

Costs of reproduction and the evolution of sexual dimorphism in a ‘flying lizard’ *Draco melanopogon* (Agamidae)

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Abstract

Life-history models suggest that ‘costs of reproduction’ can influence the evolution of sexual dimorphism, but empirical data on this effect are scarce. We tested the idea using ‘flying lizards’ (Asian agamids of the genus *Draco*), because the evolution of ‘flight’ (gliding) is likely to have increased the degree to which pregnancy affects maternal locomotor ability (and hence, we infer, has increased the ‘costs of reproduction’). As predicted, *Draco* display patterns of sexual dimorphism that are different from those seen in most other lizards. The ‘wings’ (gliding membranes) of female *D. melanopogon* are significantly larger than those of males of the same body size, a dimorphism that we attribute to natural selection on the ability to glide while encumbered with eggs. Comparisons with non-flying lizards suggest that the same selective pressure has also reversed pre-existing patterns of sexual dimorphism in body size and body proportions (relative head size, relative tail length). Measurements of wing-loading, centre of balance and gliding distances of preserved specimens support the hypothesis that a larger body, relatively larger head, and longer tail may improve a female’s aerial mobility when she is gravid. Thus, selection for locomotor ability in egg-burdened females (reduction in ‘costs of reproduction’) may have been responsible for a reversal of sexually-selected traits in this lineage.

Key words: allometry, biomechanics, gliding, life-history, locomotion, reptile

INTRODUCTION

Charles Darwin (1871) recognized that sexual selection and natural selection may work in opposition, so that the degree of elaboration of a trait may be determined by a balance between the benefits conferred by sexual selection and the costs imposed by natural selection. This kind of balance between competing selective forces may control the degree of expression of many sexually-selected traits (Andersson, 1994). One case of particular interest is the possibility that ‘costs of reproduction’ may modify the degree or direction of sexual dimorphism (Madsen & Shine, 1995). Simple models of selection suggest that the sex that benefits most from extreme development of a trait will exceed the other sex in mean value of that trait (e.g. see Trivers, 1972 for body-size models). However, more complex models that incorporate ‘costs of reproduction’ yield different predictions. For example, sexual dimorphism in adult body sizes may result from stronger selection against early maturation in one sex than another, even if the relationship between per-season reproductive success and body size is identical in the two sexes (Gibbons & Lovich, 1990; Madsen & Shine, 1995).

Although the idea that ‘costs of reproduction’ can influence the evolution of sexual dimorphism is straightforward, the idea is difficult to test. The intensity of ‘costs of reproduction’ depends on many variables – for example, energy shortage might magnify energetic costs, and an increase in predator density might increase predation costs (e.g. Bell, 1980; Shine, 1980). For comparative tests, we need a system in which two or more taxa differ *consistently* in the degree of reproductive ‘costs’ that they experience. Preferably, then, such variation in ‘costs’ should relate to traits that do not vary over the geographic range of a single species, rather than factors (such as prey availability or predator numbers) that fluctuate rapidly in time and space within the range of each species.

Phylogenetic shifts in the mode of locomotion are well-suited to such an analysis, because they are likely to impose major changes to the ‘costs’ (decrements in locomotor performance, or energy costs for travel) associated with changes in the degree of physical burdening of the organism. Thus, the degree to which pregnancy impairs maternal locomotion is likely to differ substantially between otherwise similar taxa that rely on different locomotory modes. For example,

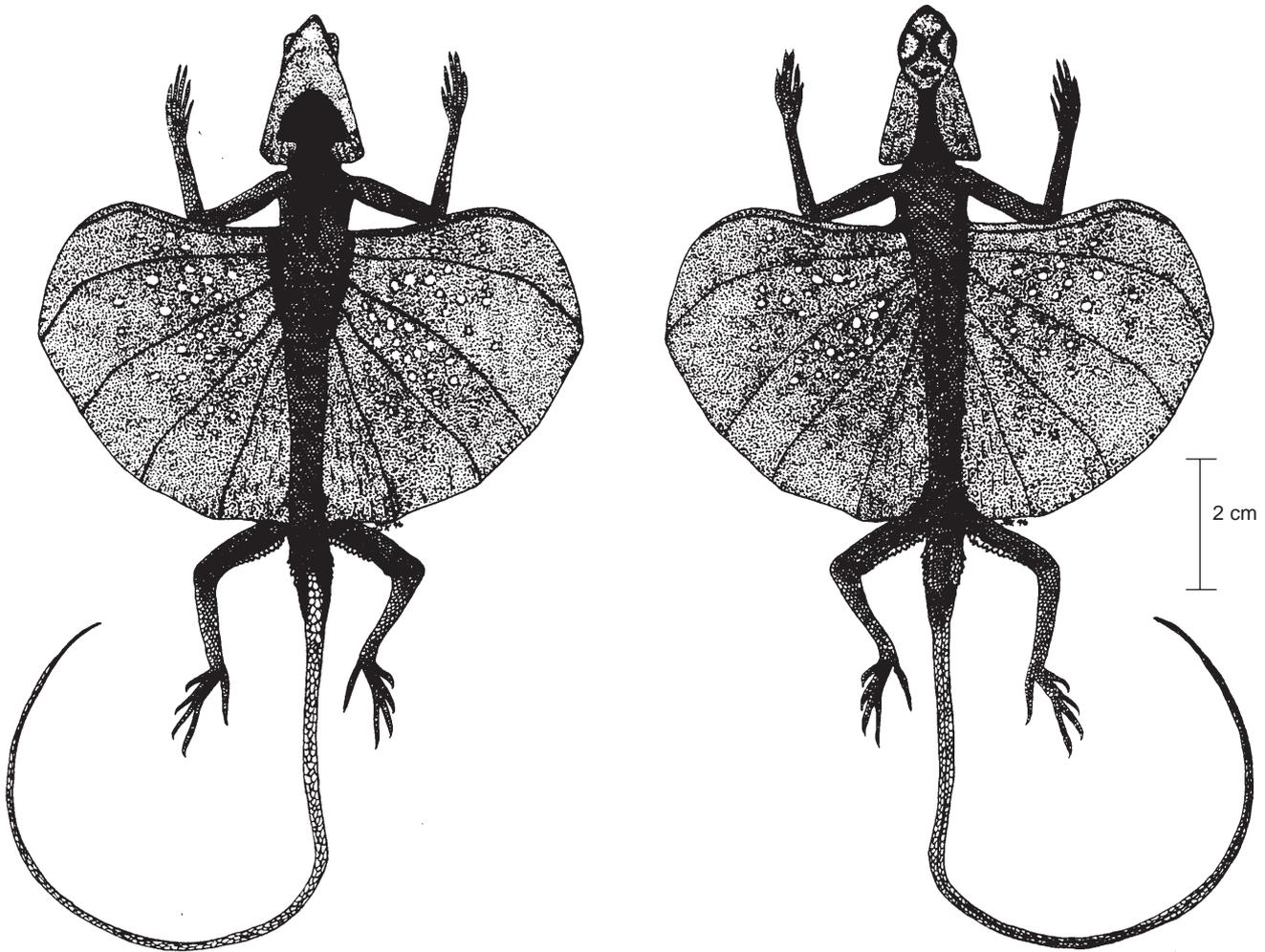


Fig. 1. Dorsal and ventral views of a male *Draco melanopogon* (Bishop Museum no. 12432), showing the outstretched 'wing' (gliding membrane). This membrane folds back against the side of the body when not in use.

phylogenetic shifts in reproductive investment patterns in snakes have been attributed to changes in the 'costs of reproduction' due to locomotor adaptations for burrowing (Gans, 1975) and swimming (Shine, 1988).

