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## THE INTERACTION OF BEHAVIORAL AND MORPHOLOGICAL CHANGE IN THE EVOLUTION OF A NOVEL LOCOMOTOR TYPE: “FLYING” FROGS

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*Abstract.*—“Flying” frogs have evolved independently several times among anurans. In all cases flyers are distinguished from their nonflying arboreal relatives by a unique set of morphological features and behavioral postures. Using both live animal field tests and wind tunnel models, this study examines the importance of this characteristic morphology and limb position on five aerial performance variables: horizontal traveling distance, minimum glide speed, maximum time aloft, maneuverability, and stability. Comparison of relative performance between a model frog with a generalized nonflying morphology and limb position and a model frog with flying morphology and limb position reveals that the morphological and positional features associated with “flying” actually decrease horizontal traveling distance but improve maneuverability. This finding suggests that maneuverability rather than horizontal travel may be the key performance parameter in the evolution of “flying” frogs.

More generally, this study illustrates that (1) derived morphological and postural features do not necessarily change a suite of performance variables in the same way, and (2) the performance consequences of postural shifts are a function of morphology. These findings indicate that the potential complexity of morphological and behavioral interactions in the evolution of new adaptive types is much greater than previously considered.

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Despite a large, older literature discussing the relative importance of behavior and morphology in the origin of new adaptive types (e.g., Mayr, 1960, 1963; von Wahlert, 1965; Christiansen, 1965), recent studies on the role of behavior in such transitions are few (Greene and Burghardt, 1978; Russell, 1979; Norberg, 1985a; Huey and Bennett, 1987; Kingsolver, 1988). To date, the origin of evolutionary novelties has been examined almost exclusively from the morphological perspective (e.g., Liem, 1973; Frazzetta, 1975; Alberch, 1980; Livesey and Humphrey, 1986; Schaefer and Lauder, 1986; Wake and Larson, 1987; Livesey, 1989). The common ideas that a behavioral shift precedes morphological or physiological change (e.g., Mayr, 1960; Ostrom, 1973; Russell, 1979; Huey and Bennett, 1987; Futuyma and Moreno, 1988) and that the effects of behavior and morphology on performance are of a similar nature although ranging in magnitude (e.g., Bock, 1970; Russell, 1979; Cople et al., 1983) have rarely been tested. Kingsolver (1988), however,

described an example of how a behavioral innovation (reflectance basking) dramatically alters the performance consequences of various wing color morphologies in butterflies, thereby affecting wing pattern evolution.

This paper reports an examination of the shift from arboreal to “flying” frogs where we evaluate the aerodynamic performance consequences of both a behavioral and morphological change. “Flying” frogs have evolved independently several times among the 3,400 species of anurans (Wallace, 1869; Siedlecki, 1909; Ayyangar, 1915; Inger, 1966; Duellman, 1970). Although the particular nonflying sister species to each flying form remains unknown, in all cases flyers are distinguished from related, nonaerial, arboreal frogs by a similar suite of morphological characters: enlarged hands and feet, full webbing on the fingers and toes, and accessory skin flaps on the lateral margins of the arms and legs. “Flying” frogs are not capable of powered flight, but do travel considerable horizontal distances during ver-

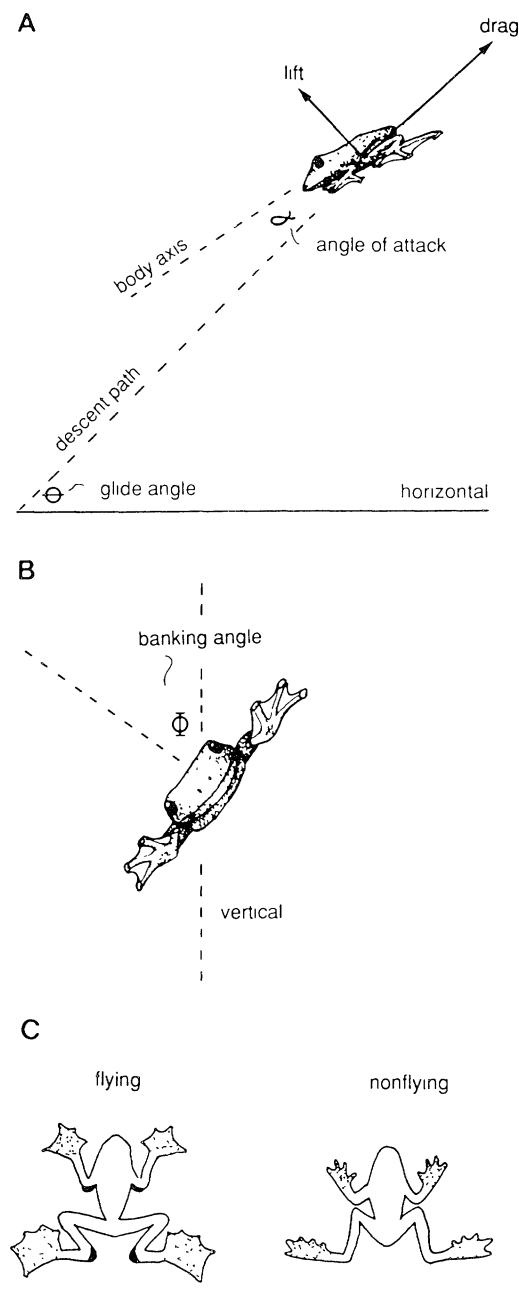


FIG. 1. A. Diagram of a side view of a gliding frog illustrating the definitions of lift, drag, angle of attack ( $\alpha$ ), and glide angle ( $\theta$ ). B. Diagram of a face-on view of a gliding frog illustrating banking angle ( $\Phi$ ). C. Silhouettes of the models of *Rhacophorus nigropalmatus* (flyer) and *Polypedates macrotis* (nonflyer), indicating the morphological features that were manipulated. Scale bar = 35 mm. The following options were available in the construction of any model: 1) flyer versus nonflyer body (including arms and legs) (indicated in white), 2) flyer versus nonflyer hands (stippled), 3) flyer versus nonflyer feet (stippled), 4) presence or absence of skin

tical descent (Inger, 1966; Scott and Starrett, 1974). They are technically classified as gliders (Oliver, 1951; Rayner, 1981; Norberg, 1985*b*) because they can descend at an angle (glide angle,  $\theta$ , Fig. 1A) less than  $45^\circ$  to the horizontal. Interestingly, arboreal frog species lacking particular morphological specializations (=nonflying frogs) drop from vertical heights as well (Stewart, 1985; Cott, 1926). These animals descend at glide angles greater than  $45^\circ$  and are, by definition, parachuting. Both "flying" and nonflying frogs move their front and hind limbs lateral to their bodies and spread their fingers and toes during aerial descent, adjusting limb position slightly during flight. This lateral position of the limbs is quite different than that observed during (1) the takeoff phase of regular jumping where fingers and toes are appressed and the limbs are held posterior and parallel to the long axis of the body, or (2) the trajectory phase of a regular jump where the forelimbs are anterior and lateral but the hind limbs remain extended posterior to the body. The functional consequences of this behavioral shift to a lateral hind limb position and the postural adjustments of the limbs during flight are unknown.

