**The gliding ability of *Agalychnis spurrelli*
(Anura: Hylidae) and the significance of size and
morphology.**

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Abstract

Morphological features were measured and flying ability tested in adult and juvenile *Agalychnis spurrelli* treefrogs. Like most anurans this species displays geometric isometry and in this respect therefore shows no particular specialization for gliding despite exhibiting other morphological adaptations such as highly pronounced webs. No correlation between size and distance was found and frogs show a positive correlation between size and speed, however the behaviour witnessed is a significant improvement on systems acting under freefall, therefore whilst not adequately equipped to glide, mechanisms facilitating parachuting are clearly in operation.

Polarization of the Costa Rican/Panamanian population into two distinct size morphs and the marked sexual dimorphism exhibited by both these morphs suggest that size is influenced by a multitude of selection pressures. Although the exact nature of these driving forces is as yet unclarified, these results implicate locomotor function as a potentially important candidate. Increasing size produces a consequent improvement in stability and control, which in all observed "flying" forms apparently prevails over the distance advantages of small size (the latter evident from the high relative jump distances seen in juveniles). Both adults and juveniles consistently adopt a stereotyped gliding posture which again emphasizes the importance of stability in development of this locomotor mechanism, supporting previous studies.

Introduction

Species description

Agalychnis spurrelli, first described by G.A. Boulenger (*1913*), is a large hylid treefrog of the subfamily Phyllomedusinae. Along with the characteristic vertical pupil common to the other seven *Agalychnis* species, *A. spurrelli* also exhibits the typical nocturnal and highly arboreal habits of the genus. It is distinguished by its dark maroon eyes, distinctive white spots on the dorsum, uniform cream/yellow ventral surface and large, extensively webbed hands and feet. Of all the *Agalychnis* species, *A. spurrelli* has the most pronounced webs and it is unusual amongst treefrogs in that development of the webbing is even evident pre-metamorphosis (see figure 1) (*Gray, 1997, Duellman, 1970, Noble, 1931*).

Newly metamorphosed froglet: note the distinctive dorsal spot pattern and webs already present on both the hands and feet.
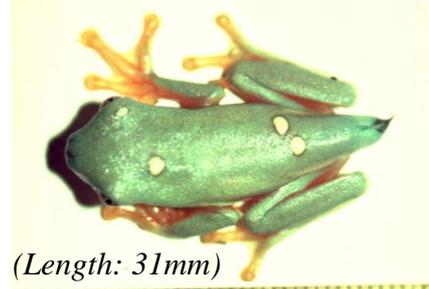
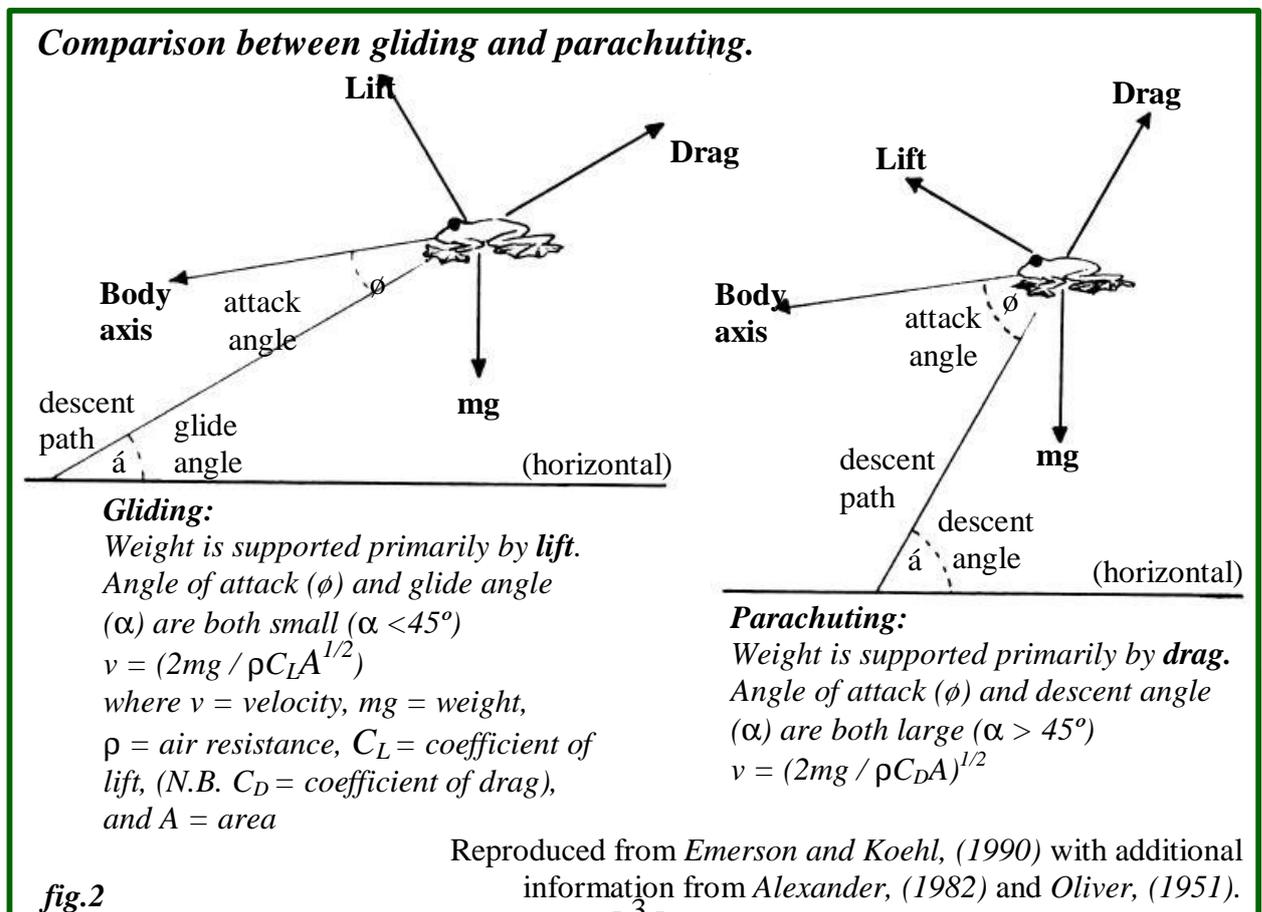*(Length: 31mm)*

Photo courtesy of A.Gray

fig.1

It is found in the humid forests of the Pacific and Caribbean lowlands of Southern Costa Rica, through Panama and into the Pacific lowlands of Colombia. As a consequence of its restriction to altitudes below 885m, the Caribbean and Pacific populations are apparently isolated from one another by the central Talamanca Chiquiri mountain range and as a result exhibit a number of significant differences in morphology and life history. One of these is a marked size discrepancy: Caribbean individuals are anything from 14 to 100% larger, with males ranging from 67.6 to 75.6mm compared with 46 to 54.5mm, and females from 81.5 to 95mm compared with 47.2 to 71.8mm. They also have considerably more extensive webbing and display distinct differences in larval characteristics and colouration. (*Gray, 1997, Cochran & Goin, 1970, Duellman, 1970, Savage & Heyer, 1967*). These factors, in combination with their very distinct calls, have even led to the suggestion that the two are different subspecies. (*Gray unpubl. obs.*).

