Biological Journal of the Linnean Society, 2007, **90**, 1–13. With 4 figures

Predator foolhardiness and morphological evolution in 17-year cicadas (*Magicicada* spp.)

UTA OBERDÖRSTER† and PETER R. GRANT*

Department of Ecology and Evolutionary Biology, Princeton University, Princeton NJ 08544–1003, USA

Received 8 June 2005; accepted for publication 15 January 2006

Periodical cicadas in the genus *Magicicada* have an unusual life history that includes an exceptionally long life cycle and a massive, synchronized emergence. Considerable effort has been put into research aimed at understanding the evolutionary history of periodical cicadas, but surprisingly little attention has been given to their morphological evolution. Their slow flight and approachability have been described as 'predator-foolhardy' behaviour. We quantified flight speeds for *M. cassini, M. septendecim,* and *Tibicen chloromera* (a nonperiodical cicada species), and interpreted them in terms of thorax musculature, body proportions and wing size and shape in relation to body size. On average, *T. chloromera* flew three to four times faster than did the two *Magicicada* species. Using empirical relationships between flight speed and body length, body mass or wing loading, we determined *M. cassini* and *M. septendecim* to be unusually slow fliers for their body size, whereas *T. chloromera* was not. The relatively slow flight speeds of *Magicicada* species could be largely accounted for by relatively small thoracic muscle masses, as indicated by thorax length × width measurements, and low wing loadings. Aspect ratio differences were contributing factors. Male *Magicicada* and female *Tibicen* were more active in mate searching than was the opposite sex, and correspondingly had relatively large aspect ratios. We interpret the morphological traits responsible for the slow flight of *Magicicada* species as being adaptations to searching for mates in dense aggregations around the canopy of trees, relatively unconstrained by the per-capita risk of predation.

ADDITIONAL KEYWORDS: aspect ratio – flight speed –mate searching – predation risk – sexual differences – thorax muscles – *Tibicen* – wing loading.

INTRODUCTION

Periodical cicadas, in the genus *Magicicada*, have an unusual life history that includes an exceptionally long life cycle and a massive, synchronized emergence. Millions of individuals emerge in May or June after spending 13 or 17 years as nymphs underground, feeding on sap from roots (Dybas & Davis, 1962; Leonard, 1964; Lloyd & Dybas, 1966a). During a brief 2–6-week period above ground, they mate, lay eggs, and die. Although their phylogenetic history is not well known, *Magicicada* are believed to be derived from a single, fully periodical ancestor that lived before the last maximum glaciation 18 000 years ago (Cooley, Simon & Marshall, 2003), and perhaps as much as or more than 3 Mya (Grant, 2005). The ancestral state is assumed to be a shorter life cycle of 2–9 years (Karban, 1986) and not aperiodic like contemporary relatives in other genera. Only seven out of 1500 species of cicadas have evolved to be periodical (Lloyd & Dybas, 1966b; Williams & Simon, 1995; Marshall & Cooley, 2000; Cooley *et al*., 2001).

The periodicity, synchrony, and extraordinary local abundance of *Magicicada* have long been a challenge for evolutionary biologists (Alexander & Moore, 1962; Lloyd & Dybas, 1966b; Heliövaara, Vaisinen & Simon, 1994; Williams & Simon, 1995). Several hypotheses have been advanced to explain the prime-number lengths of their life cycles (Karban, 1986; Cox & Carlton, 1988; Cox & Carlton, 1990; Yoshimura, 1997; Cox & Carlton, 1998), their historical and current distributions (Dybas & Lloyd, 1974; Yoshimura, 1997; Cox & Carleton, 1998; Simon *et al*., 2000; Marshall, Cooley

---

*Corresponding author. E-mail: prgrant@princeton.edu

†Current address: School of Law, Vanderbilt University, Nashville, TN 37235, USA

& Simon, 2003), their mating and courtship behaviour (Alexander & Moore, 1958, 1962; Marshall & Cooley, 2000; Cooley & Marshall, 2001, 2004; Cooley *et al*., 2001), and the genetic relatedness of populations (Lloyd, Kritsky & Simon, 1983; Martin & Simon, 1990; Simon, 1992; Williams & Simon, 1995; Simon *et al*., 2000). The long time spent underground and their synchronous emergence have been interpreted as a strategy that minimizes below-ground competition, parasitism, and above-ground predation (Lloyd & Dybas, 1966a, 1966b; Hoppenstaedt & Keller, 1976; Lloyd & White, 1976; Bulmer, 1977; Karban, 1982; Martin & Simon, 1988, 1990; Williams & Simon, 1995; Behncke, 2000).

Two traits, however, have received surprisingly little attention from evolutionary biologists. These are their extreme approachability and slow flight, in which periodical cicadas differ from all other cicadas with shorter life cycles (Beamer, 1931; Lloyd & Dybas, 1966b; White *et al*., 1983). These traits have been referred to as 'predator-foolhardy' (Lloyd & Dybas, 1966b), because, in the absence of defenses, individuals are extremely vulnerable to predation from birds and mammals (Lloyd & Dybas, 1966a, 1966b; Dybas, 1969; Karban, 1982). Predator-foolhardy traits could only have evolved after the cicadas had achieved such high population densities that predators could not reduce population sizes significantly (Lloyd & Dybas, 1966b), and indeed avian predators, which are their most significant enemies, become satiated quickly (Karban, 1983).

Of the two predator-foolhardy traits, approachability has stimulated the most discussion. Lloyd & Dybas (1966b) suggested that its converse, wariness, may be advantageous in a sparse population where secretive behaviour is required to avoid predators, but disadvantageous at high density such as found in the large and loud aggregations of mate-seeking periodical cicadas (Cooley & Marshall, 2001, 2004). The other trait, slowness in flight, has been measured but not explained in *M. septendecim* individuals (White *et al*., 1983), nor has it been accounted for in mechanistic terms of morphology or physiology. Wing morphology should be functionally relevant, but to our knowledge has only been examined in two studies. Simon (1983, 1992) studied wing venation patterns and found unsuspected differences between species, between broods of the same species, and to a small extent between populations of the same brood. Sanborn *et al*. (2001) included *Magicicada* in a study of wing morphology in relation to minimum flight temperature of 40 species of cicada, and showed that wing length increased isometrically with body size. Neither study investigated flight performance.