In the present study, we measure the effects on aerial performance of shifts in limb position and morphological features to address the following questions: (1) How do behavioral and morphological changes interact in the evolution of a novel locomotor type? (2) Do both the position of the limbs associated with aerial locomotion and the morphological features associated with "flying" frogs affect performance similarly? (3) What is the functional significance of the particular morphological characters that distinguish "flying" frogs?

#### Performance Tests Using Physical Models

To address the questions listed above, we needed to quantify the performance consequences of defined structural and postural changes. We began by comparing the aerial performance of living frogs of different mor-

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flaps (black) on arms and legs. In addition, the positions of the arms, legs, hands, and feet could be modified, as illustrated by the examples diagrammed in Figure 3.

phologies, but such comparisons suffer from two problems: (1) the structural variations that can be assessed are limited to those available in nature (i.e., we could not look at the effects of one structural feature at a time); and (2) the investigator has no control over the postures assumed by an animal during flight, hence postural effects on performance cannot be separated from morphological effects. Therefore, we supplemented our measurements of the aerial performance of living frogs in the field with a series of laboratory experiments using life-like physical models of frogs. Use of models permitted us to manipulate particular aspects of morphology and posture in a controlled fashion while holding other variables constant, and thereby enabled us to quantify the performance consequences of defined structural or postural changes. Engineers routinely use such physical models to measure the performance of airplanes, for example. Biological studies utilizing physical models to assess the fluid-dynamical performance of organisms include Koehl (1977), Kingsolver and Koehl (1985), and many others reviewed by Vogel (1981).

#### *Measures of Aerodynamic Performance*

Gliding and parachuting in arboreal animals may serve several non-exclusive biological roles (sensu Bock and von Wahlert, 1965), including energetically cheap horizontal travel (e.g., Pennycuik, 1986) relatively fast, energetically inexpensive vertical descent (e.g., Norberg, 1981; Stewart, 1985), pursuit of aerial prey (e.g., Savile, 1962; Rayner, 1981), escape from predators, or protection from injury during vertical descent (e.g., Savile, 1962). Therefore, we chose several measures of aerodynamic performance to assess the functional consequences of frog morphology and limb position.

*Gliding Performance.*—If gliding is used to travel horizontally from one place to another, then the appropriate measure of gliding performance is the *horizontal distance traveled* before landing. The horizontal distance traveled for a given loss of height during a steady-state glide is proportional to the ratio of lift to drag (e.g., Pennycuik, 1972), where drag ( $D$ ) is the component of

the aerodynamic force of the glider in the direction opposite to its motion, and lift is the component of force at right angles to the drag (Fig. 1A). Angle of attack ( $\alpha$ ) is the angle between the glider and its descent path (Fig. 1A). The lift and drag on a body can vary as a function of  $\alpha$ , and horizontal distance is greatest at the angle of attack ( $\alpha$ ) that maximizes  $L/D$ . Therefore, we used  $(L/D)_{\max}$  as a measure of horizontal traveling performance of falling frogs.

Gliders cannot generate sufficient lift to glide below a minimum airspeed. This *minimum glide speed* ( $U_{\min}$ ) might be a biologically important aspect of aerodynamic performance for several reasons. 1) In field trials frogs initially fall downwards and then break into more horizontal glides (Abdulali and Sekar, 1988; Emerson, pers. observ.), suggesting that they build up sufficient speed to glide as they fall. The lower the  $U_{\min}$  of a frog, the sooner after takeoff the animal can begin to glide. 2) The more slowly a frog can glide, the longer it can remain aloft and the less likely it is to be injured when landing. The magnitude of the force with which a gliding organism of a given mass hits the ground is proportional to the animal's speed just before impact. Indeed, such injuries may occur: although very rare, healed long-bone fractures have been found in museum specimens of nonflying frogs (Emerson, pers. observ.).

Minimum glide speed ( $U_{\min}$ ) is given by (Alexander, 1982):

$$U_{\min} = [2W/(\rho C_L)]^{1/2} \quad (1)$$

where  $W$  is the "wing" loading of the frog,

$$W = mg/S_p \quad (2)$$

where  $m$  is the mass of the frog,  $g$  is the acceleration due to gravity, and  $S_p$  is the projected area of the frog (as seen from the dorsal side);  $\rho$  is the density of air (1.205 kg/m<sup>3</sup> at 20°C (Vogel, 1981)); and  $C_L$  is the coefficient of lift,

$$C_L = 2L/(\rho U^2 S_p) \quad (3)$$

where  $L$  is the lift and  $U$  is the gliding speed.

*Parachuting Performance.*—Although lift is the force responsible for the majority of weight support in gliders, drag serves this function for parachuters (Rayner, 1981). The greater the drag force on a parachuting an-

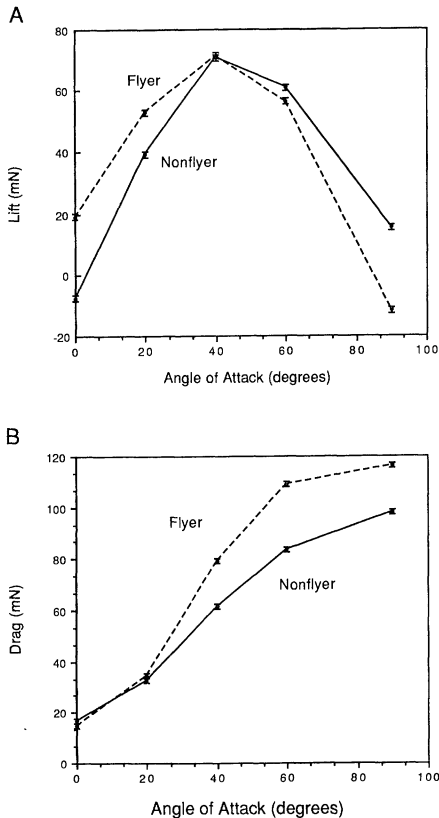


FIG. 2. Lift and drag measurements for a model of a flying and a nonflying frog in the wind tunnel at their natural airspeeds (4.5 m/sec and 6.1 m/sec respectively). Bars indicate 95% confidence intervals. A) Lift and B) Drag for flyer (dashed line) and nonflyer (solid line) models at various angles of attack ( $\alpha$ ). The flying frog experiences greater lift at low  $\alpha$ 's and greater drag at high  $\alpha$ 's than does the nonflyer.

imal of a given mass, the more slowly it falls, and hence the greater its time aloft ( $t \propto [D/m]^{1/2}$ ) (Norberg, 1985b) and the lower its force of impact when landing. Therefore, we used  $D_{90}$ , drag when  $\alpha = 90^\circ$  (i.e., the frog falling belly-first, the orientation at which drag is the greatest) as the measure of *parachuting performance*.