Clearly, the locomotor mode likely to impose the greatest additional 'costs' for a pregnant female is flight. Several major features of the reproductive biology of birds (e.g. the lack of viviparity, and sequential rather than simultaneous ovulation) may reflect selection to reduce the physical burden carried by the female (e.g. Blackburn & Evans, 1986). Decrements to flight performance due to the clutch have been advocated as the reason why the degree of sexual size dimorphism among raptorial bird species correlates with the degree to which prey capture requires complex aerodynamical performance (Andersson & Norberg, 1981; Mueller & Meyer, 1985). This principle has also been used to explain patterns of 'reversed' sexual dimorphism in bats (Myers, 1978).

Reptiles offer a particularly clear opportunity to examine the conflict between sexual selection and natural selection (costs of reproduction) as determinants of sexual dimorphism in flying species, because several

groups of squamates (lizards and snakes) include gliding species that rely on large outstretched membranes to 'fly' from tree to tree (e.g. Schiotze & Volsoe, 1959; Colbert, 1967). Although these animals glide, rather than engaging in powered flight, the selective pressures on their overall morphology are likely to be intense. Certainly, the species we studied – Asian agamid lizards of the genus *Draco* – show distinctive morphological adaptations for flight (e.g. Colbert, 1967; Inger, 1983; Musters, 1983). These lizards are very elongate, with long slender legs and remarkably distended ribs that support a pair of large 'wings' (gliding membranes: see Fig. 1).

Morphological adaptations for gliding in *Draco* have been the subject of previous studies (e.g. Colbert, 1967), and patterns of sexual dimorphism in body size and wing size in five *Draco* species have been investigated by Mori & Hikida (1992). We extend these studies by examining sexual dimorphism in another species (*D. melanopogon*), re-analysing published data on patterns of dimorphism in other *Draco* populations, and incorporating other traits (head size, tail length) into the analysis. These additional traits are of particular interest

because they permit a tighter comparison with other non-gliding agamid species. Unlike wing dimensions (which cannot be compared with non-gliding taxa) and body size dimorphism (which varies among non-gliding agamids), the direction of sexual dimorphism in relative head size and relative tail length appears to be consistent among non-gliding agamids. Putative effects of the evolution of gliding can thus be more easily evaluated, because of the lower variation among the outgroup for these traits.

MATERIALS AND METHODS

Study species

Draco melanopogon is a small (up to 90 mm snout–vent length) arboreal agamid lizard that occurs over much of south-east Asia (Musters, 1983). To eliminate possible confounding effects of geographic variation, we examined specimens collected from a single population. We quantified morphological variables on preserved museum specimens of 114 male and 128 female *Draco melanopogon* collected by Senoi aborigines in the Bukit Lagong Forest Reserve, Selangor, near Kuala Lumpur, Malaysia (Bishop Museum specimen numbers 12254–12497).

Morphological and meristic data collection

The following measurements were recorded on each specimen: snout-vent length (SVL), tail length (on undamaged tails only), maximum wing span, length of wing attachment from first wing rib to the femoral attachment, inter-limb length, head length from tip of the snout to the rear of the quadrate, maximum head width, and axial width at the shoulders. The combined wing area for each lizard was calculated from the length and width of the wings. We also dissected females and recorded the number and size of eggs and follicles (follicle diameter, and length and width of eggs and large follicles). We also recorded relative egg position by measuring the distance from vent to midpoint of each egg. To estimate egg volume, we used linear measurements in the formulae for the volume of a prolate ellipsoid ($0.5236 \times \text{length} \times \text{width}^2$).

To examine the effects of sexual dimorphism and pregnancy on wing loading, the lizard's centre of gravity, and flight performance more rigorously, we measured additional variables on a subset of 60 specimens (23 males, 37 females). These animals were chosen on the basis that all had entire tails, and their wings were fully and symmetrically extended on both sides of the body. We recorded wet mass and body length (the straight-line distance along the ventral midline, from a point between the hindlimbs to one between the forelimbs) of each of these lizards. We then balanced each lizard on a knife-edge to determine its centre of gravity, and recorded the location of this point relative to trunk length.

Because our adaptationist explanations involve the consequences of morphology for 'flight' performance, we obtained a crude measure of gliding ability from these well-preserved specimens. To do this, we held the specimen mid-abdomen and launched it horizontally and head-first, releasing the lizard 1 m above the ground, as if it was a paper aeroplane. The trials were conducted in windless conditions, and on soft substrate (grass). Each lizard was 'flown' 3 times, and launched by a different observer in each of these trials. The distance from the launch-point to each lizard's final position was measured, and the mean flight distance (average of the three trials) was used for analysis. Male and female lizards were flown in random order, with the 'launcher' unaware of the lizard's gender. We recognize that these trials offer a poor simulation of true 'gliding' as it occurs in live lizards: basically, we measured powered flight with a low (horizontal) angle of attack, whereas true gliding involves a relatively steep descent without initial propulsion. Our trials may none the less provide some insight into overall flight performance, because some of the features that enhance gliding ability also influence performance in horizontal flight (e.g. see Emerson & Koehl, 1990: fig. 2).

Statistical analysis

All meristic variables were log-transformed before statistical analysis to meet the assumptions of normality and homogeneity of variances. We used analysis of covariance (ANCOVA) to examine relationships between meristic variables where sex was the nominal variable. We also used analysis of variance (ANOVA) and *t*-tests to investigate differences in mean values of traits due to sex and age, and linear regression analysis to examine relationships among variables.

Additionally, we took advantage of extensive data tabulations from a taxonomic review of *Draco* (Musters, 1983) to investigate patterns of sexual dimorphism within this genus, in order to compare our results on *D. melanopogon* with those on congeneric species. If the unusual features of sexual dimorphism in *D. melanopogon* (see below) are indeed adaptive to gliding locomotion, we would expect to see similar features in all of the *Draco* species (since all of them use gliding flight). For such comparisons we treated data from each species (or subspecies, or population) as independent for the purposes of analysis, because our intention was simply to assess the generality of patterns. However, in order to examine relationships among traits (such as the degree to which phylogenetic changes in male vs female body size are responsible for phylogenetic changes in the degree of sexual size dimorphism), we cannot treat each population or species as independent. Similarities among closely-related taxa might reflect recent descent from a common ancestor (with a lack of change in the traits of interest) rather than resulting from selection acting on functional links