We report here a morphological study of two species of 17-year cicada, *M. cassini* and *M. septendecim.* We investigated the morphological changes that may have accompanied the evolution of predator-foolhardy behaviour by characterizing body proportions and wing size and shape in relation to body size. The closest relatives of *Magicicada* are unknown (Williams & Simon, 1995; Simon *et al*., 2000), therefore no formal phylogenetic analysis could be performed. Instead, we adopted a paired comparison method of study by including three sympatric species of the genus *Tibicen*: *T. chloromera, T. lyricen,* and *T. linnei.* Morphological differences between *Magicicada* and *Tibicen* were interpreted in terms of differences in flight performance during mate-seeking without regard to their phylogenetic relationship.

Theoretical and experimental work has established fundamental biomechanical properties of the flight apparatus of insects (Grodnitsky, 1999; Dudley, 2000; Alexander, 2002; Vogel, 2003). These studies allowed us to focus on some easily measured traits: wing length, width and area, body mass, and size of thorax. Wing size and shape have clear implications for flight speed, and thoracic muscles generate the power necessary for flight. Two other properties of the wings, wing loading and aspect ratio, are additional useful measures for interpreting the adaptive function of the overall wing morphology. Wing loading is defined as the weight of the cicada in Newtons divided by the combined area of all four wings in mm^2. The higher the value of wing loading, the faster the insect has to fly to offset the extra weight burden. The overall shape and efficiency of the wing can be described by its aspect ratio, which is the square of the wingspan divided by the combined wing area. A wing with a high aspect ratio is relatively long and narrow, and experiences less drag through the air than does a more rounded wing with a low aspect ratio; a wing with low aspect ratio has more 'tip' for its area, and this induces air vortexes that create more drag relative to lift.

The slow flight of *M. septendecim* may be the result of relatively small thoracic musculature, short wings and low wing loading, or physiological factors unconnected with morphology. Our study was designed first to quantify flight speeds of the two *Magicicada* species, second to place them in context by comparing them with other cicadas and other insects, and third to assess morphological factors as the basis of hypotheses to explain and interpret the slow flights.

MATERIAL AND METHODS

The field study of periodical cicadas was conducted from May to August 2004 on the Princeton University campus (Oberdörster & Grant, 2006a). Actively flying or singing *M. septendecim* and *M. cassini*, members of 'brood X' (Williams & Simon, 1995), were captured by hand in May and June. For the determination of flight speeds we followed the procedure of White *et al.* (1983). An individual was released in an open area near woodland after sex and species had been recorded. The mating status of females was not recorded. Flight time was measured with a stopwatch to the nearest half second; timing began when the cicada started directional flight and stopped once the cicada had landed. The distance flown was measured with a Rolatape™ 1-m distance-measuring wheel, to the nearest metre. Each animal was tested within 1 h of capture on the day of collection, and trials were conducted in the absence of wind on 4 days in late May. *M. septendecim* flight speeds were recorded under two different daily maximum temperature conditions, ~21 °C and ~30 °C. A total of 34 *M. cassini* and 81 *M. septendecim* flight speeds were recorded. Eight trials were performed with *Tibicen chloromera* in July and August at ~30 °C, and nine more were performed in the same months in 2005. These were captured by hand or with a net, or in three instances they were found as eclosing nymphs and kept for 48 h prior to release.

For morphological measurements other specimens were captured by hand. Towards the end of the *Magicicada* flying season, several specimens had worn or crinkled wings, and these were omitted from analysis. In total, 178 periodical cicadas (*M. septendecim* and *M. cassini*) were measured. Sixty-one specimens of *T. chloromera*, 25 *T. linnei* and 24 *T. lyricen* were also obtained, in one of three ways: by hand from the vegetation, from cicada-killer wasps, *Sphecius specious* (Hymenoptera), as they were dragging them to their subterranean nests, or from the ground (dead or dying). All cicadas were weighed alive or recently dead, within 1 h of capture, on an electronic balance (Denver Instruments, model TR64) to the nearest 0.01 g. Three measurements to the nearest 0.5 mm were taken from most animals with a ruler: wing length, wing width (Fig. 1) and body length with abdomen fully extended. Wing length (long axis) was measured as the distance from the shoulder joint to the wing tip of an extended forewing, and maximum width of the same wing was measured at right angles to the long axis. The combined area of a pair of wings was measured for a sample of each species by tracing an outline of the left fore- and hind-wing with a natural overlap on graph paper, and converting the enclosed number of squares to square millimeters. For the remainder, wing area was estimated from regressions of wing area on the product of wing length and width for each species separately. Measurement of length and width of the thorax were taken with calipers to the nearest 0.1 mm. Cicadas from different capture sources did not differ in mean measurements (ANOVA), and therefore we report only analyses of combined measurements for each species.