As is typical of the genus, breeding occurs near temporary or permanent ponds and swamps and eggs are laid on leaves overhanging the water into which they drop on hatching. Two breeding strategies are apparent, probably dependent on the

permanency of the water supply. "Prolonged breeding" occurs at permanent sites and involves constant, relatively low densities, particularly of males. "Explosive breeding" has been observed at temporary water sources (*Scott & Starrett, 1974*). It involves rapid aggregation of huge numbers of frogs (an estimated 13000 at one pond approximately 50m by 70m) and frenetic ("scramble") competition for partners. It is primarily during these breeding aggregations that parachuting/gliding have been observed in this species. The behaviour enables rapid aggregation of individuals from different levels in the canopy up to 10m and above, with the densest congregations occurring at 1.5 to 3m above water level. During descent females in particular have been observed to alter their course by at least 35°, gliding down towards the pool then turning at a height of about 2m and steering onto the bank.

Gliding behaviour

Gliding was first reported by Wallace in the morphologically similar Old World Rhacophorid species *Rhacophorus nigropalmatus,* (as cited by *Saville, 1962)*, and parachuting was subsequently described by Cott (*1926*) in *Hyla venulosa* (now *Phrynohyas venulosa*). Oliver (*1951*) later defined gliding and parachuting in terms of angle of descent (see figure 2).

Comparison between gliding and parachuting.

Gliding:
*Weight is supported primarily by **lift**.*
Angle of attack (ø) and glide angle
(α) are both small (α <45º)
$v = (2mg / \rho C_L A^{1/2})$
where v = velocity, mg = weight,
ρ = air resistance, C_L = coefficient of lift, (N.B. C_D = coefficient of drag), and A = area

Parachuting:
*Weight is supported primarily by **drag**.*
Angle of attack (ø) and descent angle
(α) are both large (α > 45º)
$v = (2mg / \rho C_D A)^{1/2}$

Reproduced from *Emerson and Koehl, (1990)* with additional information from *Alexander, (1982)* and *Oliver, (1951)*.

fig.2

A gliding animal is dependent on lift which requires a low angle of attack, whereas parachuting is dependent on drag and optimised by a high angle of attack (*Emerson & Koehl, 1990, Emerson et al, 1990*).

In both cases performance is dependent on a complex of morphological features, with only posture producing a significant improvement when varied independently of the rest. Fliers and non-fliers display large discrepancies in ability; fliers tend to travel much greater horizontal distances at lower descent angles, and generally fall more slowly, even when parachuting or travelling the same horizontal distance as a non-flier. Impressive turning capabilities have also been observed in certain fliers: *R.nigropalmatus* for example is able to execute turns of up to 180°. Manoeuvrability is enhanced by both enlargement of either the hands or feet and by modification of posture, and is evidently a highly significant feature of gliding. This may relate to function and the complex structure of the environment in which the species is found (*Emerson and Koehl, 1990*).

Various functions of gliding have been suggested including both pursuit of aerial prey and escape; aggregation for rapid exploitation of optimum breeding conditions as described above; and prevention of injury on landing from high falls (*Emerson & Koehl 1990, Saville 1962, Pough et al 1998*). It is also a rapid and energetically inexpensive form of horizontal and vertical travel and potentially highly advantageous considering the level of discontinuity in the arboreal substrate.
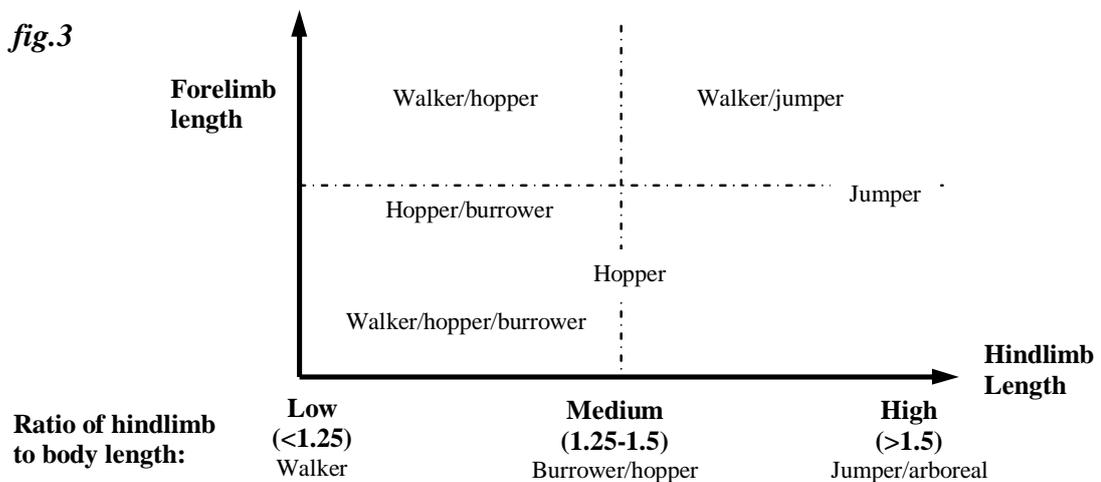
Adaptations for gliding

Many of the adaptations which have predisposed certain frogs to a predominantly saltatory mode of locomotion equally potentiate gliding behaviour.

The most important factor in take-off, both when jumping and gliding, is thrust. Jumpers have particularly elongated hind limb bones (femur, lower leg, astragalus, calcaneum, and hind foot) to provide thrust, and horizontal distance jumped correlates roughly with limb length. In addition approximately 60% of the leg musculature is comprised of pinnate muscles which exert a much greater force than ordinary muscles relative to the distance and speed at which the insertion points move. In small animals another source of energy is that stored in the elastin components of the tendons and ligaments. In frogs this energy is stored in the legs and iliosacral joint when these are placed under tension by adopting the jump

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position (*Calow & Alexander, 1973*). In *Agalychnis* the sacral diapophyses are broadly expanded and enveloped in a wide external ligament which runs from one ilium to the other superficially to the dorsal back musculature (known as a type I iliosacral joint complex) This allows considerable movement of the ilia in the horizontal plane thereby providing thrust (*Emerson, 1982, Griffiths, 1963*). Pelvic sliding is restricted in the vertical plane however (*Emerson, 1978*), which presumably contributes to maintenance of balance by preventing rotation. Streamlining is maintained by continued extension of the limb extensors even after full contraction and take off. This may also therefore contribute to maintenance of posture and balance in flight.

The importance of reducing the force with which the body hits the landing surface is augmented in gliding due to the greater heights involved. All anurans have a greatly reduced skeleton: the ribs have become vestigial as a result of the massive development of the ventral abdominal musculature and in *Agalychnis* species are lost altogether. The vertebral column is short and rigid as a result of compression of the notochord by inward bending of the invertebral discs during metamorphosis, and is strengthened against the muscles involved in jumping by the urostyle (*Macbride 1932*). The limb girdles, which articulate with the vertebral column via moveable diapophyses, are sturdy and well-ossified for dissipation of the compressive force transferred on to them on landing. (*Pough et al, 1998, Zug, 1993, Emerson 1984*). Strong jumpers tend to have moderately short scapulae and forelimbs with large forefeet for shock absorption. The chest and abdomen are also probably involved in shock absorption (*Zug, 1972*).

fig.3

Forelimb length

Walker/hopper   Walker/jumper

Hopper/burrower   Jumper

Hopper

Walker/hopper/burrower

Hindlimb Length

Ratio of hindlimb to body length:

Low (<1.25)	**Medium (1.25-1.5)**	**High (>1.5)**
Walker	Burrower/hopper	Jumper/arboreal

Emerson (1978 & 1988(b))

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Locomotor mode in frogs is influenced principally by limb proportions according to figure 3, and as one of the most arboreal genera, adapted primarily for

walking and jumping, for certain *Agalychnis* species gliding/parachuting was probably only a small step evolutionarily.