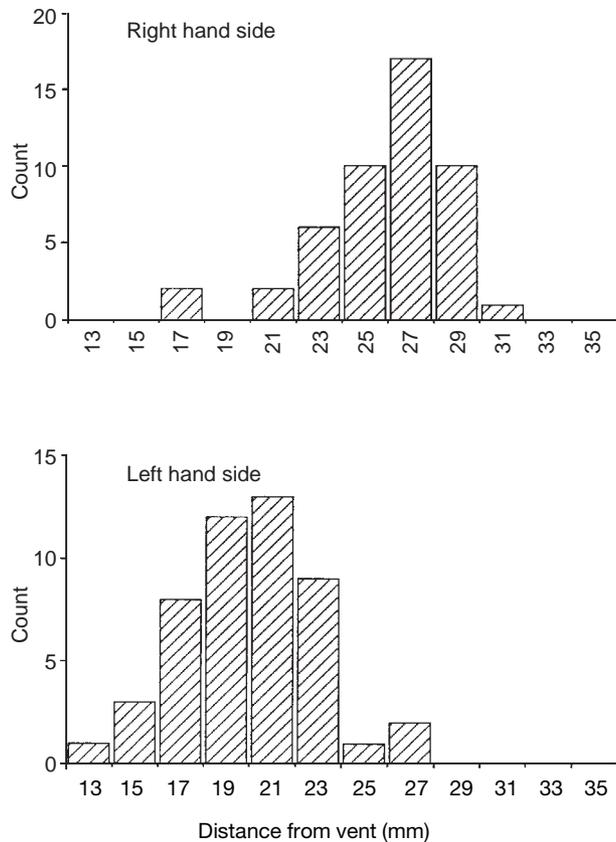


Fig. 2. Position of eggs in female *Draco melanopogon*. Virtually all females carry only two eggs, and the egg on the right-hand side of the body is consistently carried more anteriorly (upper graph) than the egg on the left-hand side (lower graph). The horizontal axis shows the distance from the vent to the midpoint of the egg.

among traits (e.g. Harvey & Pagel, 1991; Doughty, 1996a). Thus, we used the independent-contrasts method (Felsenstein, 1985; Purvis & Rambaut, 1995) to examine the degree to which phylogenetic changes in one trait were correlated with changes in another. Musters' (1983) phylogeny was used for this analysis; branch lengths were unavailable, so all were assumed to be equal.

RESULTS

Reproduction

We recorded large vitellogenic follicles or oviductal eggs in 92 of the 128 females. Of these, 90 contained two eggs each (one in each oviduct). The other two lizards contained one egg each, with distended oviducts suggesting that the other half of the clutch had been deposited recently. Larger females contained larger eggs (linear regression of SVL vs mean egg volume, $n = 52$, $r = 0.30$, $P < 0.03$). This trend was entirely due to a strong increase in egg width with maternal SVL ($n = 52$, $r = 0.38$, $P < 0.005$); egg length showed no consistent

relationship with maternal body size ($n = 52$, $r = 0.03$, $P = 0.85$). The egg on the right-hand side of the lizard's body was almost always anterior to the egg on the left (Fig. 2), with a mean difference between midpoints of 6.2 mm (SD = 0.64; against a null hypothesis of no difference, one-group $t_{42} = 9.74$, $P < 0.0001$). Eggs averaged 13.6×6.2 mm in size.

Allometry of growth

To investigate allometric changes in body proportions, we calculated the ratio of a trait (e.g. head length) to SVL, and compared this ratio between juvenile (<67 mm SVL, $n = 19$) and adult ($n = 217$) *Draco*. The size at maturity was based on examination of gonads. Because of sexual dimorphism in several traits (see below), we incorporated sex as a factor in these analyses. Thus, we used two-factor ANOVA with sex and age (adult/juvenile) as the factors, and the ratio measure as the dependent variable. No significant interactions between sex and age were detected. These analyses showed that juveniles had longer heads relative to SVL than did adults (main effect of age $F_{1,230} = 24.86$, $P < 0.0001$), but that head widths relative to SVL did not change with age ($F_{1,230} = 1.14$, $P = 0.29$). Similarly, tail length relative to SVL did not differ between adults and juveniles ($F_{1,164} = 1.32$, $P = 0.25$). Wing dimensions showed strong allometry, with both the width and length of the gliding membrane comprising a larger proportion of body length in adults than in juveniles (wing span $F_{1,230} = 63.19$, $P < 0.0001$; length of wing attachment $F_{1,230} = 5.51$, $P < 0.02$).

Sexual dimorphism

Female *Draco melanopogon* matured at the same body size as males (67 mm SVL; Table 1), but grew larger (SVL maxima of 87 vs 83 mm for adults; Table 1). Given the allometry of body proportions (see above), this size difference between the sexes inevitably translates in complex ways into sex differences in other traits. Adult females were larger than males for average values of all the meristic values we recorded (Table 1). These differences were not simply due to overall size dimorphism between the sexes, but instead resulted from allometric divergence in shape (body proportions) as well as overall size. One-factor ANCOVA (with sex as the factor and SVL as the covariate) revealed that at the same body size, females had longer tails and longer and wider heads than did conspecific males (Table 1, see Fig. 3). The slope of the relationship between SVL and other variables also showed sexual dimorphism (Table 1). The overall wing shape of males and females is very similar, but adult females have a longer wing attachment area and a wider wingspan than do males of the same SVL (Table 1). Thus, the wings of females are both longer and wider than those of males at the same body length.

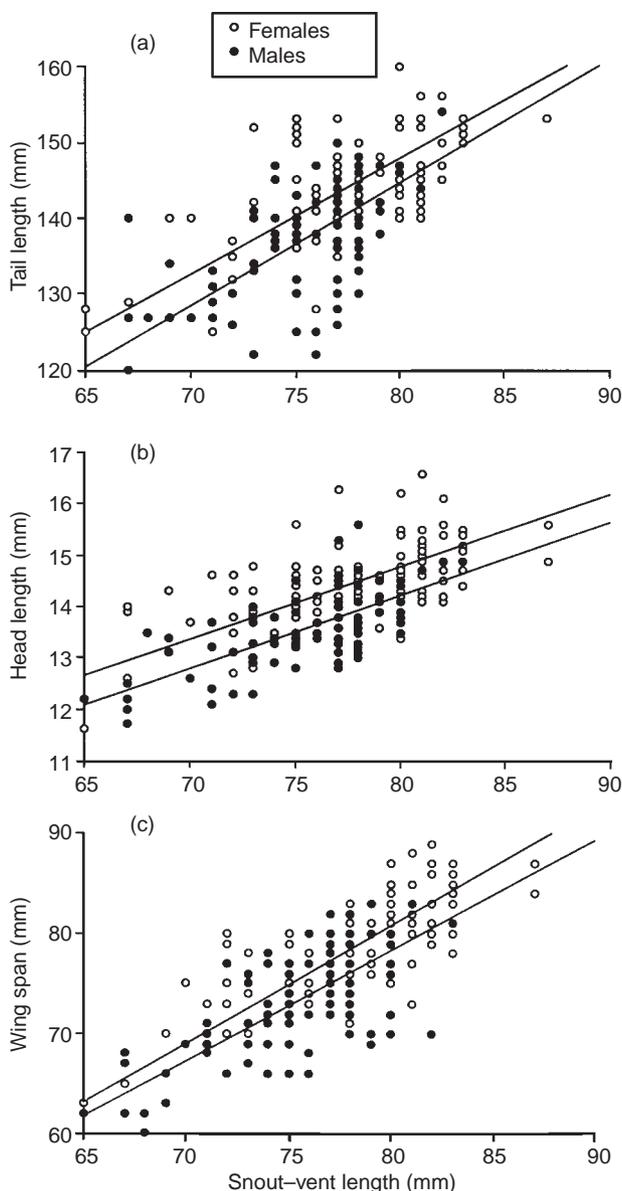


Fig. 3. Sexual dimorphism in *Draco melanopogon*. Compared to their body length, female lizards have longer tails (a), larger heads (b), and wider 'wings' (gliding membranes; c) than do males. The upper regression line represents data for females in each case, and the lower line represents data for males. See text for statistical analyses of these data.