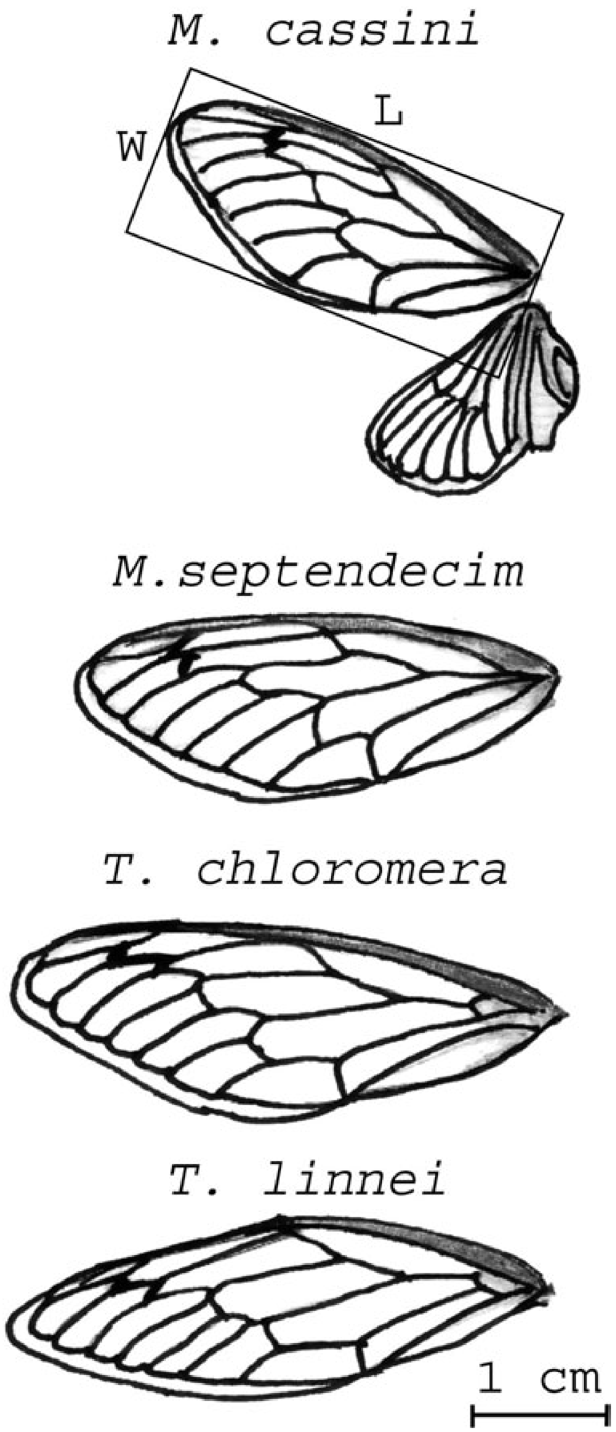

Figure 1. Wing measurements in the four study species, *Magicicada cassini, M. septendecim, Tibicen chloromera and T. linnei*. W, wing width; L, wing length.

Measurements were taken by both authors after a training session to minimize differences, and more than 100 specimens were measured independently by each observer. Measurements were standardized by adding or subtracting the difference in trait means between observers to or from the individual measurements of the first author. These differences were, on average, between 3 and 6%. For the calculations of repeatablity of unstandardized measurements by one-way ANOVA (Lessels & Boag, 1987), subsamples were measured twice, 24 h apart. Standard errors of repeatability were obtained from Becker (1992).

Both least squares regression and reduced major axis (RMA) analyses were used for bivariate analyses. Least squares regression was used for prediction and for illustrating covariation, whereas RMA was used for estimating allometric relationships between one linear trait and another, or one linear trait and overall size (mass) (Rayner, 1985). Data were ln-transformed and sex-standardized for allometric analyses. As is standard with allometric studies, all variances should be adjusted for measurement error prior to transformation by multiplying by the repeatability when it is suspected that any phenotypic variance of traits being compared will be inflated unequally by measurement error (Pagel & Harvey, 1988). Unequal measurement error directly affects the ratio of standard deviations used in an RMA model to estimate the slope of the allometric relationship. Since repeatability values of all measured traits were high, in the range 0.90–0.99 when samples of 30 individuals were measured twice (Table 1), the adjustment had little effect on the estimates of allometric slopes. Therefore, we report here only the unadjusted results. Confidence ranges for RMA slope estimates were calculated according to the method for large samples of Rayner (1985).

According to aerodynamic theory (Norberg & Rayner, 1987) the expected allometric scaling of velocity (V) with mass (m) and wing loading (p_w) when geometric similarity is maintained (Dudley, 2000; p. 80) is described by:

$$V \alpha\, m^{0.17} \quad (1)$$

$$V \alpha\, m_w{}^{0.5} \quad (2)$$

Wing loading was calculated as body weight divided by the total surface area (S) of all four wings. Aspect ratio was calculated as $4R^2/S$, where R refers to the length of one forewing. There is no expectation with respect to the scaling of aspect ratio, although a tendency for velocity to decline with increasing aspect ratio has been observed in a large sample of butterfly species (Dudley & Srygley, 1994).

Table 1. Repeatability (± SE) of measurements

Trait	*N*	Repeatability
Mass	30	0.993 ± 0.002
Body length	31	0.952 ± 0.016
Wing length	33	0.991 ± 0.003
Wing width	33	0.916 ± 0.013
Thorax length	31	0.900 ± 0.032
Thorax width	31	0.975 ± 0.009

RESULTS

FLIGHT CAPACITY

Ambient temperature had no detectable effect on the flight characteristics of male and female *M. septendecim*. The two-factor ANOVAs demonstrated that, on average, members of each sex flew at the same speed (males, $F_{1,39} = 0.529$, $P = 0.471$; females, $F_{1,38} = 1.045$, $P = 0.313$), for the same amount of time (males, $F_{1,39} = 1.576$, $P = 0.217$; females, $F_{1,38} = 0.097$, $P = 0.757$), and for the same distance (males, $F_{1,39} = 2.643$, $P = 0.112$; females, $F_{1,38} = 0.238$, $P = 0.628$) at the two temperatures. Therefore, data recorded for *M. septendecim* at the two temperatures were combined. Flight characteristics of the two *Magicicada* species and *T. chloromera* are shown in Figure 2.

The three species differed in distance flown ($F_{2,126} = 23.016$), flight duration ($F_{2,126} = 8.741$) and flight speed ($F_{2,126} = 306.724$) (all at $P < 0.001$), after controlling for possible effects of sex or sex–species interactions (all $P > 0.200$, two-factor ANOVAs; see also Table 2). On average, *M. septendecim* flew further than did *M. cassini* (Bonferroni/Dunn posthoc test, $P < 0.001$), took longer to do so ($P = 0.001$), and flew at the same speed ($P = 0.502$). In contrast, *T. chloromera* both flew significantly further distances than did *M. septendecim* and *M. cassini*, and flew much faster (Table 2) than they did ($P < 0.001$ in each case). In fact, *T. chloromera* flew almost four times faster than the *Magicicada* species, whose fastest recorded speed (5.4 ms^{-1}) was slower than the slowest speed recorded for *T. chloromera* (6.0 ms^{-1}). On average, *M. cassini* flew 27% as fast and *M. septendecim* flew 29% as fast as did *T. chloromera* (Fig. 2).

Comparisons with *T. chloromera* were not confounded by heterogeneity between years for this species; there were no significant effects of year, sex, or interaction between them in two-factor ANOVAs of distance, flight duration or speed (all $P > 0.150$). Flight speeds of two *T. linnei* males (Table 2) were close to the speeds of the larger congener, *T. chloromera*.