The existence of 'flying' forms is the result of the co-evolution of a complex of additional morphological and behavioural factors which has resulted in the improvement of four main flight performance characteristics:

1. Increased horizontal distance.
2. Reduced minimum glide speed (i.e. the speed that must be attained before gliding can occur).
3. Increased drag during parachuting, therefore increased time aloft and reduced force of impact.
4. Improved manoeuvrability due to a reduced turning radius and a low static stability. (Non-fliers have never been observed to exert any control over their speed and direction whereas control of the body during flight is a highly significant adaptation of flying frogs). (*Emerson & Koehl, 1990, Alexander, 1982*)

'Flying' frogs display two major adaptations. Firstly the feet and hands are enlarged and extensively webbed, with webbing extending up to and beyond the base of each toe disc. The toe discs are about 1.5x the size of the tympanum and both the feet and hands show a substantial increase in size relative to increasing body size (see figure 4). More significantly, all flying frogs adopt a stereotyped gliding posture during flight (see figure 5), with the webs fully extended, and the legs and arms slightly bent, spread-eagled in the horizontal plane of the body, (described by *Inger, 1966*). Non-fliers

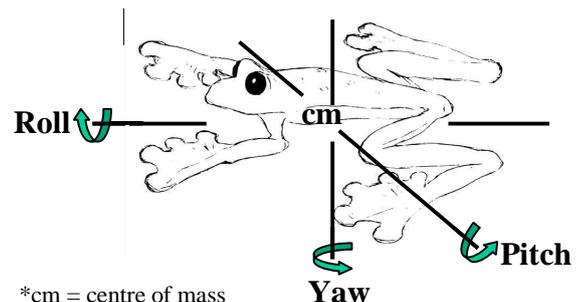*Life-size* diagrams of the foot (a) and hand (b) of an adult Agalychnis spurrelli showing the extensive webbing.*

(a)   *(b)*
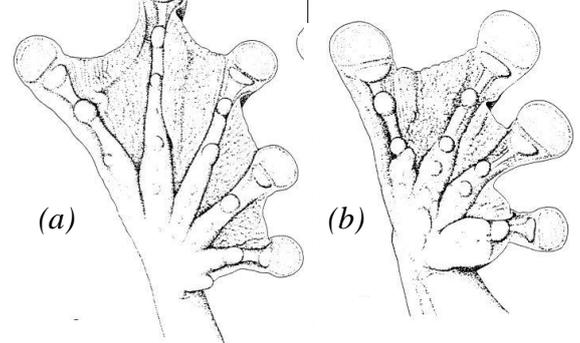
*for an adult female

fig.4   Reproduced from *Duellman (1970) p92&94.*

Gliding posture as described by Inger (1966) showing components of movement under control during flight.

Roll   cm

*cm = centre of mass   Yaw   Pitch

fig.5   Based on Inger (1966) & Caple *et al* (1983)

occasionally adopt this position, but tend to leave the legs fully extended in the taking off position.

In addition, *R.nigropalmatus*, which is thought to be the most proficient anuran parachutist, has prominent skin flaps around the edge of the body and the outer edges of the limbs. These are not present in *A. spurrelli*. Certain Rhacophorids also display a reduction in weight relative to body length which improves the aero-dynamicity by decreasing the wing-loading (*Liem 1970*).

Consideration of these factors independently highlights their marked nonadditivity, i.e. the overall improvement resulting from modification of these characteristics is much greater than the sum of the individual effects, emphasizing their synergism. Almost as crucial as the interplay of morphological factors is the interaction between morphology and size. This in itself is not remarkable; the paradox is that although size is the most important determinant of drag, the performance of large animals is significantly poorer than predicted whilst that of animals smaller than 25mm (particularly in terms of horizontal distance) is distinctly superior to that predicted. This therefore implies that gliding forms are most likely to be small whereas actually they are, in all groups, the largest representatives (*Emerson & Koehl, 1990*), and typically between 75mm (e.g.*Boophis* species) and 100mm (e.g. *Rhacophorus* species) (*Liem 1970* and see below).

Effects of size

'Flying' behaviour has evolved independently in a couple of species of New World Hylids e.g. *Hyla miliaria*, (*Duellman 1970*), and several genera of Old World Rhacophoridae: *Rhacophorus* in Malaysia; *Boophis* in Madagascar; and *Polypedates* in Southern China and the Philippines, (*Liem 1970*). The recurrence of morphological variants in different family groups is a common phenomenon in anurans which do not exhibit the increase in morphological diversity with taxonomic level typical of most animal groups (*Emerson, 1988(b), Zug, 1978*). This was initially thought to be a restriction imposed by the reduction of the anuran skeleton; however it is now generally held that the primary constraint is actually locomotor mode. Having evolved principally as jumping organisms, all frogs tend to have very similar morphologies despite their wide variation in ecologies.

Frogs are a fairly unique model for the study of variation in locomotor function with size as they maintain a fairly constant body shape over a wide size

range. Hill's model suggests that geometrically similar animals (such as frogs) should perform similarly regardless of size, for example, small frogs, whose muscles produce rapid acceleration over a short period of time should be able to jump as far as large animals whose muscles produce only slow acceleration, but have longer in which to do so. Intraspecifically, nearly all frogs exhibit strong external geometric isometry. The only exceptions are the newly metamorphosed frogs of a few species which undergo a period of allometric growth. This geometric isometry restricts speed of movement and jump distance with increasing size because relatively more power is required to produce the same acceleration. This would place large frogs at a disadvantage, as predator evasion is largely dependent on speed. However, frogs *do* jump further with increasing size despite decreasing relative jump distance (i.e. distance/bodyweight). Some species even manage to maintain constant acceleration with increasing size. Velocity increases with the distance through which the propulsive force acts which explains the slight positive correlation between hind leg length and jump distance, however this is not usually sufficient to account for the pronounced allometry in jumping performance (*Emerson, 1978, Bennet-Clark, 1977 and Alexander, 1971*).

Frogs are also unusual in that, intraspecifically, muscle mass, particularly that of the hind legs, scales isometrically, whereas most other animals violate Hill's model in this respect. The best possible explanations for the non-isometric scaling of muscular activity are therefore increased recruitment of muscle fibres in large frogs or different proportions of muscle types. Certainly the increasing energetic cost of maintaining constant acceleration requires increasing morphological specialisation and the severity of this metabolic cost is reflected in the low stamina of large frogs (*Bennet & Licht, 1974*).

The aims of this study are therefore to explore the interplay between morphology and size in relation to gliding ability, specifically:

- To investigate the relationships between different morphological characteristics of *A. spurrelli* to ascertain whether or not they conform to Hill's model.

- To determine how flying performance varies with changing size.

- To investigate the level of sexual dimorphism within the species and its effects on flying performance.

- To determine whether or not this species is capable of gliding according to the definition provided by Oliver (*1951*), and to investigate its proficiency with respect to other "flying" frogs.

- To study the growth of juveniles from the newly-metamorphosed tadpole stage, and in particular the development of the specific characteristics associated with gliding behaviour.

Methods.

Part 1. The adults.

The Animals:

Ten male and ten female adult *Agalychnis spurrelli* were selected from a group maintained in captivity at Manchester Museum under simulated natural conditions, originally collected in 2000 from a wild (Caribbean-type) Costa Rican population by A.R. Gray.

Morphological measurements:

A few days prior to the experiment the dimensions of each frog were measured as described below and the distinctive dorsal spot pattern was drawn for identification purposes.

- SVL (snout to vent length) was measured using Digimax® digital callipers whilst the frogs were resting on a flat surface.

