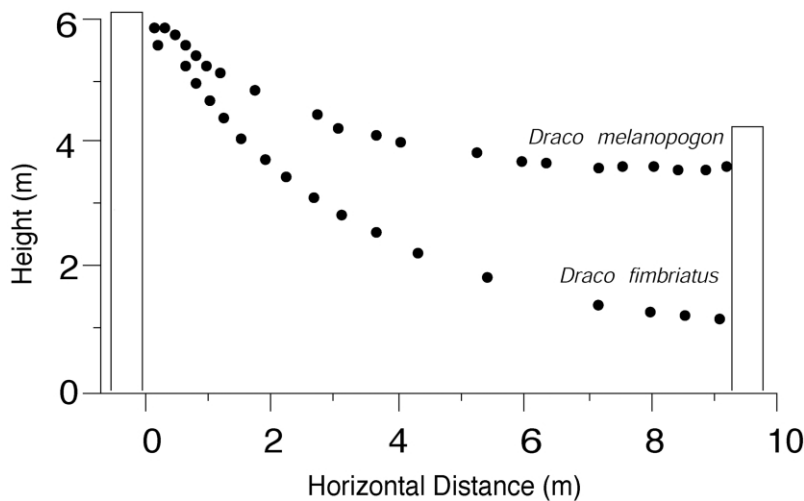


Figure 2: Representative glide trajectories for two species of *Draco* near opposite ends of the size spectrum for the genus: *Draco fimbriatus* (body mass = 21.6 g) and *Draco melanopogon* (body mass = 2.95 g). Several data points are missing from each trajectory because the lizard was not continuously visible against the mottled sky background.

Although several approaches are available, we chose to calculate independent contrasts (Felsenstein 1985) using the program CAIC, version 2.6.9 (Purvis and Rambaut 1995). We calculated independent contrasts in the context of a published phylogenetic estimate for the genus *Draco* (McGuire and Kiew 2001) that was based on maximum likelihood (ML) analysis of mitochondrial DNA sequence data. Before calculating contrasts, we first transformed the raw branch length data obtained via ML analysis, using nonparametric rate smoothing (Sanderson 1997). This allowed contrasts to be calculated in the context of a tree with ultrametric branch lengths while still permitting relaxation of a strict molecular clock. We confirmed that the contrasts were properly standardized by regressing them against their standard deviations and against the reconstructed values at adjacent nodes (Garland et al. 1992; Purvis and Rambaut 1995). Phylogenetically corrected data were then subjected to regression analysis.

Determining the appropriate regression model for use in biological studies is a contentious issue (Gould 1966; Rayner 1985; LaBarbera 1989; Harvey and Pagel 1991). The most commonly used model, ordinary least squares (OLS), may be inappropriate because it does not account for measurement error in the independent variable (Rayner 1985; LaBarbera 1989; Harvey and Pagel 1991). As an alternative, several authors have suggested use of the reduced major axis (RMA) model (Ricker 1973; Rayner 1985) because it incorporates error in the independent variable. Given that our independent variable (wing loading) almost certainly includes some measurement error, we employed the RMA in this study. We have calculated our RMA slopes by dividing the OLS slope by its correlation coefficient (Ricker 1973; Rayner 1985). However, interpretation of 95% confidence intervals with RMA regression is problematic, and care must be taken when attempting to use RMA confidence intervals for hypothesis testing (Ricker 1973; Sokal and Rohlf 1995). Because OLS will underestimate the regression coefficient when there is error in the independent variable, we conservatively present 95% confidence intervals for the OLS, which is here more relevant, given that we are primarily concerned with testing for nonzero regression coefficients. All of the data employed in the regression analyses were log transformed before calculation of regressions. All regression analyses of independent contrasts were regressed through the origin, and independent variables were posititized (Garland et al. 1992).

Motivation and Maximal Performance

One of our primary concerns in this study was the issue of motivation and its effect on locomotor performance (see Losos et al. 2002 for a detailed discussion of this issue).