BODY SIZE EFFECTS

Much of the variation in insect flight speed is due to body size, and as such the *Magicicada* species were expected to differ from the *Tibicen* species in average speed because they differed in mean body size (Table 3). Velocity tends to increase across a large range of insect body sizes (Fig. 3, taken from Dudley,

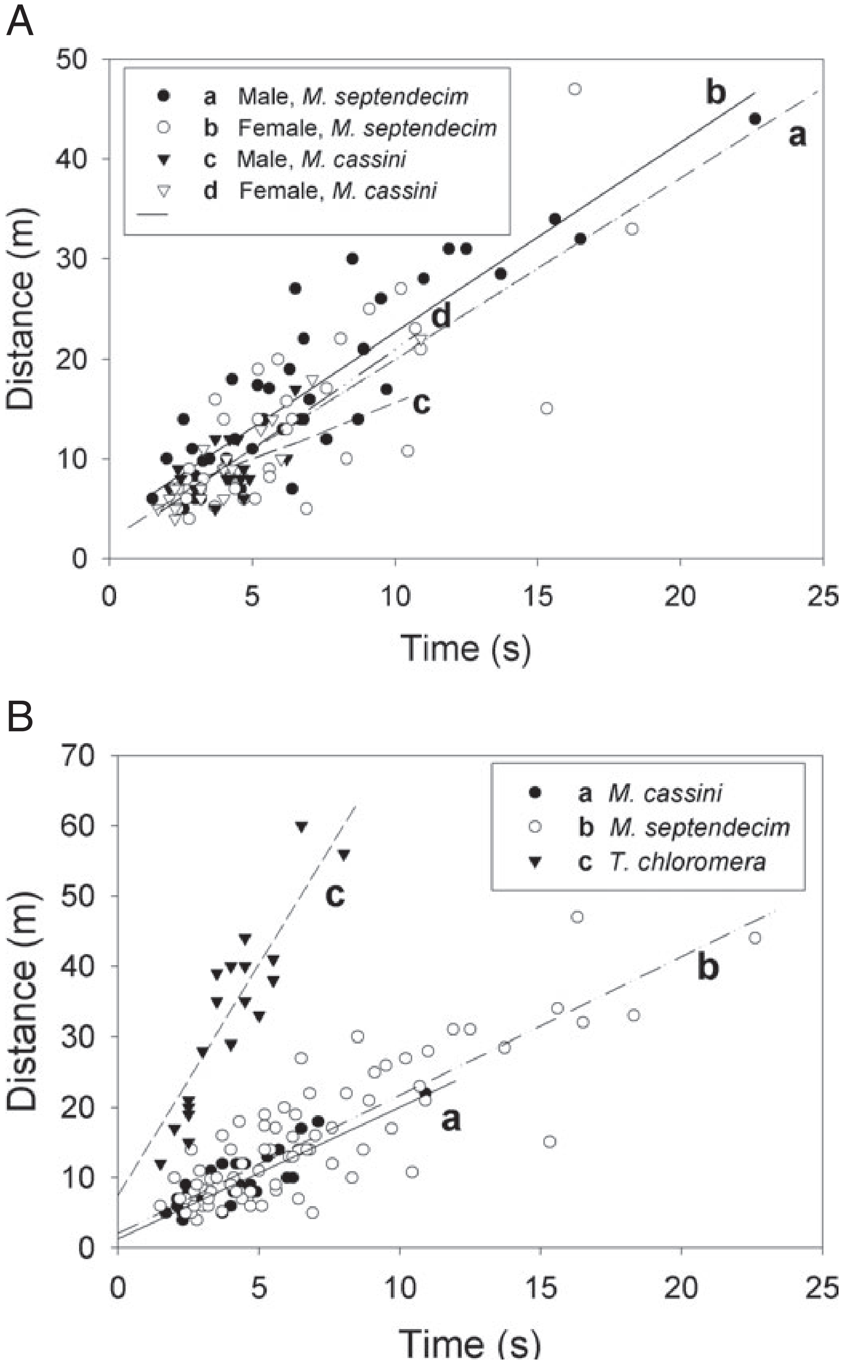

Figure 2. Least squares regressions of distance flown on duration (time) of flights. A, separate sexes of *Magicicada* species: *M. septendecim* male (●) and female (○), and *M. cassini* male (▼) and female (▽). Slopes (b ± SE): 1.74 ± 0.221 (slope a), 1.90 ± 0.161 (slope b), 1.45 ± 0.392* (slope c), 1.99 ± 0.202 (slope d); $^*P = 0.0022$, all others $P < 0.0001$. B, *Magicicada* species compared with *Tibicen chloromera*, with the sexes combined: *M. cassini* (●), *M. septendecim* (○) and *T. chloromera* (▼). Slopes (b ± SE): 1.77 ± 0.922 (slope a), 1.88 ± 0.135 (slope b), 8.16 ± 0.985 (slope c); all $P < 0.0001$.

2000). Dudley's empirical equation for log flight speed (V) as a function of log body length (BL) ($\log V = 0.86 \log BL - 0.396$), when extrapolated, predicted a velocity of 6.3 ms^{-1} for *M. cassini* and 7.2 ms^{-1} for *M. septendecim* (Fig. 3). These predicted velocities for the *Magicicada* were significantly faster than were the actual recorded speeds of 2.3 ± 0.64 ms^{-1} (mean ± SD) and 2.4 ± 0.91 ms^{-1}, respectively. Interestingly, the predicted value of 8.2 ms^{-1} for *T. chloromera* was close to the actual speed of 8.4 ± 1.36 ms^{-1} (Fig. 3);

Table 2. Flight times, distances and velocities (mean ± SD) in *Magicicada* (periodical) and *Tibicen* (nonperiodical) cicadas

Species	Sex	Time (s)	Distance (m)	Velocity (ms^{-1})
M. cassini	Male	4.15 ± 2.142 (17)	9.71 ± 4.647	2.41 ± 0.541
	Female	4.32 ± 1.536 (17)	9.00 ± 3.221	2.22 ± 0.731
	Total	4.23 ± 1.837 (34)	9.35 ± 3.953	2.31 ± 0.640
M. septendecim	Male	5.70 ± 3.194 (41)	13.61 ± 7.619	2.50 ± 0.732
	Female	8.06 ± 5.659 (40)	18.33 ± 15.417	2.38 ± 1.067
	Total	6.86 ± 4.703 (81)	15.94 ± 12.269	2.44 ± 0.909
T. chloromera	Male	3.90 ± 1.468 (10)	32.90 ± 13.617	8.40 ± 1.372
	Female	3.50 ± 1.414 (7)	29.71 ± 12.189	8.51 ± 1.447
	Total	3.74 ± 1.416 (17)	31.59 ± 12.753	8.44 ± 1.359
T. linnei	Male	6.00 (2)	42.5	7.10
	Female	–	–	–
	Total	6.00 (2)	42.5	7.10

Sample sizes are given in parentheses.