- Leg length was measured using Digimax® digital callipers from the top of the leg to the tip of the longest toe (the middle toe).
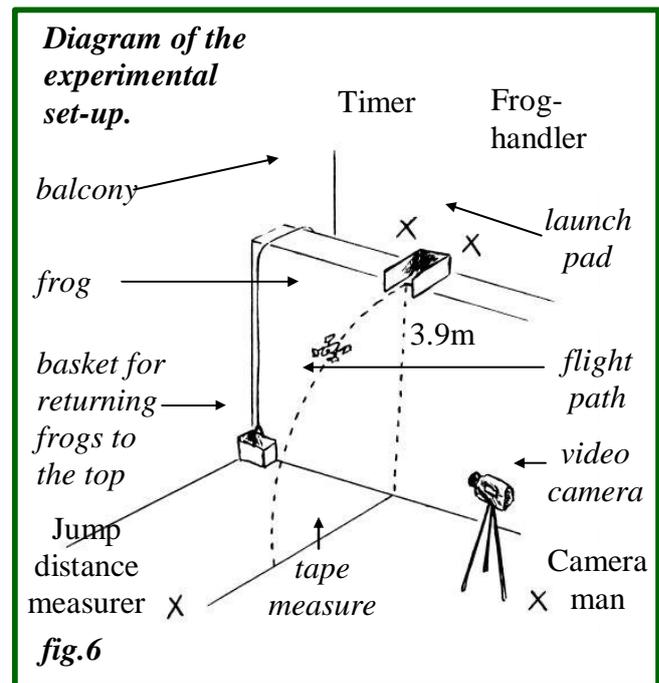
- Web area: Two drawings were made of *each* outstretched hind foot on acetate whilst the frog was stuck to a glass pane, measured using 2mm square graph paper and an average determined for a single foot.

The following day the animals were weighed both before and after urination. Relative wingloading was determined from Body mass/Area of one hind foot.

Linear regression analysis of log-log data was carried out to determine whether or not the frogs showed allometry of morphological features; a t-test was performed on the gradients of the graphs produced in order to establish if the scaling displayed was significantly different to isometric scaling. (N.B. All data analysis was carried out using SPSS version 10.1 for Windows).

The setting:

A squash hall was lined with 2cm thick foam mats and three layers of plastic sheeting. A tripod and video camera were set up approximately 4m from and perpendicular to the predicted flight path, and using a trial jump was angled in order to film the largest section of the descent possible. A launch pad constructed from a 15x25cm open box was placed about 2m from the side wall (in order to discourage jumping to the side) on

Diagram of the experimental set-up.

Timer   Frog-handler

balcony

frog

basket for returning frogs to the top

Jump distance measurer

launch pad

3.9m

flight path

video camera

Camera man

tape measure

fig.6

the balcony overlooking the court, with the sides extending about 10cm over the edge of the drop to restrict the side view and encourage jumping in a straight line. A tape measure was hung vertically from the launch pad to the floor to measure the vertical jump distance (a height of 3.90m), and all horizontal jump distances were measured from this point at the base of the wall. (See Figure 6.)

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The experiment:

Frogs were encouraged to jump by stroking their hind legs, tapping their vent, or tapping the box behind them. Each was made to jump four times in succession, each time being returned to the top of the wall using a basket tied to a piece of string. Whilst not involved in the experiment the frogs were kept in two clear plastic tanks, (males and females separated for convenience). The tanks were lined with wet tissue, and kept shaded. Jumps were timed using a stopwatch and the horizontal distance jumped was measured from the wall to the centre of the frog on landing. General motivation and behaviour were noted along with posture in jumping, turning in flight and jumping to one side. Following each jump frogs were checked for signs of stress such as rapid breathing and colour change. All pregnant females were noted and experiments on one individual were terminated due to the large number of eggs she was carrying, although she did not appear unduly stressed. All jumps were recorded in order (irrespective of whether they were discounted for any reason) due to the progressive improvement noted in some frogs' jump distances.

The main section of each flight (excluding the initial jump) was filmed using an SVHS camcorder; playing the flight back frame by frame enabled the paths to be plotted on acetates. From these the angles of the linear section of the flight path were calculated, and filming of a metre scale bar in line with the main light direction enabled calculation of velocity.

Linear regression analysis on log-log data was again performed to determine if performance is affected by size. Male and female results were compared using independent samples T-tests to establish the significance of the apparent sexual dimorphism in terms of performance. Data were compared with those of previous studies.

Part 2: The juveniles.

In August 2001, following the previous experiment, three successive broods of eggs were laid by three different test frogs (the first two batches being laid within one month of one another). Their development was followed up to metamorphosis into froglets, and once the entire first and second batches had absorbed their tails they were weighed, their body lengths measured, and their spot patterns recorded. Of

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the 72 juveniles, the development of the 30 most distinctively patterned was then followed by recording their mass and snout to vent length every four weeks for sixteen weeks. After thirteen weeks a similar experiment to that described above was carried out to investigate their flying performance for comparison with the adults. For this the entire group of (by this stage) 68 frogs were tested. The length of each was measured prior to testing by placing them on a ruler. The first 30 were made to jump twice to establish whether improvement was occurring inindividuals. As no conclusive evidence of this was found the remainder were only made to jump once. The methods and experimental conditions to which they were subjected were identical to those described in Part 1 except that the juveniles were not filmed due to their small size.

Data were averaged to determine mean development rates in terms of mass and length. Log-log plots of body length against time and jump distance were produced and linear regression analyses carried out to establish the existence of any relationships within the data. Jump data averages were used to determine relative jump distance for comparison with the adults.

Results

The Adults: Morphological Relationships.

Most of the morphological relationships observed showed isometric scaling, as seen in table 1. (An example is also given in graph 1; note the distinct grouping of the data into two sets of points).

Table 1.

Comparison of expected and observed relationships between morphological factors.

Characteristic	Expected equation	Equation of graph	T	p
Leglength:SVL	Leglength$\propto$SVL^{1}	Leglength $= 10^{.225}$ x SVL$^{.981}$	-0.306	<0.05
Area:SVL	Area$\propto$SVL^{2}	Area $= 10^{-1.074}$ x SVL$^{1.979}$	-0.131	<0.05
Mass:SVL	Mass$\propto$SVL^{3}	Mass $= 10^{-4.906}$ x SVL$^{3.339}$	1.520	<0.05

Graph

Log-log plot showing the positive correlation between body length (SVL) and body mass.
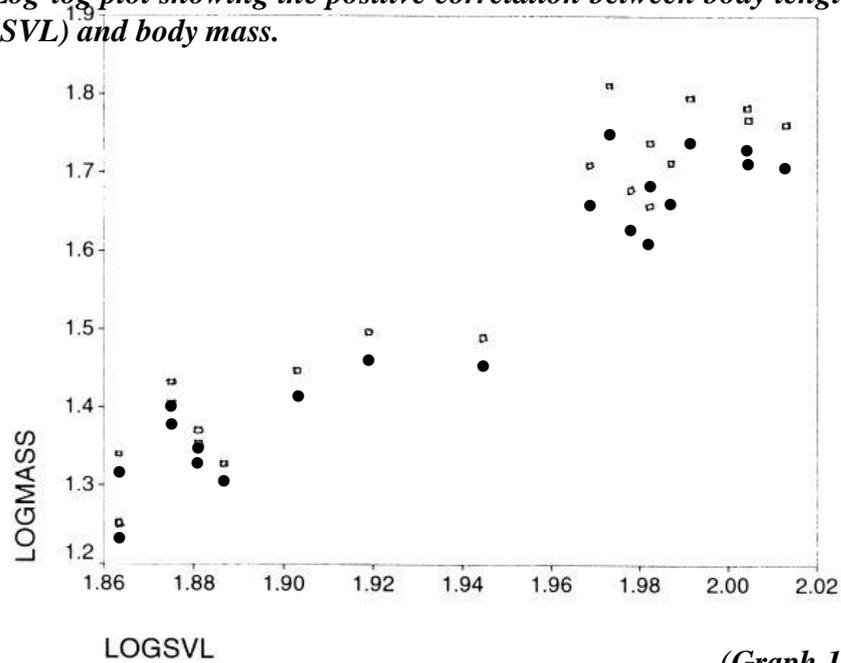
(Graph 1).