We note that gliding presents a special problem with respect to measuring maximal performance because the largely passive nature of the process does not leave any obvious signs of suboptimal "exertion," as may be detectable with sprinting lizards (Losos et al. 2002). In particular, we were concerned about motivation issues with species at the smaller end of the size spectrum. Our primary hypothesis that smaller flying lizards should be more capable gliders than larger flying lizards led us to further hypothesize that these species would exhibit greater individual and intraspecific locomotor performance variation than larger species simply because they have the flexibility to perform suboptimally while still reaching the landing pole. Larger species, on the other hand, have less flexibility, because a suboptimal glide could force them to land on the ground before reaching the landing pole. We evaluated this hypothesis by evaluating regression scatter plots with all glides considered, including multiple glides per individual and multiple glides per species. Although these data clearly violate basic statistical assumptions of independence, in this case we were interested in the shape of the cloud of data points rather than a strict evaluation of regression and correlation coefficients.

An unfortunate aspect of contemporary interspecific comparative analysis is the need to generate a single summary score or value for each included species, even when a large number of observations have been obtained for each taxon (including cases in which multiple observations have been collected for each of many individuals per species, as is the case here). Consequently, we were forced to perform the typical winnowing procedure to generate a single summary value for each species included in our phylogenetically corrected regression analyses. This massive data reduction requirement strongly influenced our decision regarding how we obtained single summary values for each species. We employed two strategies: taking the single best observed value for each species and taking the mean value for each species. In each case, we considered only glides produced by adults because within-species ontogenetic area-mass relationships are consistent with isometry in much the same manner as are interspecific area-mass relationships (thus, juveniles and subadults have lower wing loadings than do adults and are thus expected to be more capable gliders). Although we generated summary values following two different protocols, we believe that the single best value observed for a species will provide the most accurate estimate of that species' maximal performance capability, and analyses based on optimal glide events are less likely to be confounded by the unavoidable suboptimal glides (we present support for this statement below). In other words, given our null hypothesis that large size induces a constraint on gliding performance, we hoped to maximize the likelihood of using an optimal or near-

Table 1: Body mass, wing loading, and glide performance data for lizards included in this study

Species	Body mass (g)		Wing loading (N/m ²)		Adjusted glide velocity (m/s)		Height lost (m)		Glide angle (deg)	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
<i>Draco blanfordi</i> (n = 16)	11.3	3.3–16.7	14.1	9.2–17.7	6.4	5.3–7.6	4.7	3.9–5.4	26.6	22.5–30.0
<i>D. fimbriatus</i> (n = 2)	18.7	15.8–21.6	23.5	22.7–24.2	6.4	5.7–7.1	5.1	5.0–5.2	28.8	28.7–28.8
<i>D. formosus</i> (n = 13)	8.8	5.5–11.3	14.1	11.9–16.4	7.0	5.1–9.5	4.8	4.1–5.7	26.7	22.0–32.0
<i>D. haematopogon</i> (n = 9)	5.7	4.2–7.7	12.4	10.5–15.1	5.2	4.4–6.5	4.7	4.3–5.3	26.0	23.3–28.8
<i>D. maculatus</i> (n = 14)	4.0	1.7–6.3	12.9	10.4–15.1	5.8	4.9–6.8	4.1	3.8–5.2	23.9	21.8–30.0
<i>D. maximus</i> (n = 8)	15.6	5.2–32.0	16.0	11.3–22.6	6.5	5.0–7.9	5.0	4.4–5.7	28.8	21.8–30.9
<i>D. melanopogon</i> (n = 35)	3.8	1.3–5.9	9.2	7.3–12.8	5.5	3.3–6.7	4.1	2.6–6.2	24.0	15.0–32.8
<i>D. obscurus</i> (n = 3)	9.1	7.9–10.7	15.7	13.2–18.8	6.0	5.4–6.9	3.8	3.8	22.3	22.3
<i>D. quinquefasciatus</i> (n = 4)	6.5	3–8.25	10.5	9.3–11.4	7.3	5.2–10.6	4.1	3.2–5.5	20.6	18.0–23.0
<i>D. sumatranus</i> (n = 1)	6.2	6.2	14.8	14.8	7.6	7.6	4.0	4.0	23.0	23.0
<i>D. taeniopterus</i> (n = 12)	3.3	2.2–4.6	10.0	8.5–11.8	6.1	5.1–7.4	4.3	3.5–5.5	25.4	21.5–30.0

Note: Performance data are derived from best-observed glide for each individual lizard.

optimal glide for each species in order that the true relationship between wing loading and performance could be determined. We present results based on mean summary scores in part to illustrate the large effect that the data reduction protocol can have on these sorts of analyses.