*Maneuverability and Stability.*—The more maneuverable an airborne frog, the more quickly it can alter its course to avoid obstacles or to steer to landing sites. The “flying” frog, *Rhacophorus nigropalmatus*, which descends through complex tree canopies, banks to change direction during flight (Emerson, pers. observ.). The turning radius ( $r$ ) of a banking glider is given by:

$$r = 2W/(\rho C_L \sin \Phi) \quad (4)$$

where  $W$  is the wingloading (Eq. 2),  $\rho$  is the density of air,  $g$  is the acceleration due to gravity,  $C_L$  is the coefficient of lift (Eq. 3), and  $\Phi$  is the banking angle (Fig. 1B) (Pennycuick, 1971a). Hence, for a given banking angle, a frog with a high  $C_L/W$  will execute a tighter turn than one with a low ratio. Because  $C_L$  depends on  $\alpha$ , we used  $(C_L/W)_{\max}$  as a measure of *turning performance*.

Gliding and parachuting organisms can alter their direction and speed of descent by adjusting such features as the shape or position of various appendages (examples of the physics of such maneuvers are described in Pennycuick, 1971b, and Lighthill, 1975). However, a tradeoff exists between maneuverability (i.e., the rapidity of the response of the organism's orientation, speed, or flight path to such a control movement) and aerodynamic static stability (i.e., the tendency of the glider or parachuter to return to its equilibrium state after being perturbed) (e.g., Maynard Smith, 1952; Lighthill, 1975; Saunders, 1977; Gans et al., 1987).

We used static stability as a fifth measure of frog aerial performance: high static stability suggests the ability to passively stay on course and land right-side-up, whereas low static stability suggests high maneuverability. One rough index of the static stability of an organism in a particular posture is its likelihood of descending through the air without tumbling. Unfortunately, the observation that an animal descends without tumbling is not sufficient to reveal that its morphology and posture render it statically stable because the animal may be holding itself on course by active behavioral adjustments. However, the effects of active attitude control can be eliminated by observing the path of a rigid model of the organism instead. If models of various frogs in defined postures are repeatedly permitted to descend freely under the same conditions, those with relatively higher static stability should tumble less often.

## MATERIALS AND METHODS

### *Field Performance Tests*

“Flying” frogs of two species, *Rhacophorus nigropalmatus* and *R. pardalis*, as well as a number of individuals of other nonfly-

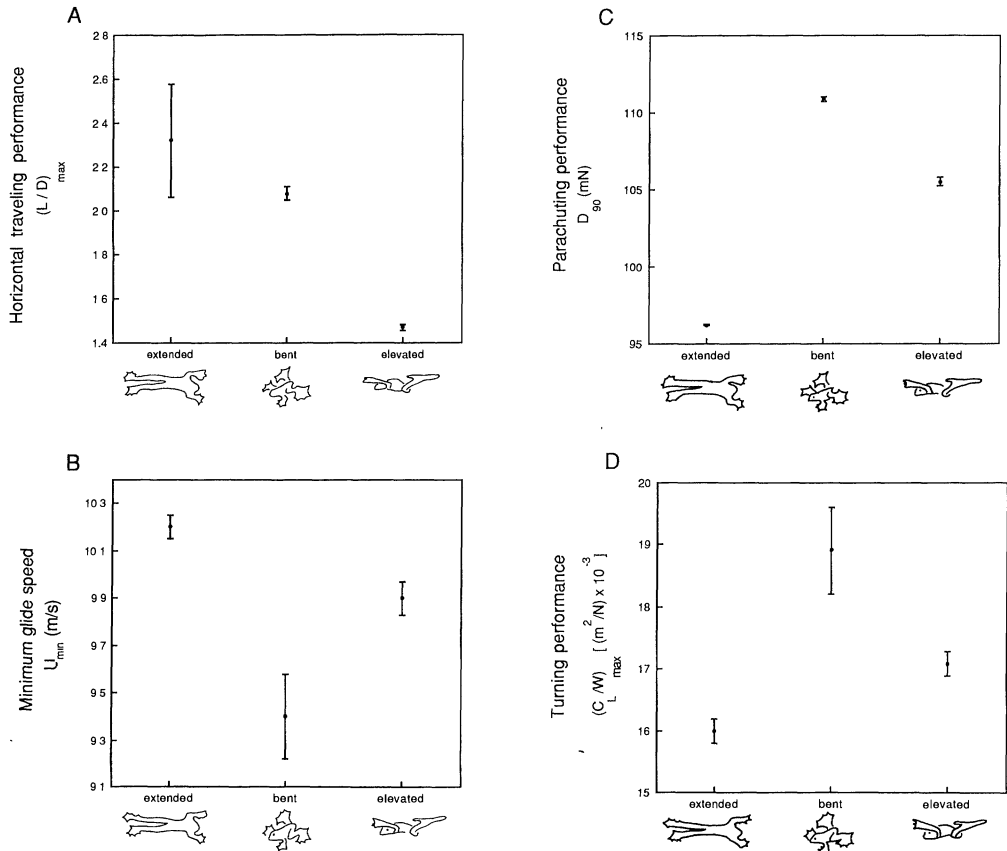


FIG. 3. Plots of performance for the three behavioral postures (extended, bent, and elevated limbs) in the flying frog model at an airspeed of 4.5 m/sec. Bars indicate 95% confidence intervals. A) Horizontal traveling performance,  $(L/D)_{max}$ . B) Minimum glide speed,  $U_{min}$ . C) Parachuting performance,  $D_{90}$ . D) Turning performance,  $(C_L/W)_{max}$ .

ing species of the family Rhacophoridae, were collected live in October–December 1986 at Danum Valley Field Centre, Sabah, Malaysia. Flying tests were conducted within 12 hours of capture. Animals were released from a platform 11.6 m high because examination of forest structure indicated that this represented an average vertical distance between the tree crowns of the two highest layers of the canopy where *R. nigropalmatus* lives.

We wanted to measure maximum gliding and parachuting performance capability. If trees were too close to the testing site, we were afraid frogs might adjust their flight path to land in the trees rather than travel maximum horizontal distances. Accordingly, the tests were conducted in a clearing so that the frogs' behavior would not be af-

ected by the presence of neighboring trees. Each frog was tested four times consecutively. Time aloft and horizontal distance of flight were recorded for all tests. The behavior of the "flying" frogs was qualitatively similar to that observed under natural conditions in the forest.

Live masses were taken for animals when captured, and the individuals were weighed again at the completion of testing. An average of the two masses was used in calculations. Animals were killed, fixed in formalin, and deposited as voucher specimens at the Field Museum of Natural History, Chicago. Linear measurements were taken later on the museum specimens. Outlines of each museum animal (in the "bent" posture with hands and feet spread, see Fig. 3) were traced onto paper, cut out, and their

plan areas determined by a Li-Cor 3,100 area meter.