Area was found to vary less with mass than expected (equation of the graph: Area = $10^{1.869}$ x Mass$^{0.570}$, t = -2.22, i.e. this is significantly different to the expected relationship: Area = 10^k x Mass$^{0.670}$, if only by a small amount). R squared values from regression analysis were very high for all these relationships.

Variation in performance

No correlation was found between distance travelled and any morphological variable includ

Graph

*Log-log plot demonstrating the absence of any correlation between distance travelled and body mass.*
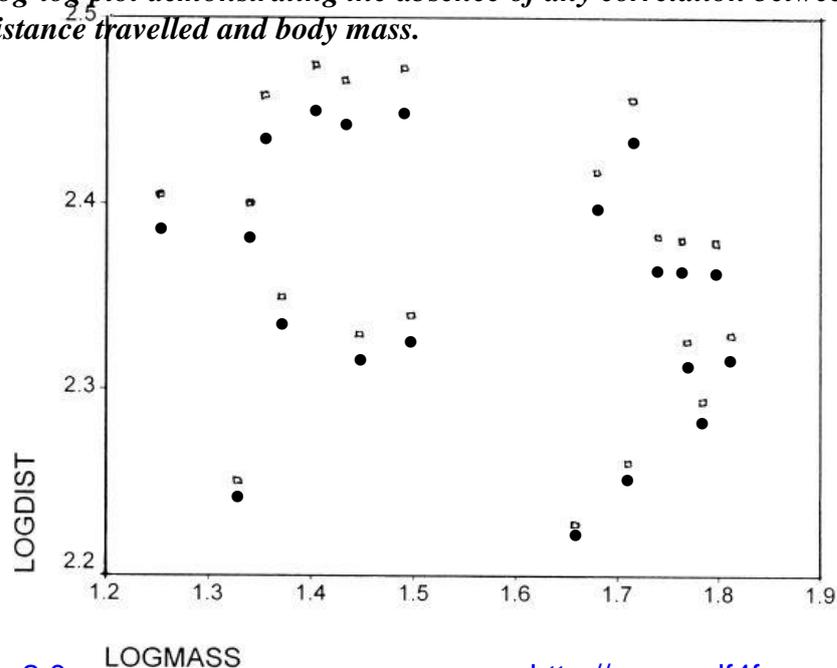
(Graph 2).

As might be expected flight time decreased with increasing mass, area, and therefore wingloading also; in each case t values calculated comparing the gradients produced (e.g. see graph 3) to a gradient of 0 indicate a significant difference, i.e. a significant relationship between time and the specific morphological characteristic.

Graph

Log-log plot showing the negative correlation between time taken for descent and mass.
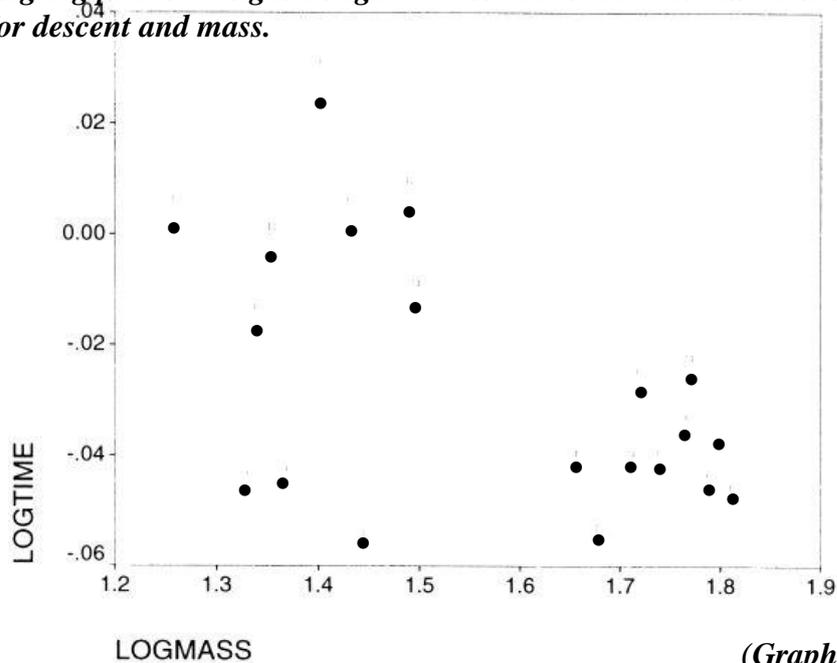
(Graph 3).

However the relationships observed are different to those expected as seen from the t values in table 2 which compare the observed gradients with the expected gradients.

Table 2.

Comparison of expected and observed relationships between time and the various morphological factors.

| Variables	Expected Relationship	Equation of the graph	t	P
Time:SVL	Time $\propto$ SVL$^{-.500}$	Time = 2.624 x SVL$^{-.228}$	3.02	>0.01
Time:Area	Time $\propto$ Area$^{-.250}$	Time = 1.795 x Area$^{-.100}$	3.40	>0.01
Time:Mass	Time $\propto$ Mass$^{-.166}$	Time = 0.661 x Mass$^{-.065}$	3.92	>0.01

No correlation was found between angle of descent and any of these morphological characteristics, however speed did show the expected relationships with dimensions as can be seen from table 3 and graph 4:

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Table 3.

Comparison of the observed and expected relationships between speed and the various morphological factors.

Variables	Expected relationship	Equation of graph	t	P
Speed:SVL	Speed $\propto$ SVL$^{.500}$	Speed = 10^k x SVL$^{.624}$	0.611	<0.05
Speed:Area	Speed $\propto$ Area$^{.250}$	Speed = 10^k x Area$^{.248}$	0.238	<0.05
Speed:Mass	Speed $\propto$ Mass$^{.166}$	Speed = 10^k x Mass$^{.183}$	0.222	<0.05

Log-log plot showing the slight positive correlation between mass and speed.
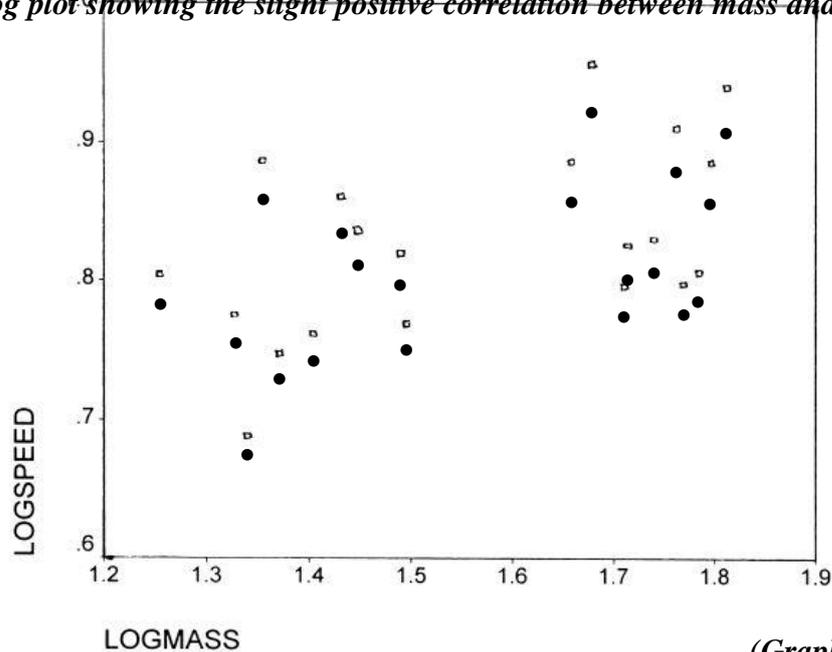
(Graph 4).