Equilibrium Gliding

In addition to the comparative analysis of gliding performance, we were also interested in determining whether the flight trajectories obtained here included equilibrium components. The equilibrium glide velocity is a theoretical expectation under steady state aerodynamics that maximizes the lift-to-drag ratio and minimizes the glide angle (McMahon and Bonner 1983; Norberg 1985, 1990); flight at the equilibrium velocity maximizes the horizontal distance traveled (this is equivalent to the maximum-range speed of powered aircraft; Alexander 1992). By definition, the equilibrium portion of a glide is characterized by a constant translational velocity (see Norberg 1990). Under experimental conditions, this theoretical expectation of constant velocity is unlikely to be met, given short-term behavioral variation in body configuration and also given measurement error imposed by the digitizing process (Walker 1998). We attempted to quantify equilibrium glides first by establishing arbitrary threshold values for consecutive percentage changes in velocity (i.e., 5%, 10%, and 15%) and then by identifying those sections of the glide over which observed velocity changes did not exceed threshold values. This approach was deemed unsatisfactory because of a strong dependence on the occasionally variable time intervals separating observed data points and because monotonic increase or decrease in velocity at increments of less than the threshold value would yield erroneous identification of an equilibrium region of the

curve. Instead, we used the program Quicksand (Walker 1997) to obtain velocity and acceleration profiles for all of our previously analyzed glides. We relied in particular on a five-point moving regression (see Lanczos 1956), which produced less extreme smoothing than did either the Butterworth filter (Winter 1990) or a quintic spline approach (Woltring 1985). Glides with velocity profiles that demonstrated a clear plateau, indicating relatively stable velocities over an extended interval, were considered to be in equilibrium over the corresponding time period.

Results

Comparative Gliding Performance

A total of 249 glides was obtained for 11 species of *Draco* lizards. Of this total, 158 glides were directly to the landing pole, and 91 were glides past the landing pole. The average horizontal wind speed for all 249 glides was 0.98 m/s, with a range of 0–3 m/s, although only six of 249 glides were accompanied by winds in excess of 2 m/s. Great interspecific variation was detected in all morphological and flight performance variables (see table 1).

Regression analysis of adjusted maximum velocity contrasts on wing-loading contrasts were nonsignificant regardless of whether the analysis was based on best observed or mean summary scores ($P = .57$ and $.68$, respectively; fig. 3; table 2). Significant positive correlations were detected when total height lost and glide angle were regressed on wing loadings ($P = .003$ and $.009$, respectively; fig. 3; table 2), as long as the analyses were based on best observed summary performance scores. Analyses based on mean summary scores were nonsignificant for both performance variables ($P = .29$ and $.41$, respectively; fig. 3; table 2). A scatter plot illustrating the relationship between height lost and wing loading when all glides are considered

together (fig. 4) suggests that variance in performance decreases with increasing wing loadings.

Equilibrium Gliding

Examination of individual velocity profiles for all glides revealed three primary glide types in the data set, each characterized by a readily identifiable velocity profile (fig. 5). Velocity profiles exhibiting a plateau (corresponding to approximately translational velocity) were termed equilibrium glides. Of 150 glides for which complete velocity profiles could be constructed, 72 (48.0%) were found to include a substantial equilibrium component. A second type of glide was characterized by a velocity profile with a sharp peak (fig. 5). These glides were characterized by acceleration through the first one-half to two-thirds of the glide, followed by rapid deceleration as the lizard approached the landing pole. This glide type generally was associated with glides to the landing pole (39 of 50 glides, or 78.0%), although lizards that glided past the landing pole occasionally began to decelerate before reaching the pole. The third glide type was characterized by a velocity profile suggesting acceleration throughout the glide (fig. 5). This glide type was almost always associated with glides past the landing pole (25 of 28 glides, or 89.3%).