Table 3. Morphological means (± SD) in *Magicicada* (periodical) and *Tibicen* (nonperiodical) cicadas

Species	Sex	Mass (g)	Wing loading × 10^4	Aspect ratio
M. cassini	Male	0.449 ± 0.034 (27)	64.84 ± 5.148 (24)	6.88 ± 0.460 (24)
	Female	0.667 ± 0.165 (14)	83.98 ± 19.108 (14)	6.47 ± 0.374 (19)
	Total	0.523 ± 0.143 (41)	71.89 ± 15.241 (38)	6.70 ± 0.468 (43)
M. septendecim	Male	0.629 ± 0.091 (48)	66.54 ± 9.949 (48)	6.47 ± 0.802 (60)
	Female	1.077 ± 0.180 (53)	106.38 ± 16.413 (53)	6.25 ± 0.679 (71)
	Total	0.864 ± 0.267 (101)	87.45 ± 24.214 (101)	6.35 ± 0.743(131)
T. linnei	Male	1.292 ± 0.110 (8)	105.90 ± 5.446 (8)	7.16 ± 0.206 (13)
	Female	1.268 ± 0.097 (6)	103.76 ± 11.297 (5)	7.44 ± 0.174 (9)
	Total	1.282 ± 0.101 (14)	105.08 ± 7.811 (13)	7.27 ± 0.235 (22)
T. chloromera	Male	1.617 ± 0.172 (20)	127.20 ± 9.614 (18)	7.04 ± 0.417 (30)
	Female	1.775 ± 0.231 (26)	131.14 ± 14.601 (25)	7.21 ± 0.248 (27)
	Total	1.706 ± 0.220 (46)	129.49 ± 12.772 (43)	7.13 ± 0.346 (57)
T. lyricen	Male	1.652 ± 0.160 (6)	130.61 ± 12.653 (6)	7.52 ± 0.315 (11)
	Female	1.636 ± 0.180 (7)	131.68 ± 14.288 (6)	7.81 ± 0.285 (8)
	Total	1.643 ± 0.167 (13)	131.44 ± 12.880 (12)	7.64 ± 0.328 (19)

Sample sizes are given in parentheses.

thus it was not abnormal when compared with other insects and therefore could be considered representative of them. Recorded speeds of 7.0 and 7.2 ms^{-1} for two *T. linnei* individuals were a little lower, by ~10%, compared with the predicted speed of 7.8 ms^{-1}. These results support our use of *Tibicen* as a standard for comparing *Magicicada* species. We can conclude that *M. cassini* and *M. septendecim* are unusually slow fliers for their body size, in relation to other insects and in relation to a nonperiodical cicada species.

The two *Magicicada* species had smaller body masses and lower wing loading values than did the three *Tibicen* species (Table 3). These differences were well-supported statistically. There were strong differences among the species in body mass (ANOVA, $F_{4,202} = 394.865$, $P < 0.001$) independent of sex differences that existed ($F_{1,202} = 33.158$, $P < 0.001$), and there were strong differences among the species in wing loading ($F_{4,197} = 129.339$, $P < 0.0001$) independent of sex differences ($F_{1,197} = 25.011$, $P < 0.0001$). All five species differed from each of the others in wing loading (posthoc tests, $P < 0.001$ in all cases), except for *T. chloromera* and *T. lyricen* ($P = 0.6971$). Males had lower wing loadings than did females in both *Magicicada* species, but not in one of the three *Tibicen* species (*T. linnei*, Table 3).

These interspecific differences in body mass and wing loading can be used to predict mean *Magicicada*

Table 4. Thoracic means (± SD) in *Magicicada* (periodical) and *Tibicen* (nonperiodical) cicadas

Species	Sex	*N*	Thorax length (mm)	Thorax width (mm)	Width × length (mm^2)
M. cassini	Male	10	6.28 ± 0.204	6.76 ± 0.097	42.45 ± 1.519
	Female	10	7.17 ± 0.295	7.19 ± 0.213	51.57 ± 3.006
	Total	20	6.73 ± 0.519	6.98 ± 0.273	47.01 ± 5.221
M. septendecim	Male	10	7.04 ± 0.398	7.66 ± 0.255	53.92 ± 3.477
	Female	10	7.88 ± 0.496	8.24 ± 0.337	65.02 ± 5.992
	Total	20	7.46 ± 0.614	7.95 ± 0.416	59.47 ± 7.425
T. chloromera	Male	24	9.93 ± 0.580	14.16 ± 0.739	142.60 ± 11.843
	Female	31	10.05 ± 0.470	14.26 ± 0.551	145.20 ± 10.002
	Total	55	10.00 ± 0.515	14.22 ± 0.558	144.01 ± 10.940
T. linnei	Male	13	8.31 ± 0.615	12.40 ± 0.454	104.36 ± 7.996
	Female	10	8.44 ± 0.599	13.05 ± 0.471	111.42 ± 8.824
	Total	23	8.37 ± 0.597	12.68 ± 0.558	107.43 ± 8.919
T. lyricen	Male	10	9.30 ± 0.694	13.39 ± 0.816	127.22 ± 16.480
	Female	9	9.37 ± 0.603	13.80 ± 0.508	130.93 ± 12.094
	Total	19	9.33 ± 0.636	13.58 ± 0.709	128.97 ± 14.298

Width × length is an indicator of cross-sectional flight muscle area.

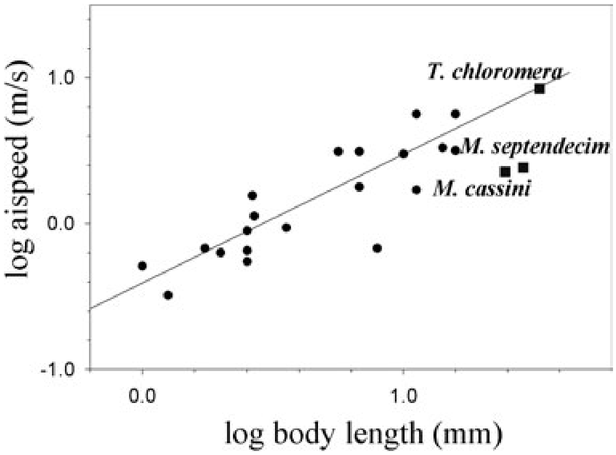

Figure 3. Scaling of allometry of insect flight speed in relation to body size (modified from Dudley, 2000, fig. 7.2). Three data points (■) have been added to Dudley's figure of several orders of insects using the average of individual airspeeds and the average of individual body lengths for *Magicicada cassini, M. septendecim,* and *T. chloromera*.

velocities using known equations relating velocity to body mass (Eq. 1) or wing loading (Eq. 2) for each species separately. We converted the equations to logarithmic form and used values of ln V and ln m (or ln p_w) from *T. chloromera* to estimate the intercept, a, in each equation. Mean velocities of the *Magicicada* species were predicted using the intercept, a, the slope, b, and estimates of mean m or mean p_w. Mean velocities of *M. cassini* and *M. septendecim* were 6.6 ms^{-1} and 7.4 ms^{-1} when estimated from their masses, and 6.1 ms^{-1} and 6.9 ms^{-1} when estimated from their wing loadings. It is interesting to note that the estimates from the empirical relationship with body length lay between these predictions. All estimates were consistent in predicting flight speeds almost three times greater than those actually flown by the periodical cicadas.