### Models

Exact replicas of frogs used in the live performance tests were cast using orthodontic cold cure methyl methacrylate (Caulk Dentsply). Molds were made by placing museum specimens in a reversible hydro-colloid duplicating gel (Surgident). The models were formed by filling the molds with resin, placing the molds in hot water inside a pressure pot (Acridense pneumatic curing unit) and applying a pressure of  $1.38 \times 10^5 \text{ N/m}^2$  for 10 minutes. Models were made of *Rhacophorus nigropalmatus* (flying species) and *Polypedates macrotis* (nonflying species). *Polypedates macrotis* was chosen for comparison to the flying species because (1) body weights of these two species overlap (25–31 g for *P. macrotis* and 27–31 g for *R. nigropalmatus*), and (2) hand and foot proportions and degree of webbing in *P. macrotis* are typical for arboreal (but nongliding) members of the Rhacophoridae (Inger, 1966; Emerson, unpubl. data). For the present study, an individual weighing 29 g (live weight) was chosen from each species to be the template for the basic model of that species. We shall report the effects of body size elsewhere (Koehl and Emerson, in prep.).

Defined morphological (Fig. 1C) and postural (Fig. 3) modifications were made to the basic models of each species. Resin limbs were cut at their joints and reattached with stiff, but adjustable, wire joints. These joints were wrapped with paper surgical tape to provide a smooth skin in each posture. The digits of the resin hands and feet were not spread, hence we constructed models of hands and feet of “flying” and nonflying frogs based on tracings of the spread hands and feet of the museum specimens from which the models were cast. The fingers and toes were made of thread-wrapped wire, and the webbing was mimicked by thin plastic membranes (Form-a-Film, Joli Plastic Co.). Paper flaps, attached with paper surgical tape to arms and legs, were also based on tracings of skin flaps on the museum specimens.

### Force Measurements on Models in the Wind Tunnel

When a frog falls through still air, the velocity of the air relative to the frog is equal

in magnitude and opposite in direction to the velocity of the frog's descent. We mimicked the air flow relative to a falling frog by blowing air past a stationary frog model in an open circuit, open jet wind tunnel (Kingsolver and Koehl, 1985; Vogel, 1981) with a working section 0.4 m in diameter. Plastic screens and epoxy honeycomb collimators were used to suppress turbulence generated by the fan and to create an even flow field in the working section of the tunnel. Wind speeds were measured using a Kurz Air Velocity Meter (Model #440). Wind speeds were representative of the falling speeds recorded for live animals of each species in the field performance tests described above: *R. nigropalmatus* at 4.5 m/sec, and *P. macrotis* at 6.1 m/sec. Each model was positioned at five angles of attack ( $\alpha$ ): 0°, 20°, 40°, 60°, and 90°.

Lift ( $L$ ) and drag ( $D$ ) forces (Fig. 1A) were measured separately using a force transducer composed of resistance-type foil strain gages (Micromasurements, Inc.) on a force beam of shimstock steel, a Gould Bridge Amplifier (Model #11,4113-01), and a digital voltmeter (see Kingsolver and Koehl, 1985). The transducer was mounted above the working section of the wind tunnel and each model was suspended from it by a hollow aluminum rod 3.3 mm in diameter. A flattened portion of the rod was epoxyed to the back of the frog model such that the rod did not protrude above the surface contour of the frog's back, and such that no shift in angle of attack ( $\alpha$ ) occurred when the wind was turned on (hence the force beam was not subjected to torsion). An extension of the mounting rod below the working section of the wind tunnel bore a sphere immersed in light Karo Syrup to damp out any small, high-frequency fluctuations in force. The force beam was calibrated with each model and damping sphere attached (to eliminate biases caused by model weight and damping viscosity) by applying known forces (via a weight-and-pulley system) at the point of attachment of the model to the rod. The steady-state lift and drag forces on each model at each angle and velocity were measured to the nearest mN. Each model was set up on three separate occasions and all force measurements repeated. Measurements of lift and drag on the mounting rod alone were also made at the relevant wind

speeds (4.5 and 6.1 m/sec). Measurements were repeated three times and the readings were identical (to the nearest mN). Lift or drag on the rod alone at the appropriate velocity was subtracted from lift or drag measured when a model was attached to the rod. Rod forces were  $\leq 17\%$  of the total force on rod plus model.

We chose four criteria to assess the aerodynamic performance of the frog models tested in the wind tunnel: 1) the horizontal distance traveled, as measured by the maximum ratio of lift to drag,  $(L/D)_{\max}$ ; 2) the minimum glide speed,  $U_{\min}$  (eq. 1); 3) the parachuting performance, as measured by the drag when  $\alpha = 90^\circ$ ,  $D_{90}$ ; and 4) turning performance, as measured by  $(C_L/W)_{\max}$  (eq. 3). We calculated  $U_{\min}$  and  $(C_L/W)_{\max}$  for each model using lift measured on the model, but mass measured on the live frog from which the model was later cast.

#### *Models in Wind Tunnel Compared to Living Frogs*

We assessed the realism of our model measurements by comparing the glide angles ( $\theta$ , the angle between the descent path and horizontal, Fig. 1A) of living individuals in field tests to the  $\theta$ 's calculated (Pennycuik, 1972) from wind tunnel lift ( $L$ ) and drag ( $D$ ) measurements made for models:

$$\theta = \arctan(D/L) \quad (5)$$

Because real frogs do not necessarily glide for the full duration of a descent, field-measured glide angles (each of which represents the average for an entire descent) should be more variable, and on average worse, than those measured for models at steady state in the wind tunnel. Nonetheless, the best (i.e., lowest)  $\theta$ 's measured for living "flying" and nonflying frogs were within three degrees of those calculated for models in the same posture.

The hands and feet on our models were stiffer than those of real frogs. Although deformation of the hands and feet of frogs gliding in the field was not obvious, we nonetheless were concerned that bending of the digits or bowing of the skin between them by aerodynamic loads might alter performance. We therefore tested whether changes in the curvature of the hands and feet of our models altered the forces measured in the wind tunnel or the tumbling of

freely falling models, and we found no significant effects, except in the case of simultaneously cambering both hands and feet, which produced a small reduction in  $D_{90}$ . Therefore, all values reported in this paper are for models with flat hands and feet.

#### *Experiments in Wind Tunnel*

We examined the effects of particular aspects of limb, hand, or foot position on the aerodynamic performance criteria listed previously. We tested three different limb positions diagrammed in Fig. 3: bent, extended, and elevated. We also tested hands and feet at the same angle of attack as the body, and feet at an angle of attack of  $30^\circ$  greater than that of the body. These limb, hand, and foot postures were taken from observations made on live animals during aerial locomotion (Duellman, 1970; Scott and Starrett, 1974; Stewart, 1985; Emerson, pers. observ.).

We assessed the functional significance of the characteristic morphological features of flying species by adding each flying modification separately to a nonflying model and recording the effect on lift and drag. The morphological features thus tested were elongated body, enlarged hands and feet with full webbing, and arm and leg flaps (Fig. 1C). We also simultaneously added flyer hands, feet, and flaps to the nonflyer body. We did not construct or test frogs intermediate in morphology between flying and nonflying forms because no such morphology exists among the living species of the Rhacophoridae.

Kruskal Wallis (K-W) (Sokal and Rohlf, 1981) tests were used to test for an overall effect of morphology and limb position on each of the four aerodynamic performance measures.