The percentage of all glides to the landing pole that were equilibrium glides was calculated for different wing-loading classes, given a null hypothesis that individuals

Table 2: Results of the regression analyses of contrasts

Data partition	OLS	<i>r</i>	RMA	<i>n</i>	<i>P</i>
Adjusted maximum velocity:					
Mean score for adults	.090	.140	.643	10	.681
Best score for adults	.229	.331	.692	10	.320
Height lost:					
Mean score for adults	.146	.278	.525	10	.409
Best score for adults	.456	.751	.607	10	.008
Total glide angle:					
Mean score for adults	.180	.354	.508	10	.285
Best score for adults	.376	.662	.568	10	.026

Note: OLS = ordinary least squares regression coefficient; *r* = correlation coefficient under OLS; RMA = reduced major axis regression coefficient; *P* value is from an ANOVA test for a nonzero regression coefficient.

with lower wing loadings were more likely to perform equilibrium glides. Among lizards with wing loadings between 6 and 9.9 N/m², more than 74% of all glides to the pole (*n* = 23) were equilibrium glides. Among individuals with wing loadings between 10 and 13.9 N/m², 50% of all glides to the pole (*n* = 38) were equilibrium glides. Among individuals with wing loadings between 14 and 17.9 N/m², 36% of all glides to the pole (*n* = 25) were equilibrium glides. For individuals with wing loadings higher than 18 N/m² (all were between 22.7 and 24.2 N/m²), 75% of glides to the pole were equilibrium glides, although sample size was small for this wing-loading category (*n* = 4). Despite the apparent trend, logistic re-

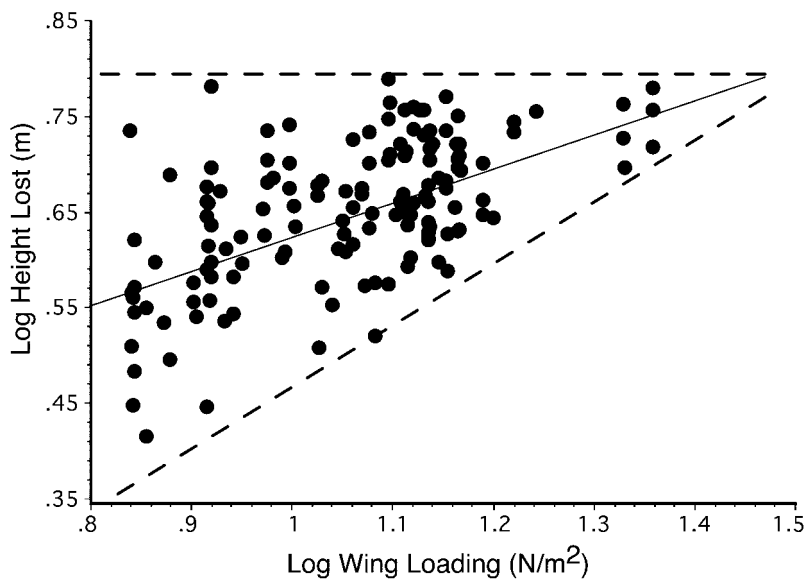
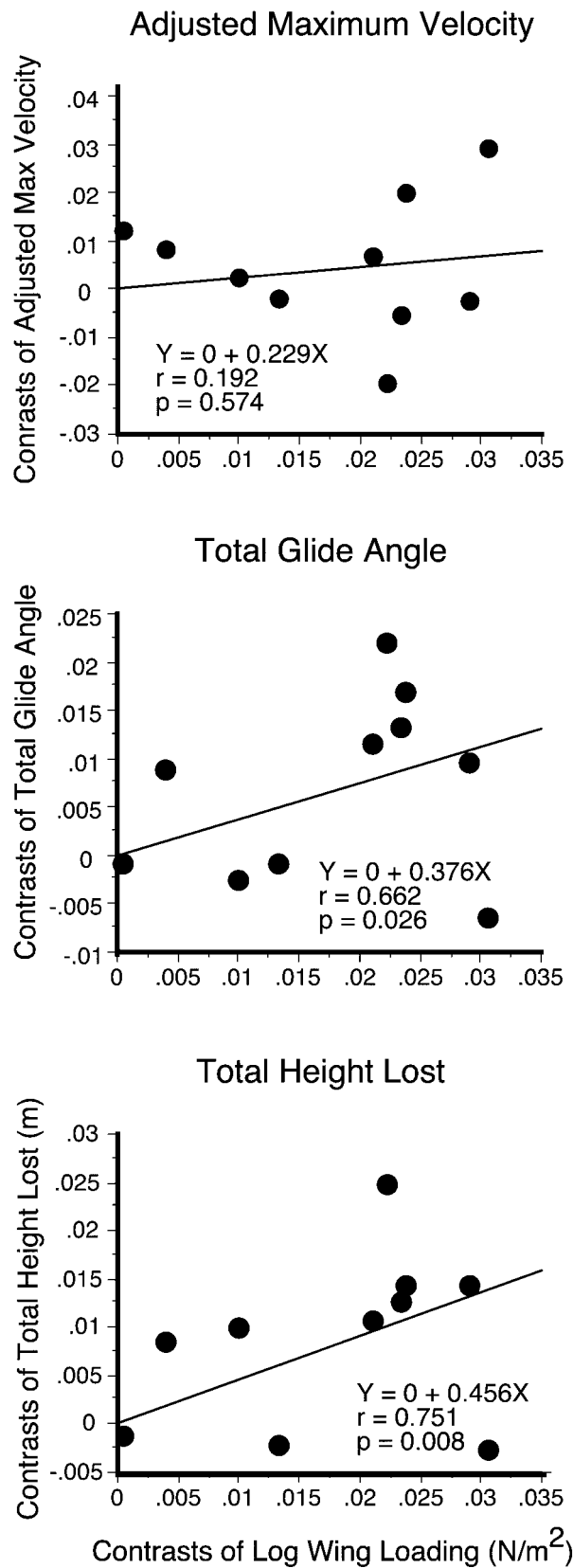