R squared values from regression analysis were very low for all these relationships.

Sexual dimorphism

Females have significantly greater dimensions than males for all measured variables. As a consequence of this they also have significantly smaller flight times and higher speeds. Only in distance and angle do the two sexes perform equally. See table 4:
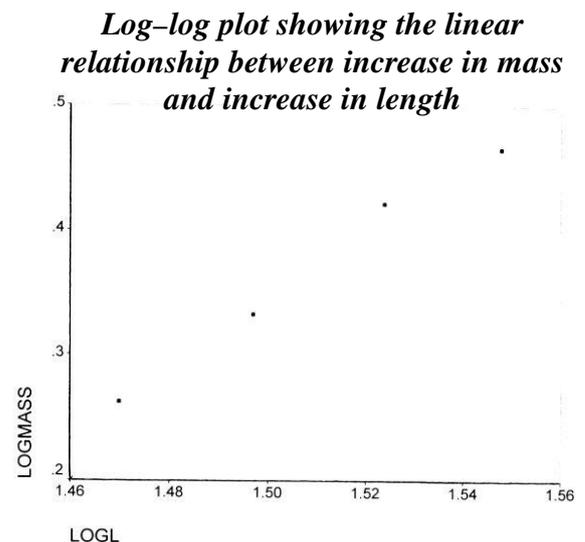
Table 4.

Comparison of morphology and performance in males and females.

	Mean		Independent Samples T-test		
	Male	Female	Mean Difference	T	P
Mass (g)	24.97	55.6	-30.64	-12.481	0.000
Area (mm^2)	452	744	-291.40	-12.366	0.000
Wingloading	0.0551	0.0750	-0.02	-5.339	0.000
SVL (mm)	77.6	97.4	-19.80	-10.795	0.000
Leglength (mm)	118.7	151.1	-32.40	-15.915	0.000
Mean distance (cm)	251.47	224.13	27.34	1.559	0.136
Angle (°)	19.65	20.50	-0.85	-0.398	0.695
Speed (ms^{-1})	6.290	7.375	-1.09	-2.566	0.019
Time (s)	0.98	0.92	0.06	2.928	0.000

During the course of the experiment six different frogs executed turns of up to 180° during a descent, landing facing in the opposite direction to take off. This turning was apparently not a result of instability during flight however, since all frogs clearly maintained the stereotyped "gliding" posture described by Inger (*1966)* with no observable pitching, rolling or wobbling.

The juveniles

For the first 16 weeks at least the juveniles demonstrated linear and isometric growth in terms of both length and mass. The relationship found between these two dimensions was not significantly different to the expected 1:3 ratio of length to mass (t = -1.67), see graph 6.

Log–log plot showing the linear relationship between increase in mass and increase in length

(Graph 6).

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Table 5.

Froglet growth over the first 16 weeks post metamorphosis

Weeks after metamorphosis	4	8	12	16
Mean mass	1.83g	2.15g	2.64g	2.92g
Mass range	1.45-2.49g	1.48-3.12g	1.41-4.16g	1.99-3.58g
Mean length	29.5mm	31.4mm	33.4mm	35.3mm
Length range	26.2-32.9mm	27.6-36.5mm	28.4-37.6mm	30.2-4.00mm

By week 16 the webbing of the larger specimens in particular was quite noticeable. On the hands webs extended approximately ¾ of the way to the toe discs. On the feet only the last two phalanges of the longest toe were unwebbed: webbing extended right to the bases of all the other toe discs.

The average length at the time of the experiment (13 weeks after metamorphosis) was found to be 34.3mm. (For the sake of speed and to avoid causing additional undue stress to the animals, length was measured prior to each jump by resting the frogs on a ruler rather than using callipers). Consequently this measurement is subject to a higher, but from the table above, apparently not significant, degree of error.

The average distance jumped was 1.107m, but jumps varied considerably, apparently depending on the motivation of the frog. The behaviour of the juveniles was less consistent than that of the adults with many simply jumping straight up into the air, however it should also be noted that the conditions of the experiment were not ideal as the squash court was particularly cold that day. The distances ranged from 0.62m ('vertical' jumps) to 2.38m (comparable to the adult distances). Log-log plots of distance and time against length do not show any correlation (t = -1.877 and –1.246, and P = 0.064 and 0.216 respectively, indicating the gradients are not significantly different to 0), however this will be discussed later.

Despite the conditions all frogs, like the adults, clearly demonstrated the characteristic gliding posture, landing upright and showing strong stability during flight with no rolling or tumbling. The flight times ranged from 0.88s to 1.21s with an average of 1.05s.

Sources of experimental error.

The greatest errors incurred were in timing as a result of the difficulty in predicting take off. Errors were also incurred in measuring the areas of the webs, mostly due to the low level of frog cooperation whilst tracing them. However in both these cases it is likely that the degree of error is fairly consistent throughout the experiment. Another source of error was the variation in mass before and after urination. This is of particular significance in the juveniles as it accounts for a relatively much larger proportion of the total mass. We would not therefore expect to observe any correlation between mass and any performance variable, especially over such a restricted size range.

There is a strong possibility that the behaviour observed does not represent the frogs' maximum capability due to the absence of strong motivational cues or visual stimuli and the general unnaturalness of the conditions, including the low temperature. However the data are still valid in terms of general trends, behavioural observations, and for facilitating comparison between studies.

Discussion

Morphological relationships

The observed isometric scaling of morphological features supports the concept that frogs follow Hill's model, but at the same time implies a lack of adaptation for gliding. As flatter objects have better aerodynamicity, one might expect allometric scaling giving a gradient significantly smaller than 3 for the log-log graph of mass versus body length, however this is not observed. In fact the reverse is true and the value obtained is significantly greater than 3 indicating a complete absence of adaptation. This contrasts with observations by Liem (*1970*) of *Rhacophorus nigropalmatus* which display the expected allometric scaling in adaptation for gliding, although the extent of this adaptation is not known due to the absence of published data on their morphology.

Effects of morphology on performance

As in Bishop's and McKay's experiments (*1999*) with the sister species *Agalychnis calcarifer*, no correlation was found between horizontal distances travelled and any morphological factor. This may relate to the function of this behaviour, indicating that absolute jump distance has been a more significant selection pressure in its development than relative jump distance. From the frequently opportunistic nature of the species' breeding strategy it seems likely that the primary function of parachuting is in rapid aggregation to exploit a temporary water source as in the smaller, non-webbed sister species *A. saltator*. Indeed it may also be that the structure of the habitat in which they live would not permit gliding long distances. The decrease in time with size and wing loading does not follow the expected ratio for an animal fully adapted to gliding. However the fact that the gradient of the graph is also significantly different to 0 shows that some compensatory mechanism is at work preventing the animals from simply free-falling.

The absence of any correlation between angle of descent and any morphological features reflects the lack of correlation with distance. The large angles to the horizontal confirm that these animals are parachuting rather than gliding. Although the height from which they were launched was not very great and therefore potentially insufficient to allow gliding to occur, the speeds reached indicated that many frogs were nearing terminal velocity at which point gliding is technically possible. However the frogs showed no indication of a change towards gliding thereby implying that this species is capable only of parachuting. This contradicts the assertion by Pough *et al (1998)* that both *R. nigropalmatus* and *A. spurrelli* can glide at angles of 18° to the horizontal, but supports Scott and Starrett's conclusion (*1974*) that *A. spurrelli* is a parachutist.