THORACIC MORPHOLOGY

The relatively slow flight speed in relation to body size of *M. cassini* and *M. septendecim* could be due to low power output. The dorsoventrally orientated flight muscles are contained in the thorax, and as a result the cross-sectional area of the thorax may be used as a plausible indicator of flight power. The two *Magicicada* species and *T. chloromera* differed in thorax length and width, as well as in the product of the two, thorax area (Table 4). Males had smaller thorax muscle areas than did females (two-factor ANOVA $F_{1,88} = 16.450$, $P < 0.001$), yet, independent of sex effects, species differed from each other ($F_{2,88} = 1338.85$, $P < 0.001$). *M. cassini* had smaller muscle areas than did *M. septendecim* (posthoc test, $P < 0.001$), and both species had much smaller muscle areas than did *T. chloromera* (posthoc test, $P < 0.001$ in each case).

On average, *M. cassini* had 33% of the thoracic muscle area of *T. chloromera,* and *M. septendecim* had 41%. On average, these two *Magicicada* species flew, respectively, at 27 and 29%, of the flight speed of *T. chloromera*. The discrepancies of 6% for *M. cassini* and 12% for *M. septendecim* were within the 95% confidence limits on estimates of both mean flight speeds and thorax muscle areas. Therefore, the relatively slow flight of the *Magicicada* species could be accounted for entirely by relatively small thoracic muscle masses.

The thorax muscle areas of the two other *Tibicen* species were smaller than were those of *T. chloromera* (Table 4), as expected from their relative body masses (Table 3), but larger than those of the two *Magicicada* species. The inclusion of *T. lyricen* and *T. linnei* in Table 4 highlights a consistent difference between the sexes in all five species; on average females had a larger thorax. This contrast was not accompanied by a consistent difference in body mass between the sexes.

ASPECT RATIO

Flight performance may also be affected by the aspect ratio of the wings. The aspect ratios of the five species were heterogeneous ($F_{4,262} = 37.721$, $P < 0.001$; two-factor ANOVA), independent of sex ($F_{1,262} = 0.052$, $P = 0.8200$). *M. septendecim* and *M. cassini* differed significantly (see Table 3), and their aspect ratios were smaller than were those of each of the three *Tibicen* species (posthoc tests, $P < 0.001$), whereas *T. linnei* did not differ from *T. lyricen* ($P = 0.0402$) or *T. chloromera* ($P = 0.3169$). On average, males had larger aspect ratios than did females in the two *Magicicada* species, but smaller aspect ratios than did females in the three *Tibicen* species (Table 3). This difference gave rise to a significant species–sex interaction in the ANOVA ($F_{4,242} = 2.970$, $P = 0.0200$).

ALLOMETRY

The two *Magicicada* species differed considerably in the way wing width scaled allometrically with wing length: negatively in *M. cassini* and positively in *M. septendecim* (Fig. 4, Table 5). Neither of the 99% confidence ranges overlapped the isometric coefficient of 1.0. The species were similar in showing negative allometry of wing length in relation to mass, again at the 99% level of support. *M. cassini* (but not *M. septendecim*) also showed negative allometry of wing width in relation to body mass at the 95% level (Table 5).

Table 5. Intraspecific allometries in *Magicicada* (periodical) and *Tibicen* (nonperiodical) cicadas: slopes of reduced major axis (RMA) model of ln-transformed and sex-standardized data (RMA = SD*y*/SD*x*)

			Actual slope (confidence range) *N*				
y variable	*x* variable	Expected slope	*M. cassini*	*M. septendecim*	*T. chloromera*	*T. linnei*	*T. lyricen*
Wing width	Wing length	1	0.97* (0.952–0.988) 43	1.357† (1.337–1.377) 131	1.192† (1.088–1.296) 61	1.077 (–) 25	1.207 (–) 24
Wing length	Mass	0.33	0.214* (0.192–0.236) 41	0.236* (0.215–0.257) 101	0.306 (0.268–0.344) 61	0.383 (–) 14	0.318 (–) 12
Wing width	Mass	0.33	0.208* (0.092–0.324) 41	0.318 (0.264–0.372) 101	0.306 (0.272–0.340) 44	0.642 (–) 14	0.385 (–) 12
Thorax length	Mass	0.33	0.474 (–) 20	0.35 (–) 20	0.43 (0.261–0.599) 44	0.827 (–) 14	0.758 (–) 12
Thorax width	Mass	0.33	0.143 (–) 20	0.229 (–) 20	0.364 (0.283–0.445) 44	0.605 (–) 14	0.385 (–) 12
Aspect ratio	Mass	–	0.416 (0.264–0.568) 41	0.567 (0.472–0.662) 101	0.405 (0.131–0.679) 44	0.309 (–) 14	0.418 (–) 12
Wing loading	Body length	3	5.172 (–) 20	3.17 (–) 20	2.939 (–) 42	1.721 (–) 14	2.806 (–) 12

Significant departures from the slope expected from isometry are indicated (*negative allometry, †positive allometry). Confidence ranges, in parentheses below the slopes, are calculated according to the large sample method of Rayner (1985) for sample sizes > 30. Samples sizes are below the confidence ranges.