#### *Static Stability*

Using a technique similar to that of Wootton and Ellington (1988), we assayed the relative static stability of flyer and nonflyer models in several postures by observing whether they tumbled when descending freely through the air.

Whether an airborne animal or model tumbles depends on the position of its center of mass relative to its centers of lift and drag (e.g., Saunders, 1977). If the distribution of mass in a model frog mimics that of



TABLE 1. Field performance of living frogs.

Species	N	Mean maximum horizontal distance $\pm$ 95% C.I. (range)	Mean $\theta$	Lowest $\theta$	Range of airspeeds (m/sec)
"Flying" frogs					
<i>Rhacophorus pardalis</i>	10	9.9 $\pm$ 3.78 (0.6–18.0)	43°	33°	3.6–5.3
<i>Rhacophorus nigropalmatus</i>	8	15.7 $\pm$ 9.91 (2.3–29.3)	37°	25°	4.2–5.8
Pooled nonflying species*	8	5.9 $\pm$ 3.63 (0.8–13.7)	69°	60°	5.7–6.2

\* *Polypedates macrotis*, *Polypedates leucomystax*, *Rhacophorus rufipes*.

the prototype real frog, then the shift in the position of the center of mass that is produced by a given postural change will be the same for both. We assessed the distribution of mass in models and in the preserved frogs on which they were based by weighing isolated components (e.g., a foot, a leg) of each. We found that the fraction of total body weight represented by each of these various components did not differ by more than 1 to 2% between the model and the prototype.

Models of flying and nonflying morphology were gently thrown (belly down) horizontally from a platform 5.25 m in height such that their average flight speed (length of descent path/[time aloft]), 5.7 m/sec (SD = 0.68,  $N = 225$ ), fell within the range of speeds measured in field tests with living frogs of both species (Table 1). Each morphology was tested 15 times in each of three limb positions: bent, extended, and elevated. Flight distance was measured with a tape measure to the nearest 0.01 m, time aloft was measured to the nearest 0.1 s with a stopwatch, and frog orientation upon landing was noted. Average distance traveled and time aloft for each treatment did not vary by more than 14% and 13% respectively. For each trial we also recorded whether the model tumbled in pitch (body rotating in a vertical plane with its nose moving up or down), roll (body rotating in a vertical plane about its long axis), or yaw (body rotating in a horizontal plane with its nose swaying to the left or right).

In the field, "flying" frogs were observed to begin gliding only after first parachuting some vertical distance, and nonflyers were observed only to parachute (Abdulali and Sekar, 1988; Emerson, pers. observ.). In our model trials we were interested in comparing relative stability of the two morphologies and three postures under similar conditions. We therefore chose glide angles in

the parachute range (greater than 45°) for the stability tests. The "flying" frog model had an average glide angle of 48° with a range from 44–59°. The nonflying frog model averaged a 51.5° glide angle with a range from 46–67.5°. The effects of posture and morphology on each of the four aspects of stability (pitch, roll, yaw, and landing orientation) were examined separately using log linear analysis (Sokal and Rohlf, 1981).

## RESULTS

### *Field Performance Tests: Flyers vs Nonflyers*

Both parachuting and gliding were observed in the "flying" frogs during field trials. On occasion, both species of flyers executed bank turns of up to 180° while gliding. In contrast, nonflying frogs were never observed to glide (Table 1) or turn during aerial descent. Once launched, "flying" frogs always placed their hands and feet in the bent position lateral to the body. Nonflying frogs usually assumed the bent limb position during descent, but on occasion left the legs partially extended behind the body.

The performance of individual frogs (both flyers and nonflyers) was highly variable from trial to trial. However, because we are examining how the flyer morphology might extend the range of possible performance for a falling frog, we consider the maximum (rather than the average) performance shown by each individual. As expected, nonflying frogs have a steeper angle of descent and travel shorter horizontal distances than "flying" frogs (Table 1). Overall, "flying" frogs take longer to descend than nonflying individuals of the same mass. Interestingly, this difference holds even when both morphologies are parachuting and travel roughly the same horizontal distance [mean maximum time aloft 2.90 sec for *Rhacophorus*

TABLE 2. Performance of models in wind tunnel.

Morphology	Performance variable [mean + (range), $N = 3$ ]			
	$(L/D)_{\max}$ : horizontal traveling performance	$U_{\min}$ : minimum glide speed [m/sec]	$D_{90}$ : parachuting performance [N]	$(C_L/W)_{\max}$ : turning performance [ $(m^2/N) \times 10^{-3}$ ]
Nonflyer*	1.21 (1.17–1.28)	12.23 (12.19–12.25)	97.8 (96.9–98.4)	11.1 (11.1–11.2)
Flyer*	1.53 (1.52–1.54)	8.98 (8.94–9.01)	116.20 (114.9–117.0)	20.6 (20.5–20.8)

\* Both models were in the bent posture (illustrated in Fig. 3).

*nigropalmatus* (flyer,  $N = 7$ ) vs 1.86 sec for similar sized *Polypedates macrotis* (nonflyer, 4);  $t = 7.03$ ,  $df = 9$ ,  $P < 0.0005$ ].

#### Wind Tunnel Performance Tests: Flyers vs Nonflyers

Table 2 compares the performance of models of nonflying and “flying” frogs in the wind tunnel at their natural airspeeds (6.1 m/sec and 4.5 m/sec respectively, Table 1). (We tested all models at both velocities. All the differences between a flyer and nonflyer discussed below are even more pronounced if the two morphologies are compared at the same velocity.)

The horizontal distance traveled by a glider is proportional to the lift to drag ratio ( $L/D$ ). Flyers have greater  $(L/D)_{\max}$  because they have higher lift at low angles of attack ( $\alpha$ ) (Fig. 2A). As a consequence, “flying” frogs, on the average, travel longer horizontal distances than nonflying frogs during aerial flight (Table 1). Conversely, at high angles of attack the “flying” frog produces more drag (Fig. 2B). Consequently, “flying” frogs take longer on average to descend when parachuting ( $\alpha = 90^\circ$ ) than nonflyers.

#### Behavior and Performance

Figure 3 shows the effects of limb position on aspects of aerial performance for the “flying” frog. Limb position significantly affects each performance variable (all  $H = 7.20$ ,  $P < 0.02$ ), but different limb positions produce the highest values for each performance variable. The extended limb position results in the highest  $(L/D)_{\max}$  (corresponding to a coefficient of lift,  $C_L$ , of 0.20). In contrast, behaviorally switching to the bent position results in the lowest minimum glide speed ( $U_{\min}$ ) and the best turning performance [ $(C_L/W)_{\max}$ ] (both corresponding to a  $C_L$  of 0.53), as well as the best parachuting performance ( $D_{90}$ ). Changing hand or foot angle can also simultaneously improve some

aspects of performance, worsen others, and leave some unchanged. For example, if a “flying” frog (with flat hands and feet) in the bent limb position tilts its legs so that its feet are at an  $\alpha$  of  $30^\circ$  to the body, its horizontal travel, parachuting, and turning performance are all worsened ( $(L/D)_{\max}$  is reduced by 22%,  $D_{90}$  by 11%, and  $(C_L/W)_{\max}$  by 19%), whereas its minimum glide speed is somewhat improved ( $U_{\min}$  is lowered by 6%).