The relationships observed between speed and morphological dimensions were very close to those expected for gliding or parachuting animals, confirming once again that despite exhibiting no particular adaptation for gliding they perform considerably better than if under free fall conditions.

The low R squared values for all the performance analyses indicate that the variables under study are not the only factors influencing performance and a considerable amount of variation is due to a combination of other factors which have not been tested, probably largely a consequence of varying take-off speed. Predictably only the morphological relationships showed high R squared values.

Sexual dimorphism

The pronounced sexual dimorphism is evident in the graphs as the scatter of data in virtually all the variables shown (with the exception of relative wingloading) shows fairly clear division into two groups representing the two sexes. Females are considerably larger than males in all the dimensions studied, although the two still conform to Hill's model of isometric scaling. As a consequence of this size discrepancy females fly significantly faster than males resulting in significantly shorter flight times. No significant difference is seen in horizontal distance travelled however (although females have a slightly lower mean value), which again emphasizes the lack of correlation between size and horizontal distance overall. The size discrepancy may therefore relate more closely to breeding strategy, for example whilst in amplexus females would require significantly larger hands and feet to maintain a grip on a leaf in order to compensate for the additional weight of the male.

There was also some evidence of a difference in motivational state of males and females. Generally males required much less encouragement to jump and jumped increasingly willingly as the trial progressed, whereas females were reluctant, regardless of how many times they had jumped previously. The only three exceptions to this were the three females carrying eggs which jumped very willingly: possibly because the escape instinct was enhanced in these animals as a result of their condition. A commonly observed behaviour was urination on take off. Urination is frequently witnessed as an alarm response; however in this case it may serve a dual function in improving flight performance. Observation of the distance and speed at which urine is ejected suggest potential propulsive capabilities. Although no experimental verification of this was attempted, frogs were weighed prior to and following urination and urination was found to produce an average 11% weight loss in adults and up to 25.5% in juveniles. In terms of propulsion this is a considerable mass of liquid, however even if the purpose were not propulsion the

reduction in weight would produce a significant reduction in wingloading and slowing of the descent. Therefore it seems likely that at least in one respect this mechanism improves flying performance.

Behavioural observations

Improvement in performance over the course of the trial was a fairly general trend (in the adults) with eleven out of the twenty frogs (seven male) showing a gradual improvement in jump angle, and ten (five of each sex) showing a gradual improvement in horizontal distance. This may be evidence of learning, or growing accustomed to the height from which they are jumping. It is not known how much (if any) calculation of height is carried out in the natural habitat prior to jumping, although this substrate probably provides more visual cues on which to base any assumptions than the (virtually bare) squash court. Certainly many frogs were observed to aim for a particular target (e.g. the camera, side wall or measurer), although best attempts were made to maintain a forward direction by blinkering the view of the sides from the launch pad. In the event most frogs jumped in a more or less straight line perpendicular to the wall.

Turning behaviour observed in a few individuals did not appear to result from any kind of instability during flight with all frogs rigidly maintaining the stereotyped "gliding" posture. Gliding and parachuting are thought to require active stabilization as the low aerodynamicity of the frog shape produces low passive stability. Evidence suggests that inherent instability is actually advantageous in facilitating more rapid turning ability and lower minimum speeds (*Maynard-Smith, 1952*) and that unstable flyers and gliders actually evolved from more primitive, passively stable ones once they developed a certain degree of active control over their bodies during flight. Studies involving other species suggest that posture is extremely influential in the control of static stability, having a far more significant effect than morphology. (Postural changes exaggerate radial asymmetry deflecting air around the body in directions other than that parallel to the direction of travel, producing deviation from the straight path). This in itself appears to emphasize the importance of manoeuvrability in the evolution of this locomotor type: the bent limb position adopted by all "flying" frogs studied improves parachuting performance by increasing drag and significantly improves stability and control of flight, yet it is favoured above other postures which produce a significant increase in horizontal

distance by providing greater lift (*Emerson & Koehl 1990, Emerson et al 1990*). General observation of these frogs in captivity has highlighted their proficiency in manoeuvring, supporting the theory that this rather than horizontal distance has been the driving force in development of this behaviour.

The juveniles

As the test conditions were identical in both experiments, comparison with the adults is possible in terms of relative jump distance. This statistic indicates an impressive performance by the juveniles with a relative jump distance of 41cm g^{-1} compared to 10 cm g^{-1} for the males and 4cm g^{-1} for the females. The log-log plots of distance against length show no clear correlation, but given the small size range involved this is unsurprising. However, the large number of results mask a small number of particularly long jumps performed by the largest individuals ($\approx$40mm) in the group. These suggest that the maximum achievable distance may increase with size to a certain maximum value, (quite probably one which had not been attained at the time of the experiment), at which point further mass increase then enters the pronounced negative correlation with distance as witnessed. This is also apparently supported by Scott and Starrett's data which imply a relative jump distance intermediate between the juveniles and the adult males in this experiment (as befits their size) however the absence of any mass measurements prevent direct comparison. There may be a sudden improvement in jumping performance at a particular size, relating to other developmental changes occurring at this stage, for example an increase in muscle mass as opposed simply to an increase in bulk. (It is known that some species exhibit a phase of uncharacteristic allometric growth). Comparison of mass increase with length increase shows that the juvenile group as a whole had not undergone any allometric growth within the first 16 weeks of development. The primary question then concerns the selective forces driving the evolution of size beyond that which optimises this mode of locomotion. During a number of flights juveniles were apparently observed using their forefeet as air brakes, a behaviour not observed in the adults. The function of this is naturally speculative, but most probably relates to postural control since posture was rigidly and consistently maintained during all tests. If so this once again highlights the significance of stability and the benefits of larger size for control. Alternatively the

problem may be viewed from the reverse angle, taking into account Bennet and Licht's studies of the negative correlation between stamina and size (*1974*) and the suggested use of gliding simply as an energetically inexpensive mode of travel (*Norberg, 1981*); i.e. gliding/parachuting as a means of travel may permit exploitation of the advantages of large size whilst avoiding the usual compromise in speed, or the expensive physiological adaptations otherwise required in compensation.

Comparison with other studies.

Although statistical comparison with other studies is not possible due to the different experimental conditions, a basic comparison of the results is still of some use. Comparison with Scott and Starrett's data for Pacific coast specimens (*1974*) highlights the significant size discrepancy between these and the Caribbean forms. The two sets of data correlate well in terms of proportions emphasizing the adherence to Hill's model seen in this species as a whole. This morphological investigation shows that the Caribbean specimens have both larger feet with respect to body length and also more extensive webbing between the digits, (webbing in some Pacific forms studied only extends as far as the penultimate phalanges, whereas that in Caribbean forms extends at least to the base of the toe pads and on some toes right to the centre of the disc), (*Gray, unpubl. data, Duellman, 1970*). Yet gliding ability also appears to scale fairly uniformly. This therefore prompts the question as to what has driven the divergence in size on the opposite coasts as adaptation to enhance parachuting performance in one or another population is evidently not a factor. The observation of breeding aggregations involving several thousand individuals in a very small area prompts speculation as to the influence of density-dependent factors. This draws on findings by Rose (*1960*) that growth of tadpoles in certain *Rana* species is inversely proportional to density and that, even more significantly, certain individuals within a population are able to produce a water-borne growth retarding factor which inhibits the growth of conspecifics in the immediate vicinity. Although the existence of this behaviour has not been investigated in this particular species, the possibility of a similar mechanism acting under conditions involving explosive breeding is a feasible one, especially if the size discrepancy between the two coasts is mirrored by a discrepancy in the predominant breeding strategy.