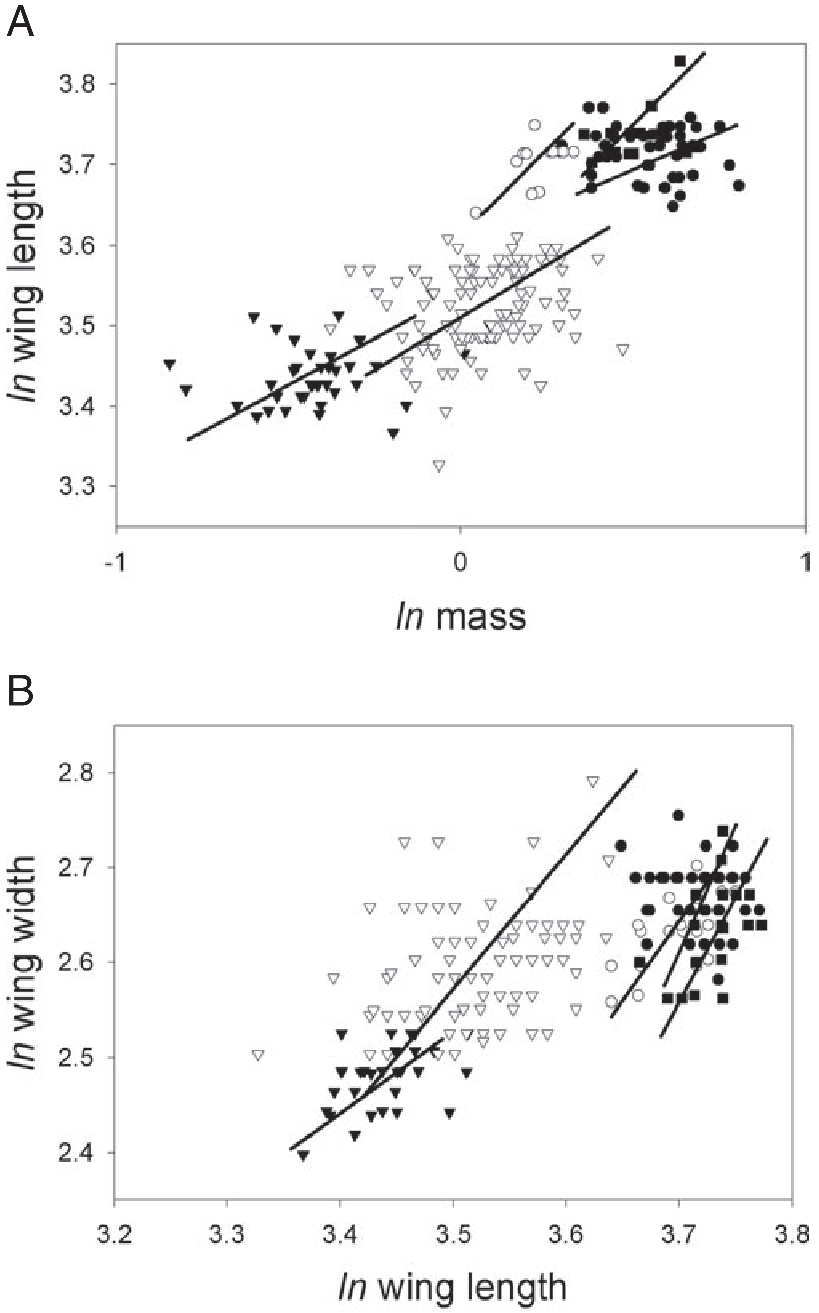

Figure 4. Intraspecific scaling of wing width and length using reduced major axis models. Wings are relatively short in *Magicicada* species in relation to body size (A) and wing width (B) when compared with *Tibicen* species. ●, *T. chloromera*; ○, *T. linnei*; ■, *T. lyricen*; ▼, *M. cassini*; ▽, *M. septendecim*.

Thus, the two species have diverged in wing proportions: the larger the species, the longer the wings, with some offset (Fig. 4A), but wing width increased faster in relation to wing length in one species (*M. septendecim*) compared with the other (*M. cassini*; Fig. 4B). Allometries of the *Tibicen* species were generally steeper. Like *M. septendecim*, *T. chloromera* displayed positive allometry in the way wing width scaled with wing length. Allometric coefficients for the aspect ratios of the two *Magicicada* species and *T. chloromera* lay mainly between 0.3 and 0.5 (Table 5).

DISCUSSION

Periodical cicadas display the predator-foolhardy behaviour of conspicuously slow flight (Beamer, 1931;

Lloyd & Dybas, 1966b). Our goal was to quantify it, explore morphological reasons for it, and suggest an evolutionary interpretation. We included *Tibicen* species in the study as a standard against which to compare *Magicicada* species because they display predator-evasive behaviour typical of cicadas in general. In the absence of a phylogeny for cicadas, we made paired comparisons, within and between genera, of traits considered alone or in the context of allometry. The use of *Tibicen* for comparative purposes was strengthened by an interordinal analysis of flight speed in relation to body size based on experimental measurements made by Lewis & Taylor (1967) and summarized by Johnson (1969). The analysis showed that *Tibicen* flight speeds are accurately predicted by body size, whereas flight speeds of the two *Magicicada* species are not. *Magicicada* species are unusually slow in flight, and their slow speeds need to be accounted for morphologically and evolutionarily.

There are no other data available for nonperiodical cicadas; hence the need for the future is to expand the sample size of flight speeds measured on other cicada species under standardized conditions. In contrast, one other study has quantified speeds of a periodical cicada species. White *et al*. (1983) reported an average ± SD flight speed of $2.1 \pm 0.9\ \mathrm{ms}^{-1}$ for 18 *M. septendecim* in natural flight over distances of up to 78 m. In a larger open space, eight healthy individuals tossed into the air flew an average distance of 206 ± 48 m at an average speed of $2.8 \pm 0.3\ \mathrm{ms}^{-1}$. The fastest individual flew at a speed of $3.8\ \mathrm{ms}^{-1}$. Our estimates of average flight speeds of *M. septendecim* males ($2.5 \pm 0.73\ \mathrm{ms}^{-1}$) and females ($2.4 \pm 1.07\ \mathrm{ms}^{-1}$) over shorter distances fell within this range, as did estimates of *M. cassini* males ($2.4 \pm 0.54\ \mathrm{ms}^{-1}$) and females ($2.2 \pm 0.73\ \mathrm{ms}^{-1}$). Thus we confirmed the slow flight speed of *M. septendecim*, and showed with *M. cassini* that slow flight is not restricted to one species in the genus. *Magicicada* flight speeds were between one third and one quarter of the average flight speed of *T. chloromera* ($8.4 \pm 1.36\ \mathrm{ms}^{-1}$).

The contrast between *Magicicada* and *Tibicen* flight performance in these trials could be misleading if flight distance per unit time was underestimated more in *Magicicada* than in *Tibicen*. This could happen if *Magicicada* took longer to accelerate to a normal equilibrium cruising speed upon release, climbed or descended more, or in other ways took more complicated three-dimensional flight trajectories than did *Tibicen*. In our experience, however, was contrary to this. If there was any recording bias arising from differences in erratic flight paths, flight distances of *Tibicen* would have been underestimated.