Wing loading, centre of balance, and gliding performance

Our data allow us to examine several assumptions underlying the notion that the burden of eggs impairs female gliding, and that this 'cost' has been responsible for the evolution of sexual dimorphism in size and shape in *Draco*.

1. *The mass of the eggs is a significant component of adult female body mass.* If this statement is not true, the degree of burdening due to eggs should be trivial, and thus unlikely to act as a selective force for sex-specific morphological adaptation. We could not weigh eggs separately (because this would have caused excessive

damage to the specimens), but we could assess the validity of this assumption indirectly in two ways. If eggs are a substantial component of body mass, we expect that females burdened with eggs should weigh more than males at the same SVL, as indeed they do (ANCOVA with sex as the factor, SVL as the covariate, and mass as the dependent variable: slopes $F_{1,57} = 3.62$, $P = 0.06$; intercepts $F_{1,58} = 170.94$, $P < 0.0001$). Also, the mass of a female should be significantly correlated with the volume of her eggs, as indeed it is ($r = 0.72$, $n = 36$, $P < 0.0001$).

2. *The mass of the eggs contributes significantly to the degree of wing-loading.* Wing-loading (body mass divided by wing area) should be an important determinant of gliding ability. Given that females are heavier than males (see above), we expect that they are also likely to show a higher average wing-loading, despite their larger wing area. Our analyses confirm that wing-loading averages higher in females than in males (mean wing-loading indices of 1.24 vs 0.83; unpaired two-tailed t -test, $t_{59} = 12.14$, $P < 0.0001$), and show that the degree of wing-loading of a female is correlated with the size (volume) of her eggs ($r = 0.48$, $n = 36$, $P < 0.004$).

3. *The eggs carried by a female lizard affect her centre of balance, and thus (potentially) her gliding ability.* In keeping with this assumption, the centre of balance is located more posteriorly in females than in males (as a proportion of trunk length, means of 0.44 vs 0.41; unpaired two-tailed t -test, $t_{59} = 4.75$, $P < 0.0001$) and the centre of balance of a female is a function of the size of her eggs (egg volume vs centre of balance; $r = 0.33$, $n = 36$, $P < 0.05$).

4. *The larger head of females enhances gliding ability.* This hypothesis makes at least three predictions. First, since not all females carry full-sized eggs, we would expect mean flight distance to be higher in females than in males, as was indeed the case in our gliding trials with preserved lizards (means of 3.27 vs 2.97 m; unpaired two-tailed t -test, $t_{56} = 2.76$, $P < 0.008$). Second, we would expect an overall relationship between relative head size and flight ability; lizards with relatively larger heads would be expected to travel further in our trials. We tested this prediction using residual values from the linear regression of head length on SVL as our measure of relative head size, and the analysis confirmed our prediction (distance 'flown' vs relative head size: $r = 0.31$, $n = 57$, $P < 0.02$). Third, if this result is due to head size rather than to some other (unmeasured?) sex difference in body proportions, we expect that the males and females with similar relative head sizes will 'fly' for similar distances. As predicted, analysis of covariance (with sex as the factor, relative head length as the covariate, and distance 'flown' as the dependent variable) showed no sex difference in this relationship (slopes $F_{1,53} = 0.12$, $P = 0.73$; intercepts $F_{1,54} = 2.88$, $P = 0.10$).

Comparative analysis

We obtained data on 30 *Draco* populations (representing 26 subspecies and 13 species) from Musters'

Table 1. Sexual dimorphism in adult *Draco melanopogon* from Malaysia based on preserved museum specimens. This table compares mean values for males versus females (using unpaired two-tailed *t*-tests), and also uses analysis of covariance (ANCOVA) to examine sex differences in the relationship between snout-vent length (SVL) and other variables. These ANCOVAs all have sex as the factor, and SVL as the covariate; if slopes differ significantly, intercepts tests are meaningless and hence were not carried out. Degrees of freedom for ANCOVAs can be calculated from sample sizes. Raw data (in mm) are presented for mean values, but statistical tests were performed on transformed (natural log) data. Individuals with broken tails were excluded from these analyses

Variable	Females		Males		Unpaired <i>t</i> -tests			ANCOVA			
	<i>n</i>	Mean ± SD (range)	<i>n</i>	Mean ± SD (range)	<i>t</i>	d.f.	<i>P</i>	Slopes test		Intercepts test	
								<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
SVL	108	77.9 ± 4.1 (67–87)	106	75.7 ± 3.4 (67–83)	4.17	212	<0.0001	–	–	–	–
Tail length	80	145.1 ± 7.1 (125–161)	77	136.8 ± 7.7 (120–154)	6.91	155	<0.0001	0.82	0.37	14.95	0.0002
Wing span	108	78.4 ± 5.0 (65–89)	106	73.6 ± 5.0 (60–83)	6.05	212	<0.0001	0.06	0.81	17.74	0.0001
Wing attachment	108	45.6 ± 3.1 (38–53)	106	43.6 ± 3.0 (35–51)	4.60	212	<0.0001	2.01	0.16	4.82	0.03
Inter-limb length	108	43.8 ± 2.7 (36–51)	106	42.2 ± 2.5 (36–48)	4.22	212	<0.0001	14.18	0.001	–	–
Head length	108	14.5 ± 0.7 (12.6–16.6)	106	13.6 ± 0.8 (8.7–15.6)	8.60	212	<0.0001	0.70	0.40	49.95	0.0001
Head width	108	9.4 ± 0.5 (8.1–10.3)	106	8.9 ± 0.6 (7.7–12.3)	6.17	212	<0.0001	0.60	0.48	10.02	0.001
Axial width	108	10.6 ± 0.9 (8.9–13.2)	106	10.1 ± 1.0 (7.7–12.7)	3.26	212	0.0013	3.60	0.05	–	–

(1983) detailed taxonomic study, which provides data on mean SVLs of males and females in each of these populations, as well as on sex differences in head lengths and tail lengths relative to SVL. However, Musters does not provide sex-specific data on wing dimensions. Sample sizes are low for some populations, but any resultant error should obscure patterns in the data rather than generate them (Shine, 1987). Treating the values from each population as independent data points, our analysis shows a very strong trend for female *Draco* to have larger heads relative to SVL than do conspecific males (true for 24 of 30 comparisons, with no sex difference in the other six cases; paired two-tailed $t_{29} = 8.61$, $P < 0.0001$), and a weaker (but still significant) trend for females to attain larger mean SVLs than males (true for 19 cases, with males larger in the other 11 taxa; paired two-tailed $t_{29} = 2.19$, $P < 0.04$). However, tail lengths relative to SVL do not differ consistently between male and female *Draco* (females with relatively longer tails in 17 cases, males with longer tails in another 10 cases, and no difference in the remaining 3; paired two-tailed $t_{29} = 1.70$, $P = 0.10$). Thus, the sexual dimorphism that we documented in *D. melanopogon* (females with greater SVLs, and relatively larger heads and tails) reflects a condition that is widespread in the genus *Draco*.