Figure 3: Scatter plot depicting the relationship between wing loading and height lost when all glides (regardless of statistical independence) are considered. The plot suggests a monotonic reduction in performance variation as wing loading increases. Dashed lines simplify emphasize the shape of the cloud of data points. Data are log transformed.



gression failed to detect a significant correlation between wing loading and equilibrium gliding ($\chi^2 = 1.9460$, $df = 1$, $P = .16$). However, analysis after exclusion of the four *Draco fimbriatus* observations that comprise the highest wing-loading category reveals a highly significant negative correlation between wing loading and equilibrium gliding ($\chi^2 = 7.6151$, $df = 1$, $P = .006$).

Discussion

Comparative Gliding Performance

We hypothesized, on the basis of known area-mass scaling relationships (McGuire 2003) and aerodynamic theory, that large *Draco* species are relatively poor gliders relative to their smaller congeners. More specifically, we predicted, first, that larger species require greater absolute glide velocities in order to generate sufficient lift, given that their wings must support greater mass per unit area; second, that the need for greater velocities consequently requires longer ballistic dives such that larger species lose more height over the course of standard glide distances; and third, that longer ballistic dives result in increased glide angles for larger species. Thus, we expected to find positive correlations between wing loading and each of these performance parameters. Our results when considering the best observed glides for each species were largely congruent with these predictions, as we found significant positive correlations between wing loading and both height lost and total glide angle, despite relatively small sample sizes (249 observed glides reduced to 10 independent contrasts). Although we did not detect a significant correlation between wing loading and glide velocity, we suggest that this might be more reflective of low statistical power and the technical challenges of accurately extracting clean velocity data from video footage (see “Material and Methods”) than of an absence of such a relationship. Regardless of whether velocity and wing loading prove to be correlated, we believe that our findings provide convincing evidence that larger *Draco* species are indeed less capable gliders than are smaller species.

We detected no significant correlations between performance and wing loading when considering mean summary performance values for each species. We believe that this illustrates an important issue for interspecific performance studies, which will often be hampered by small

Figure 4: Regression plots (ordinary least squares) illustrating results when adjusted maximum velocity, total glide angle, and total height lost are regressed on wing loading. The data are phylogenetically corrected (independent contrasts) summary values for each species. The data are log transformed.