Comparison with Emerson's data for *R. nigropalmatus* and other Rhacophorids (*1990*) show that the former at least are considerably more proficient parachutists achieving much greater glide distances and lower glide angles. These are similar in body length, but have more extensive webbing (between 50 and 120% more than *A. spurrelli*), (*Inger 1966*), and differences in body form: *A. spurrelli* do not have the characteristic body flaps seen in some *Rhacophorus* species and possibly have a much higher bodyweight to body length ratio. These results suggest that body form is of considerably greater significance than suggested by Emerson's results, which serves to emphasize once again the high levels of nonadditivity of morphological characteristics brought to light in those experiments. Despite better gliding performances in *Rhacophorus* (*R. nigropalmatus* is capable of true gliding), the same bias is seen in *A. spurrelli* towards adaptation for improved manoeuvrability above improved horizontal distance.

Conclusion

Like the majority of anurans *A. spurrelli* conforms to Hill's model of geometric similarity with all dimensions scaling isometrically. Pronounced sexual dimorphism is observed, however its effects on performance are relatively minor, accounting only for a slight weight-related correlation with speed. Although not capable of true gliding and distinctly less proficient a flyer than *R. nigropalmatus*, this species does show parachuting behaviour. Parachuting is facilitated by the enlarged and extensively webbed feet and hands, however a large number of other factors synergistically influence performance, for which it is impossible to test individually. Of these probably the most significant factor is posture. *A. spurrelli* consistently adopts the characteristic gliding posture as described by Inger (*1966*), and evidence suggests that the principle purpose of this stance is to improve stability and control, with the implication that this, rather than distance has been the driving factor behind evolution of this locomotor type.

There is great potential for further study in this area, particularly concerning determination of size and, relating to this, the factors producing the observed geographical size dimorphism in the species. This would probably require a thorough investigation of behaviour in the natural environment and analysis of the different ecological factors influencing the two populations.

Acknowledgements

References

Alexander, R.McN. 1971 "Size And Shape Studies In Biology (29) 59pages Arnold, London

Alexander, R.McN. 1982 "Locomotion Of Animals" p54-61 Chapman and Hall, New York

Bennet, A.F. and Licht, P. 1974 "Anaerobic metabolism during activity in amphibians" Comp. Biochem. Physiol. A **48** 319-327

Bennet-Clark, H.C. 1977 "Scale Effects Of Animal Locomotion" pages185-201 Acadenic Press. New York

Bishop, K.L. 1999 Abstract. Amer. Zool. **39(5)** 501

Boulenger, G.A. 1913 "On a collection of batrachians and reptiles made by Dr.H.G.F. Spurrell, F.Z.S., in the Choco, Colombia" Proc. Zool. Soc. **LXVIII** 1019-1046

Calow, L.J. and Alexander, R.McN. 1973 "A mechanical analysis of the hind leg of a frog (*Rana temporaria)*" Lond. J. Zool. **171** 293-321

Caple, G., Balda, R.P. and Willis, W.R. 1983 "The physics of leaping animals and the evolution of preflight" Amer. Nat. **121(4)** 455-475

Cochran, D.M. and Goin, C.J. 1970 "Frogs of Colombia" Bull. Smithsonian Institution U.S. Nat. Mus. **288** 149-151

Cott, H.B. 1926 "Observations on the life habits of some batracians and reptiles from the Lower Amazon and a note on some mammals from Marajo Island" Proc. Zool. Soc. Lond. **4** 1159-1178

Duellman, W.E. 1970 "The Hylid frogs of Middle America" Monograph Mus. Nat. Hist. Uni. Kansas vol.1 90-95 & 124-130

Emerson, S.B. 1978 "Allometry and jumping in frogs: helping the twain to meet." Evolution **32** 551-564

Emerson, S.B. 1982 "Frog post-cranial morphology: identification of a functional complex" Copeia 603-613

Emerson, S.B. 1984 "Morphological variation in frog pectoral girdles: testing alternatives to a traditional adaptive explanation" Evolution **38** 376-388

Emerson, S.B. 1988(b) "Convergence and morphological constraint in frogs: variation in post-cranial morphology" Fieldiana: Zool. (New Series) **43** 1-19

Emerson, S.B. and Koehl, M.A.R. 1990 "The interaction of behavioural and morphological change in the evolution of a novel locomotor type: 'flying' frogs" Evolution **44(4)** 1931-1946

Emerson, S.B., Koehl, M.A.R. and Travis, J. 1990 "Functional complexes and additivity in performance – A test case with 'flying' frogs" Evolution **44(4)** 2153-2157

Ennos, A.R. 1999 "Statistics And Data Handling Skills In Biology" Addison Wesley Longman Ltd 144 pages

Gray, A.R. 1997 "Observations on the biology of *Agalychnis spurrelli* from the Caribbean lowlands of Costa Rica" J. Int. Herpet. Soc. **22(2)** 61-70

Griffiths, I. 1966 "The phylogeny of the salienta" Biol. Rev. **38** 241-292

Inger, R.F. 1966 "The systematics and zoogeography of the amphibia of Borneo" Fieldiana: Zool. **52** 1-402

Liem, S.S. 1970 "The morphology, systematics and evolution of the Old World treefrogs (Rhacophoridae and Hyperoliidae)" Fieldiana: Zool. **57** 1-145

MacBride E.W. 1932 "Recent work on the development of the vertebral column" Biol.Rev. **7** 108-148

Maynard-Smith, J. 1952 "The importance of the nervous system in the evolution of animal flight" Evolution **6** 127-129

McKay, M. 1999 Abstract. Amer. Zool. **39(5)** 614

Noble, G.K.1931 "The Biology Of The Amphibia" 577pages McGraw-Hill Book Company, Inc. London

Norberg, U.M. 1985 "Evolution of vertebrate flight: An aerodynamic model for the transition from gliding to active flight" Amer. Nat. **126** 303-327

Oliver, J.A. 1951 "Gliding in amphibians and reptiles with a remark on arboreal adaptation in the lizard *Anolis carolinensis carolinensis". Amer. Nat.* **85** 171-176

Pough, F.H. Andrews, R.M. Cadle, J.E. Crump, M.L. Savitzky, A.H. Wells, K.D. "Herpetology" 2nd ed. 612pages Prentice Hall ltd. London

Rose, S.M. 1960 "Feedback mechanisms on growth control: possible stunting resulting from high density populations". Ecol. **41** 188-199

Savage, J.M. and Heyer, W.R. 1967 "Variation and distribution in the treefrog genus Phyllomedusa in Costa Rica, Central America" Bietr. Neotrop. Fauna **5** 111-131

Saville, D.B.O. 1962 "Gliding and flight in the vertebrates" Amer. Zool. **2** 161-166

Scott, N.L. and Starrett, A. 1974 "An unusual breeding aggregation of frogs with notes on the ecology of *Agalychnis spurrelli* (Anura: Hylidae) Bull. South. Calif. Acad. Sci. **73(2)** 86-94

Zug, G.R. 1972 "Anuran locomotion: structure and function. Preliminary observations on the relationship between jumping and osteometrics in the appendicular axial skeleton" Copeia 613-624

Zug, G.R. 1978 "Anuran locomotion - structure and function: Jumping performance of semiaquatic, terrestrial, and arboreal frogs" Smithsonian Contributions to Zoology **276** 1-31

Zug, G.R. 1993 "Herpetology" 527pages Academic Press Inc. London