Why are females larger than males in some *Draco* species, whereas males are larger than females in others? To investigate this question, we calculated Gibbons & Lovich's (1990) index of sexual size dimorphism (SSD) for each taxon (the size of the larger sex divided by the size of smaller sex, arbitrarily defined as positive if females are the larger sex and negative if males are larger). Our analysis reveals strong allometry in SSD within *Draco*, with the ratio of female size to male size being greatest in the smallest species (Fig. 4; correlation between SSD and mean SVL: $r = -0.54$, $n = 30$, $P < 0.003$). Closer inspection reveals that this pattern is due to interspecific variation in male body size rather

than female body size (SSD vs male SVL, $r = -0.68$, $P < 0.0001$; SSD vs female SVL, $r = 0.31$, $P = 0.09$). That is, males are smaller than females in species with small males, whereas female size is not significantly correlated with the degree of sexual size dimorphism. Phylogenetic analysis using independent contrasts yielded the same result, with evolutionary changes in male (but not female) body size being accompanied by shifts in the degree of sexual size dimorphism (changes in SSD vs changes in male size, regressed through the origin, $r = -0.62$, $n = 15$ contrasts, $P < 0.02$; changes in SSD vs changes in female size, $r = -0.12$, $n = 15$, $P = 0.65$). We note, however, that Musters (1983) provides little explanation as to how he derived his phylogenetic hypothesis, and it would be advisable to

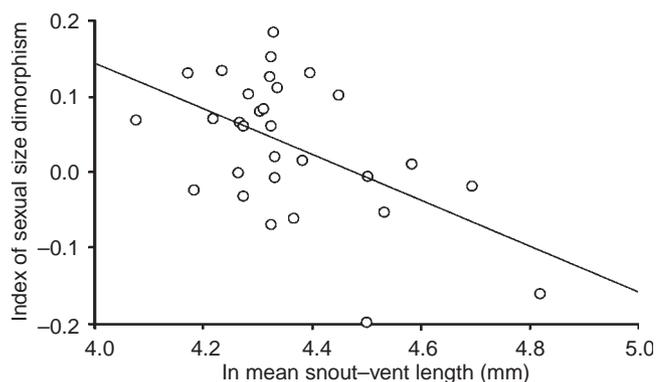


Fig. 4. Sexual size dimorphism among different taxa of 'flying lizards' within the genus *Draco* is related to mean body size; larger species tend to have males larger than females, whereas the reverse is true for smaller species. Each data point represents a single population. 'Mean snout-vent length' = arithmetic mean of male and female values. The index of sexual size dimorphism is calculated using Gibbons & Lovich's (1990) technique; the more positive the score, the larger the female relative to the male. Raw data are taken from Musters (1983); see text for statistical analysis.

repeat the above analysis with a more rigorously based phylogeny.

DISCUSSION

Our measurements reveal that *Draco melanopogon* displays a series of unusual features in reproductive biology and sexual dimorphism, that plausibly might be associated with the evolution of gliding locomotion.

Reproductive output

The most notable feature is the low and essentially invariant clutch size (i.e. two eggs) in all females. This situation offers a strong contrast to most lizard species, in which clutch sizes are highly variable and are typically correlated with maternal body size (e.g. Fitch, 1970). However, despite its invariant clutch size, total clutch volume increases with female body size in *Draco* because of an increase in egg size (width but not length) in larger females. Both of these patterns are unusual, but not unique, among lizards (e.g. Werner, 1989; Doughty, 1996b, 1997). Low and invariant clutch sizes have evolved in several lineages of lizards, usually in species of small body sizes (Shine & Greer, 1991). In particular, several lineages of tropical arboreal lizards have independently evolved a constellation of traits involving a slender body, a low clutch volume, and frequent production of small clutches (e.g. Andrews & Rand, 1974; Vitt, 1986).

The slender body form and low clutch volume may represent adaptations for arboreal mobility, with the evolution of gliding favouring even more extreme development of these features. It is tempting to attribute the evolution of a fixed clutch size of two eggs to the need for female *Draco* to maintain balance while gliding, a problem whose solution may be facilitated by an even rather than odd number of eggs. However, the independent evolution of two-egg clutches in many non-gliding lizard lineages (Shine & Greer, 1991) suggests that this explanation is unnecessarily complex. Records of larger clutches in other *Draco* species (Musters, 1983; Mori & Hikida, 1993) also militate against this hypothesis.

The situation is similar with respect to the increase in egg volume with maternal body size. This trend is consistent with maintenance of constant weight-loading during gliding, but an analogous phenomenon is seen in many (but not all) non-gliding lizard species with fixed clutch sizes (e.g. Vitt, 1986; Michaud & Echternacht, 1995; Doughty, 1996b, 1997). Given that a female *Draco* cannot increase her clutch size, and that maternal body volumes constrain reproductive output in many reptiles (Shine, 1992), it seems likely that larger female *Draco* simply take advantage of available abdominal space by increasing egg size. The increase occurs by way of egg width rather than egg length, supporting the notion that space constraints within the female's body (or pelvic diameter) may determine maximal egg size. The consis-

tent anterior-posterior placing of eggs on either side of the body (Fig. 2) could also be interpreted in terms of enhancing maternal stability during gliding (by spreading the payload: Norberg, 1990) but again, similar spacing also occurs in non-flying lizard species (Doughty, 1996b, 1997). Hence, we see no compelling reason to interpret the low and invariant clutch size of *Draco*, the increase in egg size with maternal body size, or the anterior-posterior displacement of eggs on either side of the body, as adaptations to gliding locomotion.

Sexual dimorphism

Patterns of sexual dimorphism in *D. melanopogon* may be linked more directly to locomotor mode. Female *D. melanopogon* grow larger than males, and have larger heads and longer tails relative to body length. All of these traits are unusual among agamid lizards, and the two latter conditions appear to be unique to *Draco*, and, possibly unique among all lizards. Thus, *D. melanopogon* is unusual among agamids, but not unique, in having females that attain larger body sizes than males. Although males are generally the larger sex in agamids, the direction of sexual dimorphism in adult body size varies considerably among species (Table 2; see also Greer, 1989) and the same is true even within the genus *Draco* (Musters, 1983; Inger, 1983; Mori & Hikida, 1992). Our analyses of Musters' (1983) data indicate a significant allometry in the degree of sexual size dimorphism, with males attaining larger body sizes than females only in the largest *Draco* species (Fig. 4). The same kind of allometry, in the same direction, has been documented in a diverse array of other reptilian groups (e.g. Berry & Shine, 1980; Shine 1994), as well as in other kinds of animals (e.g. Shine, 1979; Reiss, 1989). It is tempting to interpret patterns of sexual dimorphism in *Draco* in adaptationist terms. For example, functional constraints associated with gliding might impose stronger selection for some aerodynamically optimized body size in females than in males, possibly explaining why the latter sex shows more variation in mean body size (and thus, largely determines the direction of sexual size dimorphism). However, the common occurrence of this kind of allometry suggests that there is no need to invoke *Draco*-specific explanations for the phenomenon.