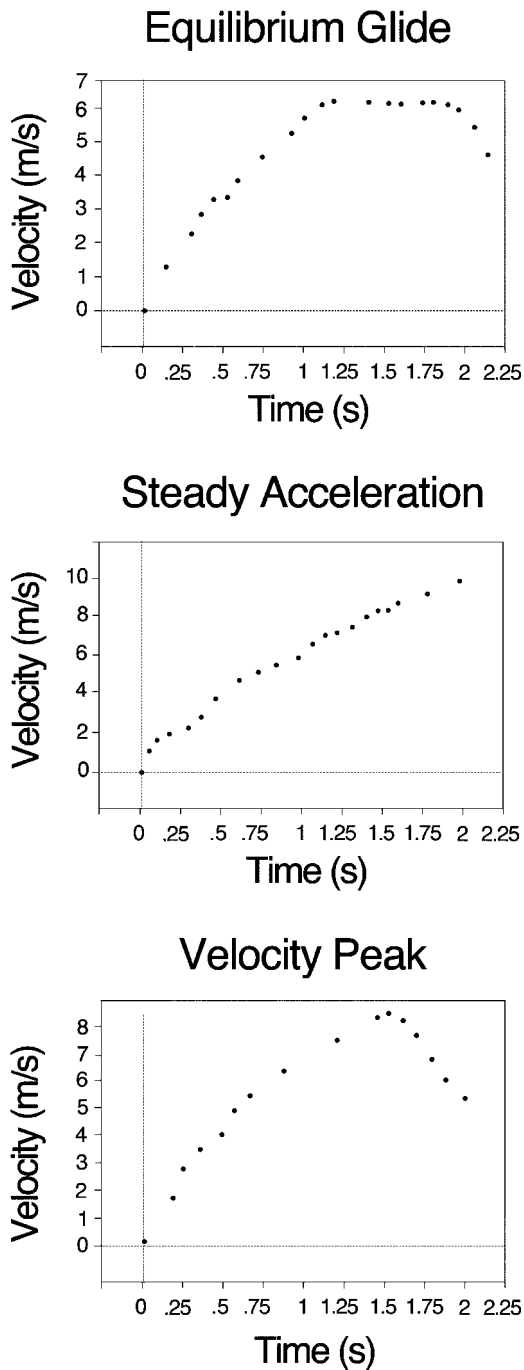


Figure 5: Velocity profiles illustrating the three patterns observed in this study. The velocity data were smoothed using the Lanczos five-point moving regression (Lanczos 1956). The equilibrium glide was obtained from a *Draco melanopogon* with wing loading of 7.37 N/m². The glide exhibiting steady acceleration was obtained from a *Draco blanfordi* with wing loading of 14.32 N/m². The glide exhibiting the velocity peak was obtained from a *Draco taeniopterus* with wing loading of 10.54 N/m².

sample sizes. If the goal is to understand the relationship between some morphological feature and maximal performance, it is important to account for nonoptimal performance trials in a manner that does not dilute assessment of a species' maximum performance capacity (see Losos et al. 2002). We believe that our own analyses based on mean summary performance values were compromised in this way. The primary problem appears to be tied to motivation (or lack thereof) and the challenges we face when attempting to convince any organism to perform maximally. The issue of motivation is discussed further in our assessment of performance variation below.

Wing Loading and Performance Variation

We made an additional prediction beyond the basic hypothesized relationships between body size and overall gliding performance. We suggested that, should smaller species prove to be more accomplished gliders, they would exhibit greater individual and intraspecific performance variation in gliding trials than would larger species. The logic behind this prediction was that smaller species might not be motivated to land as high on the landing pole as they were capable—perhaps just reaching the landing pole is sufficient. In other words, an individual with lower wing loading may be able to glide over a broad range of angles according to behavioral context, whereas a heavier individual with higher wing loading is restricted to steeper glides and an overall reduced range of potential glide angles. Examination of the scatter plot presented in figure 4 suggests that this is indeed the case. For example, individuals at the lower end of the wing-loading spectrum exhibit glide angles ranging from 15° to 35°, whereas all glides by individuals with wing loadings greater than 16 N/m² exceed 25° (range of 25°–34°). This result is illustrative in a number of ways. First, it indicates that mean scores for smaller species with lower wing loadings would almost certainly underestimate maximum performance capabilities for the species. This would introduce bias to an analysis based on mean species values, because larger species are more likely to perform closer to their maximum capability. This outcome would tend to underestimate the regression slope if mean species values are employed rather than the best observed values.