#### Morphology and Performance

Morphology, like limb position, can have a significant effect on each measure of performance ( $H$  statistic for K-W tests 13.2–13.5; all  $P < 0.02$ ), and different aspects of morphology maximize each of the performance variables (Fig. 4). Enlarged fully webbed hands or feet increase  $(L/D)_{\max}$  similarly (Fig. 4A). In contrast, neither flaps nor body form have a significant effect on  $(L/D)_{\max}$ . Note that *changing* limb position (“behavior,” in Fig. 3A) has as large an effect on  $(L/D)_{\max}$  as does changing morphology.

Enlarged hands or feet lower (improve) minimum glide speed ( $U_{\min}$ ) (Fig. 4B) more than does a change in limb position (Fig. 3B). Flaps slightly worsen  $U_{\min}$ , whereas body form has no effect on minimum glide speed.

Enlarged, webbed hands and enlarged, webbed feet are the morphological features that most affect the drag experienced by a frog parachuting at  $\alpha = 90^\circ$  (Fig. 4C). However, body form has a surprisingly large influence on drag as well. Skin flaps also increase the drag, but to a much smaller degree. Whereas altering limb position (Fig. 3C) also can change the drag, morphology has a much larger effect.

Although skin flaps and body form do not improve turning performance, enlarged hands and feet do (Fig. 4D). Changing limb

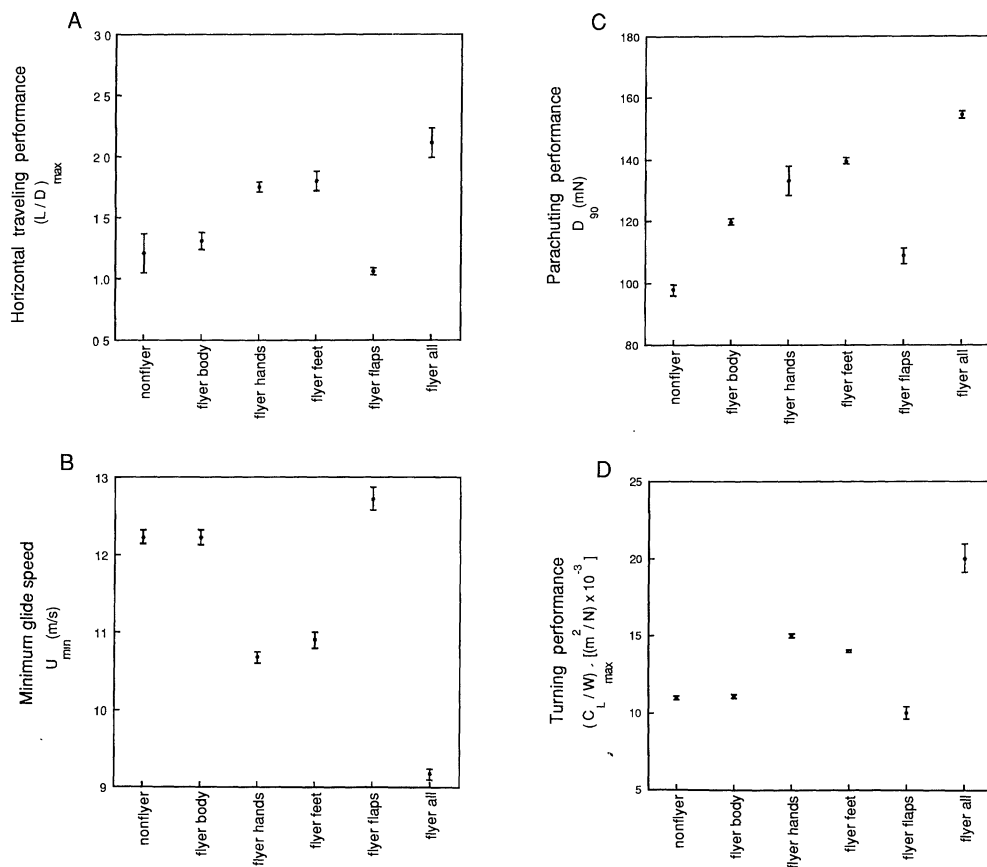


FIG. 4. Flight performance of models with different morphologies in the bent posture (see Fig. 3) at an airspeed of 6.1 m/sec: nonflyer = model of actual nonflying frog; flyer body = model constructed from the body of a flying frog whose hands and feet are replaced by those of a nonflyer and whose skin flaps are removed (to test effects of body shape alone); flyer hands = nonflyer whose hands are replaced by those of a flying frog (to test effects of large, fully-webbed hands alone); flyer feet = nonflyer whose feet are replaced by those of a flying frog (to test effects of large, fully-webbed feet alone); flyer flaps = nonflyer bearing on its arms and legs the skin flaps of a flying frog (to test effects of skin flaps alone); flyer all = nonflyer whose hands and feet are replaced by those of a flying frog and whose arms and legs bear flyer skin flaps (to test effects of all these flyer features together). Error bars indicate 95% confidence intervals. A) Horizontal traveling performance,  $(L/D)_{max}$ . B) Minimum glide speed,  $U_{min}$ . C) Parachuting performance,  $D_{90}$ . D) Turning performance,  $(C_L/W)_{max}$ .

position (Fig. 3D), however, can enhance turning performance almost as much as the enlargement of hands *or* feet alone (although enlargement of both simultaneously has a much greater effect than does limb position).

#### *Consequences of Limb Position for Different Morphologies*

Limb position appears to have a larger effect on some aspects of performance when coupled with the nonflying morphology ver-

sus the flying morphology (Fig. 5). In other words, for horizontal travel  $[(L/D)_{max}]$  and turning performance  $[(C_L/W)_{max}]$ , the flying morphology renders a frog less sensitive to the changes in limb position we tested. Morphology can also determine the *direction* in which a behavioral shift in limb position alters performance. For example, a change from the extended to the bent limb position reduces  $D_{90}$  in the nonflying morphology, but increases it in the flying morphology (Fig. 5C). Only in minimum glide speed did