More surprisingly, female *D. melanopogon* have larger heads and longer tails than males at the same body length. We do not know of any prior records of these conditions in lizards. Head sizes relative to body size are frequently dimorphic, but always (to our knowledge) in the direction of larger head sizes in males than in same-sized females (see Table 2). Similarly, in all other agamid species for which we could find information, males have tails at least as long as those of females of the same body length (Table 2). In view of the generality that male lizards have never been reported to have smaller heads or shorter tails than conspecific females of the same body size, we see these patterns in *Draco* as the most surprising results from our study. Musters' (1983)

Table 2. The direction of sexual dimorphism in agamid lizards (excluding *Draco*), based on published and unpublished data. This table shows which sex achieves the larger mean adult body size, the larger head relative to snout–vent length, and the longer tail relative to snout–vent length (SVL). M = male; F = female

Species	Sex with larger mean body size	Sex with larger head relative to SVL	Sex with longer tail relative to SVL	Authority
<i>Agama agama</i>	M	M	M	Harris, 1964; Chapman & Chapman, 1964
<i>A. tuberculata</i>	M	M	M	Waltner, 1991
<i>Amphibolurus muricatus</i>	M	M	M = F	J. E. Taylor, pers. comm.
<i>Calotes cristatellus</i>	M	M	M	Ota & Hikida, 1991
<i>Chlamydosaurus kingii</i>	M	M	?	Shine, 1990
<i>Ctenophorus caudicinctus</i>	M	M	M	Storr, 1967; pers. obs.
<i>C. fionni</i>	M	M	M	Johnston, 1996
<i>C. maculosus</i>	M	M	M	M. Olsson, pers. comm.
<i>C. nuchalis</i>	M	M	M	J. Koenig, pers. comm.
<i>Hypsilurus boydii</i>	F	M	M = F	G. Torr, pers. comm.
<i>H. spinipes</i>	M	M	M	A. Manning, pers. comm.
<i>Japalura swinhonis</i>	M	M	?	Lin Jun, 1978
<i>Lophognathus gilberti</i>	M	M	M = F	P. Harlow, pers. comm.
<i>L. temporalis</i>	M	M	M = F	P. Harlow, pers. comm.
<i>Physignathus lesueurii</i>	M	M	M	P. Harlow, pers. comm.
<i>Pogona</i> , 3 species	M	M	M	Badham, 1976
<i>P. minor</i>	M = F	M	M	Witten, 1994
<i>P. vitticeps</i>	M	M	M	Witten, 1994
<i>Tympanocryptis adelaidensis</i>	F	?	M	Bamford, 1992

data suggest that the larger relative head size of females is a consistent feature of many (all?) *Draco* species, but that longer tails in females are not.

Given uncertainties about the phylogenetic affinities of *Draco*, coupled with the scarcity of reliable data on patterns of sexual dimorphism in body sizes or body proportions among agamids in general, we are unable to quantitatively test the proposition that the condition seen in *Draco* is truly unique, and represents a set of traits that evolved at about the same time that gliding developed in this lineage. Thus, we cannot be confident of any functional link between gliding and the unusual sexual dimorphism seen in *D. melanopogon*. However, given the fact that *Draco* is highly unusual both in its locomotor mode and in its sexual dimorphism relative to other lizards in general, we will proceed to explore possible causal pathways that might link these two traits. Additional information on the phylogenetic relationships and reproductive traits of Asian agamid lizards might show that the scenarios described below are overly simplistic.

The patterns of sexual dimorphism in *D. melanopogon* are potentially explicable in several ways, but some of these arguments are much stronger than others. Below, we review these alternative hypotheses.

1. *The sex differences are due to age differences rather than adaptation.* If males are on average younger than females (because of higher mortality rates in males), the size difference between the sexes (Table 1) might be due to this factor rather than adaptation. However, this hypothesis is not supported by available survival data from field populations of *Draco* (Mori & Hikida, 1993), and in any case cannot explain the sex divergence in body proportions.

2. *The sex differences reflect adaptations to enhance gliding ability in egg-carrying females.* The larger body sizes, relative head sizes and relative tail lengths of female *Draco* may be viewed as a set of adaptations that enhance a female's ability to glide while she is carrying eggs. That is, decrements in locomotor performance of gravid females may constitute a 'cost of reproduction' in this species, such that natural selection has favoured a suite of morphological changes that reduce the magnitude of this cost. Plausibly, lowered mobility might reduce a female's ability to evade predators, to capture prey, to move to egg-laying sites, and so forth. By growing to a larger body size, females achieve a lower relative clutch mass, and hence reduce the extent of wing-loading (i.e. lower payload relative to surface area of the wing; Norberg, 1990). By having large heads and long tails relative to body size, females have stabilizing mass at either extreme of the body, in locations that would plausibly enhance aerial mobility and gliding stability (e.g. Morris, 1984). Perhaps the best analogy is with paper aeroplanes; we suggest that the large head of a female *Draco* serves the same function as a paper-clip attached to the front of the glider (Morris, 1984). Although our gliding trials with preserved specimens offer only a crude simulation of natural 'flight', it is interesting to note that flight distances were significantly enhanced by larger relative head sizes. Previous studies have also interpreted the larger body size of females in flying organisms as adaptations to reduce the relative mass of the clutch and hence, the degree of locomotor impairment of gravid females. For example, this hypothesis has been used to explain the trend for females to grow larger than conspecific males in most raptorial birds (e.g.

Andersson & Norberg, 1981). In bats, females not only grow larger in many species, but tend to have larger wings relative to body size (Myers, 1978).

3. *The small body size of males is an adaptation to increase manoeuvrability while gliding.* If male *Draco* glide more often than females, in the context of social interactions among competing males, manoeuvrability may be more important for this sex (Mori & Hikida, 1992). Aerodynamic models suggest that smaller body size might enhance manoeuvrability (Norberg, 1990). A similar hypothesis (sexual selection for small male size to enhance agility in three-dimensional contests) has been advocated to explain the 'reversed' (males smaller) dimorphism of some species of birds and seals (Alexander *et al.*, 1979; Andersson, 1994), and is also broadly consistent with patterns of sexual dimorphism in aquatic vs terrestrial turtles (Berry & Shine, 1980). Under this hypothesis, the smaller heads and shorter tails of male *Draco* could be interpreted as adaptations for additional manoeuvrability. This hypothesis is similar to the one listed directly above, in that it relies upon sex-specific adaptations to gliding.