Further support for the contention that smaller species with lower wing loadings have greater flexibility with respect to glide performance is provided by the range of glide angles exhibited by individual lizards. Extreme examples include one *Draco melanopogon* (no. 1702; wing loading of 8.72 N/m²), which yielded glides at angles of 26.2°, 24.4°, and 16.3°; another *D. melanopogon* (no. 1811; wing loading of 12.75 N/m²) produced glides at 32.8° and 19.8°; and a third *D. melanopogon* (no. 1740; wing loading

of 8.01 N/m^2) yielded glides at 26.1° and 18.0° . Such variability suggests that smaller *Draco* lizards can utilize biomechanically different gliding strategies when traversing equivalent horizontal distances. This observation also suggests that any single glide observation is unlikely to be a true reflection of the performance limits for that individual.

Equilibrium Gliding

About half of the glides in this study for which complete data were available exhibited an obvious plateau in the plot of air velocity versus time, indicating equilibrium gliding. This is the first study to document quantitatively the occurrence of equilibrium gliding in nonpowered flying animals. Because available theory pertaining to gliding locomotion is based on steady state aerodynamics and thus is strictly relevant only to equilibrium glides, our finding that *Draco* lizards enter equilibrium during at least some glides indicates that steady state aerodynamic theory can be relevant to flying lizard locomotion and probably to that of other animal gliders.

In addition to equilibrium glides, we observed two qualitatively different classes of nonequilibrium glides. One nonequilibrium glide form was characterized by a distinct peak in velocity, followed by deceleration. In such glides, it seems likely that the lizard either could not or did not reach an equilibrium velocity before initiating the deceleration phase of the glide. Most of these glides (78%) were directly to the pole, suggesting that the associated deceleration was in preparation for landing. The second nonequilibrium glide type was characterized by continuous acceleration throughout the glide and was almost always associated with glides past the landing pole. This observation suggests one of two possibilities—either these lizards had not yet achieved their potential equilibrium glide velocity by the time they passed the landing pole or some extended glides are not undertaken at equilibrium velocities (perhaps it is sometimes more important to make a fast getaway than to maximize horizontal glide distance).

The distance separating takeoff and landing poles for our gliding trials (9.3 m) is comparable with the spacing of tree trunks utilized by *Draco* in Southeast Asian dipterocarp rainforest (J. A. McGuire, personal observation). Thus, our finding that more than half of the fully analyzed glides in this study did not reach equilibrium suggests that nonequilibrium flight may be important to flying lizards in nature. Although we did not detect a significant correlation between wing loading and equilibrium gliding in our analysis of all glides to the landing pole, this result was dependent on the unexpected finding that *Draco fimbriatus*, with the highest wing loading of any species included in the study, produced multiple equilibrium glides

to the landing pole. Analysis after exclusion of the *D. fimbriatus* samples results in a significant negative correlation between wing loading and the tendency to perform equilibrium glides. This finding suggests that many large *Draco* species either require takeoff heights greater than 6 m or horizontal transit distances greater than 9 m to achieve equilibrium glides. Nevertheless, it is clear that these dimensions do not necessarily preclude equilibrium gliding in heavier species—especially *D. fimbriatus*.

Ecological and Evolutionary Consequences

Results of this study are concordant with predictions derived from aerodynamic models of animal gliding (see Norberg 1990; McGuire 2003). Larger species, with their greater wing loadings, are markedly less capable gliders than are smaller species with respect to both height lost over a standard horizontal distance and glide angle. Gliding ability is of daily importance in the lives of flying lizards and almost certainly has important consequences in contexts of both natural and sexual selection. Why, then, have larger species not evolved either disproportionately larger wings or other compensatory mechanisms for the size-dependent degradation of gliding performance?