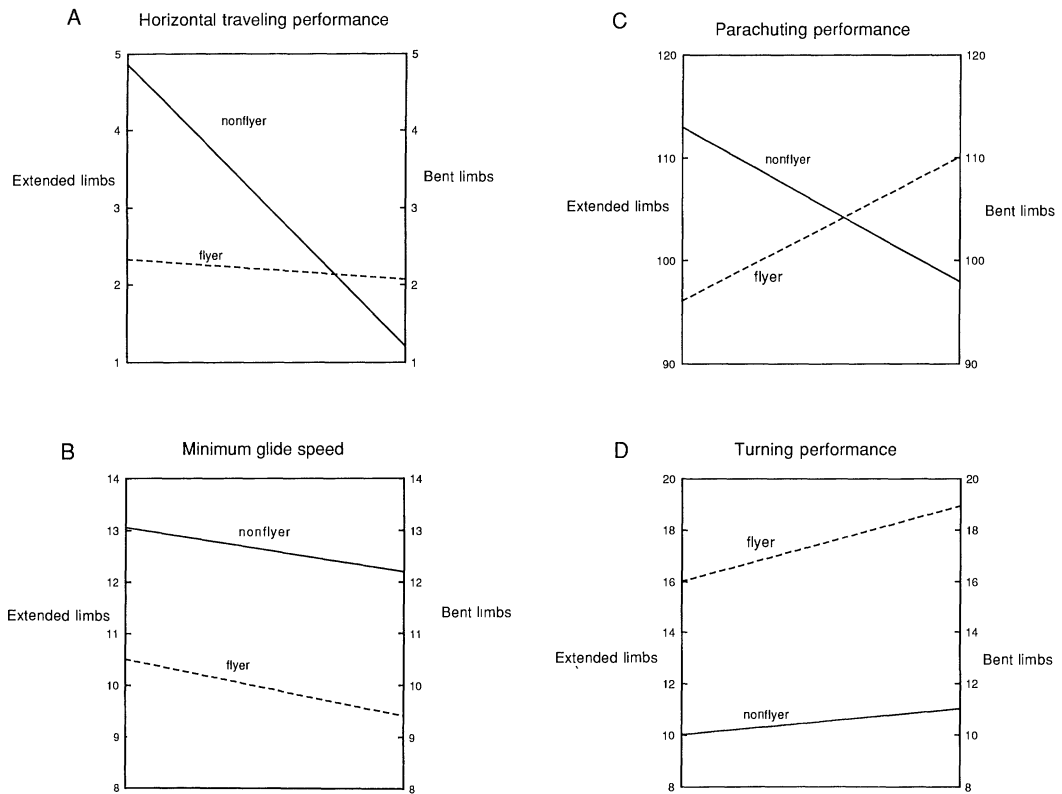


FIG. 5. Diagrams showing the effects of bent or extended limbs on the performance of flying and nonflying morphologies. The nonparallel lines indicate that there is a morphology-specific effect of limb position on the performance variables.

behavioral changes in limb position have similar effects on both the flying and nonflying morphologies (Fig. 5B).

#### Static Stability

The proportion of falls in which a model does not tumble is a rough indicator of its static stability relative to other models. The tumbling in pitch, roll, and yaw of models of "flying" and nonflying frogs in various postures is summarized in Table 3. If the number of falls in which a tumble occurs are rank ordered for both morphologies in all postures, the flyer tumbles in pitch significantly more than the nonflyer (Mann-Whitney-Wilcoxon (Gibbons, 1976), one-tailed,  $P = 0.027$ ), although the two morphologies do not differ significantly in yaw. Another indication that the nonflyer shows a higher degree of static stability than the flyer is that the nonflyer lands right-side-up

(on its belly) significantly more than does the flyer (Mann-Whitney-Wilcoxon, one-tailed,  $P = 0.0425$ ).

Log linear analyses reveal significant overall effects of both posture and morphology on landing position, and on the tendency to yaw or pitch (Table 4). Posture, but not morphology, has a significant effect on the tendency to roll. In all cases posture had a stronger effect on static stability than did morphology, and in no case did morphology and limb position show a significant interaction (Table 4).

#### DISCUSSION

##### *Functional Significance of "Flying" Morphology*

The major morphological features that distinguish "flying" from nonflying frogs are: 1) full webbing on the hands and feet; 2) enlarged hands and feet; and 3) additional

TABLE 3. Tumbling performance of "flying" and nonflying frog models.

Type of tumbling	Extended legs		Bent legs at 90°		Bent legs, hands & feet close to body		Elevated legs	
	Flying	Nonflying	Flying	Nonflying	Flying	Nonflying	Flying	Nonflying
Pitch	15*	15	13	0	10	1	5	7
Roll	8	7	1	2	10	1	0	0
Yaw	3	6	7	14	11	14	14	14
Belly landing	0	1	12	13	6	15	15	15

\* Number of trials in which a particular type of tumbling occurred; total number of trials (15).

flaps of skin on the arms and legs (Inger, 1966; Emerson, pers. observ.). To a large degree, the wind tunnel experiments verify the expected: the increased plan area of these modifications reduces the "wing" loading ( $W$ , eq. 2) for animals in the bent flying posture, and 1) improves the lift/drag ratio or horizontal traveling distance; 2) lowers the minimum speed required to glide; 3) increases the drag at  $\alpha = 90^\circ$  and hence lowers force of impact and raises time aloft during parachuting; and 4) reduces the turning radius (Table 2).

The skin flaps on the arms and legs of "flying" frogs comprise only a small percent of the total plan area (e.g., 3.8% for our model), and their functional significance has been somewhat of an enigma. These flaps are particularly intriguing because small protuberances and ridges occur at a variety of body locations among nonflying species of Rhacophoridae (Inger, 1966). Our data

indicate that the presence of skin flaps results in a small but significant increase in drag. Accordingly, protuberances and ridges in nonflying species may represent exaptations (sensu Gould and Vrba, 1982) for aerial locomotion.

#### *Interaction of Morphology and Behavior in the Evolution of "Flying" Frogs*

One assumption of most models for the evolution of new adaptive types is that behavioral change is not morphology-specific in affecting performance. Our results strongly contradict that assumption. Limb positions that improve the performance of one morphological type can worsen the performance of another (Fig. 5). Bending the limbs significantly worsens both the parachuting performance and horizontal travel of the nonflyer, but markedly improves the parachuting of the flyer while having little effect

TABLE 4. Log likelihood statistics and significance values of log linear analyses on the interaction of morphology, limb position, and performance.

Interaction	G-value	Significance
I. Pitch		
morphology · performance	19.43	$P < 0.005$
morphology · limb position	5.68	$P > 0.200$
performance · limb position	49.97	$P < 0.005$
II. Roll		
morphology · performance	4.80	$P < 0.05$
morphology · limb position	1.07	$P > 0.800$
performance · limb position	33.26	$P < 0.005$
III. Yaw		
morphology · performance	11.36	$P < 0.005$
morphology · limb position	3.67	$P > 0.300$
performance · limb position	40.34	$P < 0.005$
IV. Belly landing		
morphology · performance	11.62	$P < 0.005$
morphology · limb position	7.20	$P > 0.06$
performance · limb position	91.33	$P < 0.005$

on its horizontal travel. Conversely, bending the limbs improves (lowers) the minimum glide speed of the nonflyer, but has little effect on that of the flyer (Fig. 5). Turning index is the only performance variable altered in the same direction by both the nonflyer and the flyer when a behavioral shift to the bent limb position occurs. Thus, although a range of limb positions were observed in the field for both nonflying and "flying" frogs, these postures interact differently with the two morphologies. Kingsolver (1988) found a parallel situation in butterflies where the consequences of the changes in color pattern were behavior-dependent.