4. *The larger body size of females is due to fecundity selection.* Larger body size does not increase clutch size in *D. melanopogon* (because almost all clutches consist of two eggs), but genes for large size in females may have been favoured because larger females tend to produce larger eggs, and they might also produce eggs more frequently (although we have no evidence of the latter phenomenon). However, this hypothesis cannot explain the apparently distinctive pattern of sexual dimorphism in relative head size or tail length of *D. melanopogon*, and we see no reason why fecundity selection should be more intense on female *Draco* than on females of other lizard species.

5. *The small body size of males is due to less intense sexual selection on this sex.* If males do not fight (or if success in fighting does not enhance male reproductive success), they may be under less sexual selection for larger body size and head size; hence, other (energy-based?) advantages of smaller size might result in an evolutionary reduction of these traits in males. Available data do not fit this hypothesis; male *Draco* are territorial (Mori & Hikida, 1994), and larger body size seems to enhance reproductive success in this sex (Mori & Hikida, 1993, 1994).

6. *The small head size of males is an adaptation related to the large dewlap of this sex.* Male *Draco* have large dewlaps which they extend in social displays. Conceivably, smaller head size might facilitate maximal extension of the dewlap, by reducing the size of the lingual process of the hyoid which must be rotated dorsally as the dewlap is extended (S. Emerson, pers. comm.). However, a reduction in male head size does not occur in other male agamids with prominent display structures erected by hyoid movement (e.g. *Chlamydosaurus*, *Pogona*, Table 2), leading us to doubt the biomechanical underpinnings of this hypothesis. The same objection can be levelled against the idea that small head size in males is adaptive because it somehow

facilitates display effectiveness (e.g. if females or other males respond to dewlap size relative to head size).

7. *Sex differences in body size reflect adaptations to thermal biology.* If the sexes differ in activity patterns, microhabitats, or thermal preferences, differences in body size may affect their thermal regimes. Although these kinds of thermal issues may be significant for some ectotherms (e.g. butterflies, Gilchrist, 1990), they seem unlikely to play a role in thermoconforming lizards in tropical forest with high stable ambient temperatures (Mori & Hikida, 1993; Rummery *et al.*, 1995). Also, this hypothesis does not predict sex differences in body proportions.

8. *The sexes have evolved to fill different ecological niches.* This hypothesis does not explain why it should be females rather than males that are the larger sex, and available data do not support the idea of sex divergence in diets in *Draco* (Mori & Hikida, 1994).

It is important to recognize that these hypotheses are not mutually exclusive; indeed, the observed patterns of sexual dimorphism in *D. melanopogon* may be due to a complex mixture of several such processes. Unfortunately, some of these hypotheses make similar predictions; for example, both the 'female burdening' and 'male manoeuvrability' hypotheses (see hypotheses 2 and 3 above) predict that females should glide less often, and less readily, than males. Thus, verification of this prediction (Mori & Hikida, 1994) does not help to eliminate either hypothesis. Nonetheless, it should be possible to evaluate the importance of each of these hypotheses with further work. Experimental manipulations (e.g. adding 'loads' to different parts of the body) would enable strong tests of our ideas concerning the effects of dimorphic traits on gliding ability. One of the most exciting aspects of this topic is its enormous potential for comparative studies on independently-evolved systems, and hence for strong tests of the generality of these ideas. For example, gliding has evolved independently in several lineages of reptiles including agamid, iguanian, gekkonid, and lacertid lizards, and colubrid snakes (e.g. Schiotze & Volsoe, 1959; Russell, 1979; Losos, Papenfuss & Macay, 1989; Garland & Losos, 1994) as well as in various mammalian lineages including flying lemurs, flying squirrels, and gliding possums. Many evolutionary transitions between flying and non-flying forms have been documented also in both insects and birds, and gliding has evolved in frogs and fishes (Duellman & Trueb, 1986; Hildebrandt, 1995). These independently-evolved systems provide ideal material with which to test predictions from adaptationist hypotheses, such as the idea that the expression of sex differences in morphology is influenced by sex differences in 'costs of reproduction'.