One possibility is the presence of a design constraint, given that the glissant locomotion employed by flying lizards is relatively straightforward, compared to flapping flight, and is enabled principally by morphological and, to a secondary extent, behavioral features. The most obvious means by which selection might act to maintain gliding performance as body mass increases is through positively allometric changes in wing size. However, potential modification of wing area is limited by the architecture of the gliding apparatus. The area of the patagial membrane is a direct function of rib length, because the wings are folded next to the body when not in use. If this length is constrained by the distance between the forelimb and hind limb insertions, then wing area will not be free to vary independently of trunk length. This suggestion is consistent with the empirically determined allometry of wing area in *Draco* (McGuire 2003). Also, the patagium of flying lizards is attached to the proximal portions of the hind limbs, which may actively control patagial camber during gliding by way of depression of the hind limbs relative to the longitudinal body axis. The need for such a control mechanism, which might be disabled if the ribs were extended beyond the hind limbs, may effectively prevent further elongation and thereby preclude disproportionate increases in wing area.

The finding that larger *Draco* species are relatively poor gliders compared to their smaller congeners has important ecological implications for flying lizards. Larger species cannot utilize lower forest strata to the same extent as can

smaller species while maintaining the ability to complete glides to adjacent trees. Consistent with this prediction is the finding by Inger (1983) that, of six sympatric species of *Draco*, the two with the lowest wing loadings were also found most frequently in the lowest levels of the forest. A similar pattern would be predicted for ontogenetic variation within species of *Draco*. The exclusive occurrence of large species in sympatry with smaller species (McGuire 2003) suggests that there is indeed a fitness cost to being large that is overcome only in the ecological presence of other flying lizards. Whether that cost derives exclusively from the locomotor penalties identified here or is related to other aspects of flying lizard biology, such as diet, remains to be rigorously evaluated through careful ecological study. It would be of particular interest to evaluate potential habitat partitioning by body size in multispecies assemblages to determine whether structuring rules parallel those for the well-studied *Anolis* communities of the Caribbean (Williams 1983; Losos et al. 1998).

Implications for Other Glissant Taxa

We have confirmed that gliding performance among flying lizards is consistent with predictions derived from area-mass scaling relationships and that larger flying lizards are unable to compensate for their higher wing loadings by physiological or behavioral means. These findings indicate that approximate, if not precise, gliding locomotor performance should, in fact, be predictable from structural (morphological) data alone, just as they would be for an inanimate object such as a model airplane, a possibility that requires empirical confirmation. In other glissant taxa, such as flying squirrels, flying frogs, and flying geckos, it is as unlikely as in *Draco* that behavioral or physiological compensatory mechanisms are available to overcome the adverse allometry of wing area. We are therefore confident that our general finding that larger species of *Draco* are comparatively poor gliders relative to smaller species will pertain to other glissant lineages that exhibit isometry in wing area.

Finally, we emphasize that the most important performance parameters evaluated in this study—height lost over the course of a standard glide distance and the correlated total glide angle—are generally not considered in theoretical treatments of animal gliding. Rather, steady state aerodynamics are emphasized, with the glide angle generally considered only from the standpoint of the equilibrium phase of a glide. From an ecological perspective, we argue that the total height lost over the course of a glide (and the corresponding total glide angle, including the ballistic dive component) may have more direct fitness consequences than the more restricted parameter of total height lost during the equilibrium portion of a glide. Con-

sequently, in the absence of applicable aerodynamic theory, we suggest that predictions of locomotor performance in glissant taxa, at least in the near term, will likely require direct empirical study. Thorington and Heaney (1981), for example, used both aerodynamic theory and empirical performance data for hang gliders to predict gliding performance capabilities in flying squirrels, which, like *Draco*, exhibit isometric area-mass scaling relationships. Based on aerodynamic theory, Thorington and Heaney (1981) correctly concluded that small and large flying squirrels should be characterized by similar glide ratios, with larger species requiring greater glide velocities during equilibrium. However, we hypothesize that the greater velocity requirements of larger species will necessitate that they lose significantly more height during the ballistic portion of the glide, as shown here for flying lizards. The equivalent glide ratios expected among small and large flying squirrels are probably of little consequence, whereas the spatial demands of the ballistic dive must have important ecological and evolutionary implications for flying squirrels and, presumably, all glissant taxa.

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