A second assumption of most models for the evolution of new adaptive types is that behavioral changes generally precede morphological shifts, but both types of changes are in the same direction along a particular performance gradient. Again, our results contradict that assumption. The actual historical transformation (sensu Lauder, 1981) that occurred in the evolution of the "flying" frog *Rhacophorus nigropalmatus* cannot be determined at this point because we lack a phylogenetic hypothesis for this species and its relatives. However, because no intermediate morphologies exist between flying and nonflying forms, we can use these two endpoints to examine the possible order and interaction of morphological and behavioral change in the evolution of "flying" frogs. If we assume that the nonflying morphology and extended limb position (the posture shown by all frogs when they begin to jump) represent the primitive condition and the flying morphology and bent limb position to be derived, the performance consequences of changing only limb position, only morphology, or both posture and morphology together are different, discontinuous and unpredictable (Table 5, Fig. 6).

The ability of animals to cover longer horizontal distances is often mentioned as the biologically most important performance parameter in the evolution of "flying" frogs. Yet, gliding performance is decreased both by the flyer morphology alone and by the bent limb position alone, hence neither change by itself could lead to improved gliding. Coupled morphological and behavioral change decreases gliding perfor-

TABLE 5. The effects of behavioral and morphological change on performance capability.

Condition	Performance parameter*				Stability and landing position
	Horizontal gliding performance ( $(L/D)_{max}$ )	Parachuting performance ( $D_{90}$ )	Turning performance ( $(C_L/W)_{max}$ )	Minimum glide speed ( $U_{min}$ )	
Nonflying morphology with a behavioral shift to bent limb position	large decrease	small decrease	small increase	small decrease	stable in pitch, land right-side-up
Extended limb position with a morphological shift to the flying morphology	moderate decrease	large increase	large increase	moderate decrease	unstable in pitch, land upside down
Morphological and behavioral shifts to the flying morphology and bent limb position	small decrease	large increase	very large increase	large decrease	unstable in pitch, land right-side-up

\* Measured relative to the performance of a nonflying morphology in the extended limb position.

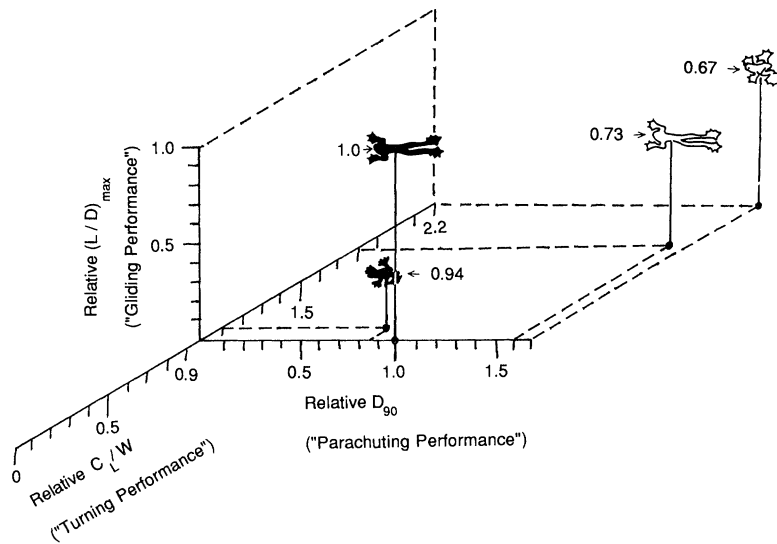


FIG. 6. Three-dimensional representation of the performance capability of frogs with: 1) nonflying morphology (black frog) in the extended limb position; 2) nonflying morphology (black frog) in the bent limb position; 3) flying morphology (white frog) in the extended limb position; and 4) flying morphology (white frog) in the bent limb position. The mean value for a performance parameter (at 6.1 m/sec) is divided by the mean value of that parameter for the nonflying morphology in the extended limb position (the "primitive" state) to yield a relative performance value. A relative performance value  $> 1$  indicates improved performance, and  $< 1$  indicates worsened performance for  $D_{90}$ ,  $(L/D)_{\max}$ , and  $(C_L/W)_{\max}$ . The numbers next to the circles indicate the relative  $U_{\min}$  for each morphology plus posture. In contrast to the other relative performance variables, a relative  $U_{\min} > 1$  indicates worsened performance and  $< 1$  indicates improved performance relative to the "primitive" state. All performance variables are significantly different from those of the primitive condition.

mance least, but there is still a loss of ability relative to the primitive condition (Fig. 6). In contrast, turning performance improves with either behavioral or morphological change alone. Furthermore, with a combined behavioral and morphological shift, the magnitude of improvement is greater than the sum of the effects of each of the changes acting alone (Fig. 6). Also, the possible importance of maneuverability rather than horizontal distance to "flying" frogs is consistent with the natural history of *Rhacophorus nigropalmatus*. This species occurs high in the canopy of primary rain forest in Borneo (Inger, 1966), but breeding takes place on the ground around water holes and wallows made in the forest by large animals and fallen trees (Emerson, pers. observ.). Maneuverability would be a definite advantage in negotiating the spatially complicated but relatively open understory of the Bornean rain forest (Emmons and Gentry, 1983).

Behavioral or morphological change alone affects two performance parameters, para-

chuting ability and stability, in opposite ways, rather than in the same direction as would be expected if morphological changes enhance the effects of behavioral innovations (Table 5). These opposite effects make it impossible to predict a priori the results of coupled morphological and behavioral change on parachuting and stability.

The increased stability that results from only a behavioral shift may explain why nonflying frogs usually place their limbs in a bent position during descent. The unlikelihood of a flying morphology in the extended limb position of landing right-side-up may explain why that combination has never been observed in living frogs. Interestingly, only a combined morphological and behavioral shift maximizes turning during a glide while retaining the ability to land right side up (Table 5).

A behavioral shift to the bent limb position permits nonflying frogs to parachute more "safely"—reducing the force of impact slightly as well as improving stability (Table 5, Fig. 6). Many arboreal frogs make

daily vertical movements for feeding, breeding, and locating resting sites (Stewart, 1985, and references therein). Given this vertical migration, parachuting rather than walking or hopping down a tree trunk should certainly lower the predator encounter rate for a frog. Frog predators such as snakes and large arthropods are common in trees. Some data also suggest that parachuting down and climbing up a tree is energetically less costly than climbing both up and down (Stewart, 1985). The fact that a behavioral shift alone improves parachuting performance may help to explain why this form of vertical locomotion has evolved independently so many times among nonflying frogs (Stewart, 1985).

To conclude, this study demonstrates that behavioral and morphological shifts do not necessarily affect the same performance variables or change them in the same way. Knowledge of the function of a particular limb position or morphology alone does not always allow a prediction of performance when behavioral and morphological changes are coupled. Behavioral shifts show a morphology-specific effect on performance. Our data suggest that the general model for the evolution of new adaptive types—a sequence of initial behavioral changes amplified by subsequent morphological shifts—should be considerably elaborated. In its present form, this simple model largely overlooks the potential complexity of morphological and behavioral interactions in producing change.

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