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REFERENCES

- Alexander, R. D., Hoogland, J. L., Howard, R., Noonan, K. M. & Sherman, P. W. (1979). Sexual dimorphism and breeding systems in pinnipeds, ungulates, primates and humans. In *Evolutionary biology and human social behaviour*: 402–435. Chagnon, N. A. & Irons, W. D. (Eds). North Scituate, Massachusetts: Duxbury Press.
- Andersson, M. (1994). *Sexual selection*. New Jersey: Princeton University Press.
- Andersson, M. & Norberg, R. A. (1981). Evolution of reversed sexual size dimorphism and role partitioning among raptors, with a size scaling of flight performance. *Biol. J. Linn. Soc.* **15**: 105–130.
- Andrews, R. & Rand, A. S. (1974). Reproductive effort in anoline lizards. *Ecology* **55**: 1317–1327.
- Badham, J. A. (1976). The *Amphibolurus barbatus* species group. *Aust. J. Zool.* **24**: 423–443.
- Bamford, M. J. (1992). Growth and sexual dimorphism in size and tail length in *Tympanocryptis adelaidensis* (Lacertina: Agamidae). *Herpetofauna* **22**: 25–30.
- Bell, G. (1980). The costs of reproduction and their consequences. *Am. Nat.* **116**: 45–76.
- Berry, J. F. & Shine, R. (1980). Sexual size dimorphism and sexual selection in turtles (Order: Chelonia). *Oecologia (Berlin)* **44**: 185–191.
- Blackburn, D. G. & Evans, H. E. (1986). Why are there no viviparous birds? *Am. Nat.* **128**: 165–190.
- Chapman, B. M. & Chapman, R. F. (1964). Observations on the biology of the lizard *Agama agama* in Ghana. *Proc. zool. Soc. Lond.* **143**: 121–132.
- Colbert, E. H. (1967). Adaptations for gliding in the lizard *Draco*. *Amer. Mus. Novitates* **2283**: 1–20.
- Darwin, C. (1871). *The descent of man and selection in relation to sex*. London: Murray.
- Doughty, P. (1996a). Statistical analysis of natural experiments in evolutionary biology: comments on recent criticisms of the use of comparative methods to study adaptation. *Am. Nat.* **148**: 943–956.
- Doughty, P. (1996b). Allometry of reproduction in two species of gekkonid lizards (*Gehyra*): effects of body size miniaturization on clutch and egg sizes. *J. Zool. (Lond.)* **260**: 703–715.
- Doughty, P. (1997). The effects of 'fixed' clutch sizes on lizard life-histories: reproduction in the Australian velvet gecko, *Oedura lesueurii*. *J. Herpetol.* **31**: 266–272.
- Duellman, W. E. & Trueb, L. (1986). *Biology of amphibians*. New York: McGraw-Hill.
- Emerson, S. B. & Koehl, M. A. R. (1990). The interaction of behavioral and morphological change in the evolution of a novel locomotor type: 'flying' frogs. *Evolution* **44**: 1931–1946.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.* **125**: 1–15.
- Fitch, H. S. (1970). Reproductive cycles in lizards and snakes. *Univ. Kans. Mus. Nat. Hist. Misc. Publ.* **52**: 1–247.
- Gans, C. (1975). Tetrapod limblessness: evolution and functional corollaries. *Am. Zool.* **15**: 455–467.
- Garland, T. Jr. & Losos, J. B. (1994). Ecological morphology of locomotor performance in squamate reptiles. In *Ecological morphology: integrative organismal biology*: 240–302. Wainwright, P. C. & Reilly, S. M. (Eds). Chicago: University of Chicago Press.
- Gibbons, J. W. & Lovich, J. E. (1990). Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). *Herpetol. Monogr.* **4**: 1–29.
- Gilchrist, G. W. (1990). The consequences of sexual dimorphism in body size for butterfly flight and thermoregulation. *Funct. Ecol.* **4**: 475–487.
- Greer, A. E. (1989). *Biology and evolution of Australian lizards*. Sydney, New South Wales: Surrey Beatty & Sons.
- Harris, V. A. (1964). *The life of the rainbow lizard*. London: Hutchinson.
- Harvey, P. H. & Pagel, M. D. (1991). The comparative method in evolutionary biology. In *Oxford studies in ecology and evolution*: 1–239. May, R. M. & Harvey, P. H. (Eds). Oxford: Oxford University Press.
- Hildebrandt, M. (1995). *Analysis of vertebrate structure*. 4th edn. New York: John Wiley.
- Inger, R. F. (1983). Morphological and ecological variation in the flying lizards (genus *Draco*). *Fieldiana (Zool), New Series* No. 18: 1–35.
- Johnston, G. R. (1996). Behavioural ecology of the Peninsula Mallee Dragon lizard, *Ctenophorus fionni*. unpublished PhD thesis, School of Biological Sciences, Flinders University, Adelaide, South Australia.
- Lin Jun, I. (1978). Reproductive biology, and seasonal fat body and liver cycles in the Taiwan tree dragon: *Japalura swinhonis formosensis*. *Biol. Bull. Dept. Biol., Coll. Sci., Tunghai Univ.* **49**: 1–12.
- Losos, J. B., Papenfuss, T. J. & Macay, J. R. (1989). Correlates of sprinting, jumping, and parachuting performance in the butterfly lizard, *Leiolepis belliani*. *J. Zool. (Lond.)* **217**: 559–568.
- Madsen, T. & Shine, R. (1995). Costs of reproduction influence the evolution of sexual size dimorphism in snakes. *Evolution* **48**: 1389–1397.
- Michaud, E. J. & Echternacht, A. C. (1995). Geographic variation in the life history of the lizard *Anolis carolinensis* and support for the pelvic constraint model. *J. Herpetol.* **29**: 86–97.
- Mori, A. & Hikida, T. (1992). A preliminary study of sexual dimorphism in wing morphology of five species of the flying lizards, genus *Draco*. *Japanese J. Herpetol.* **14**: 178–183.
- Mori, A. & Hikida, T. (1993). Natural history observations of the flying lizard, *Draco volans sumatranus* (Agamidae, Squamata) from Sarawak, Malaysia. *Raffles Bull. Zool.* **41**: 83–94.
- Mori, A. & Hikida, T. (1994). Field observations on the social behaviour of the flying lizard, *Draco volans sumatranus*, in Borneo. *Copeia* **1994**: 124–130.
- Morris, C. (1984). *Advanced paper aircraft construction Mk. II. More easy-to-make flyable models*. Sydney: Angus & Robertson.
- Mueller, H. C. & Meyer, K. (1985). The evolution of reversed sexual dimorphism in size: a comparative analysis of the Falconiformes of the western Palearctic. *Curr. Ornithol.* **2**: 65–101.
- Musters, C. J. M. (1983). Taxonomy of the genus *Draco* L. (Agamidae, Lacertilia, Reptilia). *Zool. Verh.* No. 199: 1–120.
- Myers, P. (1978). Sexual dimorphism in size of vespertilionid bats. *Am. Nat.* **112**: 701–711.
- Norberg, U. M. (1990). *Vertebrate flight*. New York: Springer-Verlag.
- Ota, H. & Hikida, T. (1991). Taxonomic review of the lizards of the genus *Calotes* Cuvier 1817 (Agamidae Squamata) from Sabah, Malaysia. *Trop. Zool.* **4**: 179–192.
- Purvis, A. & Rambaut, A. (1995). Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Comput. Appl. Biosci.* **11**: 247–251.

- Reiss, M. J. (1989) *The allometry of growth and reproduction*. Cambridge: Cambridge University Press.
- Rummery, C., Shine, R., Houston, D. L. & Thompson, M. B. (1995). Thermal biology of the Australian forest dragon, *Hypsilurus spinipes* (Agamidae). *Copeia* **1995**: 818–827.
- Russell, A. P. (1979). The origin of parachuting locomotion in gekkonoid lizards (Reptilia: Gekkonidae). *Zool. J. Linn. Soc.* **65**: 233–249.
- Schiotze, A. & Volsoe, H. (1959). The gliding flight of *Holapsis guentheri* (Gray), a West African lacertid. *Copeia* **1959**: 259–260.
- Shine, R. (1979). Sexual selection and sexual dimorphism in the Amphibia. *Copeia* **1979**: 297–306.
- Shine, R. (1980). 'Costs' of reproduction in reptiles. *Oecologia (Berl.)* **46**: 92–100.
- Shine, R. (1987). Sexual selection in amphibians: a reply to Halliday and Verrell. *Herpetol. J.* **1**: 202–203.
- Shine, R. (1988). Constraints on reproductive investment: a comparison between aquatic and terrestrial snakes. *Evolution* **42**: 17–27.
- Shine, R. (1990). Function and evolution of the frill of the frillneck lizard, *Chlamydosaurus kingii* (Sauria: Agamidae). *Biol. J. Linn. Soc.* **40**: 11–20.
- Shine, R. (1992). Relative clutch mass and body shape in lizards and snakes: is reproductive investment constrained or optimized? *Evolution* **46**: 828–833.
- Shine, R. (1994). Sexual size dimorphism in snakes revisited. *Copeia* **1994**: 326–346.
- Shine, R. & Greer, A. E. (1991). Why are clutch sizes more variable in some species than in others? *Evolution* **45**: 1696–1706.
- Storr, G. M. (1967). Geographic races of the agamid lizard *Amphibolurus caudicinctus*. *J. Roy. Soc. Western Aust.* **50**: 49–56.
- Trivers, R. L. (1972). Parental investment and sexual selection. pp. 136–179. In *Sexual selection and the descent of man 1871–1971*. B. Campbell (Ed.). Chicago: Aldine.
- Vitt, L. J. (1986). Reproductive tactics of sympatric gekkonid lizards with a comment on the evolutionary and ecological consequences of invariant clutch size. *Copeia* **1986**: 773–786.
- Waltner, R. C. (1991). Altitudinal ecology of *Agama tuberculata* Gray in the Western Himalayas. *Univ. Kans. Mus. Nat. Hist. Misc. Publ.* **83**: 1–74.
- Werner, Y. L. (1989). Egg size and egg shape in near-eastern gekkonid lizards. *Israel J. Zool.* **35**: 199–213.
- Witten, G. J. (1994). Relative growth in *Pogona* (Reptilia: Lacertilia: Agamidae). *Mem. Qld. Mus.* **37**: 345–356.