Flight behaviour may vary in relation to population density, as suggested for the Japanese epidemic cicada *Morgannia iwasakii* (Nagamine & Itô, 1980; Itô & Nagamine, 1981). Our study was conducted solely at very high densities of periodical cicadas and was therefore unable to detect a possible effect of crowding. If such an effect existed, it would confound flight comparisons between the middle of the emergence period and the beginning or the end, when adult cicada numbers are low and the risk of predation is high (Karban, 1982; Williams *et al*., 1993).

To account for the large difference in flight speeds between the genera *Magicicada* and *Tibicen*, we investigated the cross-sectional area of the thorax. This is a plausible indicator of flight muscle strength, although its fidelity needs to be determined. Power output and flight velocity depend upon flight muscle strength, and strength in turn depends on cross-sectional area of the dorsoventral flight muscles in the thoracic cavity (Dudley, 2000; Alexander, 2002). In the absence of direct measurements of the muscles, we used length × width of the thorax to approximate cross-sectional area. Relative to *Tibicen* species as a standard for comparison, *Magicicada* species had a much reduced cross-sectional area and corresponding reduced flight speeds. Quantitatively, the relatively slow flights of the *Magicicada* species were well predicted by their relatively small thoracic muscle masses. Small discrepancies – thorax muscle areas did not fully account for reduced flight speeds (by a few percent) – can be attributed to sampling error. Alternatively, they may be explained by the relatively low aspect ratio of their wings (discussed below).

Reduced muscle area was not a simple consequence of reduced body size. If this were the case, the thorax muscle area should scale interspecifically to the two-thirds power of mass, giving average values of $64\ \mathrm{mm}^2$ for *M. cassini* and $76\ \mathrm{mm}^2$ for *M. septendecim*. The actual values (Table 4) were much lower; $47.01 \pm 5.221\ \mathrm{mm}^2$ and $59.47 \pm 7.425\ \mathrm{mm}^2$, respectively.

There may be additional morphological, physiological, or behavioural reasons to explain why *Magicicada* fly relatively slowly. One factor could be their small size, permitting energy to be saved from slow flight. *Magicicada* species are smaller than are *Tibicen* species, and their lower wing loadings can be interpreted in energetic terms. The cross-sectional area of an insect decreases with decreasing body size more slowly than does its mass, therefore the force produced per gram of insect increases with decreased size. As a consequence, less power is needed to maintain a given speed, less energy is required (Alexander, 2002), and they can fly slower.

The evolutionary divergence of the two *Magicicada* species from each other is further reflected in the different allometric scaling of their wing dimensions. The maximum contrast observed was in the scaling of wing width in relation to wing length; this was negatively allometric in *M. cassini* and positively allometric in

M. septendecim and *T. chloromera*. These differences deserve attention, because they imply subtle differences in flight performance among individuals of different size.

Functional differences in flight performance are similarly implied by differences in aspect ratios among the cicada species. The aspect ratio affects the relationship between energy expenditure and speed. Power requirements for flight are a U-shaped function of speed, and a lower power curve can be obtained with a high aspect ratio (Norberg, 1990; Dudley, 2000; Alexander, 2002). Aspect ratios are not expected to vary systematically with body size (Norberg, 1990; Dudley, 2000). Nevertheless Dudley & Srygley (1994) found a tendency for the aspect ratio to vary inversely with body size among butterfly species, whereas Norberg & Rayner (1987) found an opposite tendency in bats and Norberg (1990) demonstrated the same with birds. The reasons for these trends are not known (Norberg, 1990; Dudley, 2000).

The two *Magicicada* species were smaller compared with the three *Tibicen* species, and had smaller aspect ratios. Two tendencies ran counter to this association. First, within each genus, the species with the largest aspect ratio was the smallest in size: *M. cassini* and *T. linnei* (Table 4). The high aspect ratio of *T. linnei* was achieved partly by an unusual departure from an elliptic wing shape in the direction of a pointed tip (Fig. 1). Second, males, the smaller sex, had higher average aspect ratios than did females in the two *Magicicada* species, whereas the difference was reversed in the three *Tibicen* species.

We interpret the sex differences adaptively in terms of the different mating systems of the two genera. *Tibicen* females approach acoustically signalling, stationary, males, whereas *Magicicada* males approach females (Cooley, 2001; Cooley & Marshall, 2001, 2004). Thus, in both genera the actively seeking sex had the higher aspect ratio. The intersexual differences in aspect ratios did not covary in a simple manner with body size, wing loading or thorax size differences. A relatively high aspect ratio is advantageous to the more active flyers because it confers low drag in relation to lift and is thus aerodynamically more efficient than is a low aspect ratio. In birds, a high aspect ratio is often, but not always, associated with fast flight over short distances (Norberg, 1990). Wickman (1992) found a similar association between aspect ratio and the tactics used by male butterflies when seeking mates; aspect ratios were higher in species that fly fast, and in bursts of activity, than they were in slower, patrolling species. Unlike the cicadas, however, males and females strongly covaried in aspect ratios.

Low wing loading and low aspect ratio contribute to slow speeds and high maneuverability when wing length is constrained, for example by flying in abrasive vegetation (Norberg, 1990). These circumstances are experienced by mate-seeking *Magicicada* males. We found several *Magicicada* individuals (mainly males) with abraded wings towards the end of the flight season, but none of the *Tibicen* had abraded wings. The hypothesis of greater maneuverability of *Magicicada* should be tested experimentally in an enclosure with obstacles to be avoided by flying insects, since natural observations such as ours are unlikely to be sufficiently precise for a reliable test.

We conclude that relatively small thoracic muscle mass and low wing loading are major factors responsible for the slow flight of *Magicicada* species, with small body size and low aspect ratios contributing additional influences. We interpret them as being evolutionary adaptations to searching and competing for mates in dense aggregations in the canopy of trees, relatively unconstrained by the risk of predation. Periodical cicadas do not have to fly far to find a mate, but they do have to compete with many others, and frequent flights over short distances rather than flying longer distances appear to enhance success (Karban, 1981; Cooley & Marshall, 2001, 2004). In other words, their slow flight is not simply permitted by a low risk of predation, it is advantageous on short flights when searching for mates. In contrast, the per-capita risk of predation is much higher for the scarcer *Tibicen*. *Tibicen* are chased by grackles (*Quiscalus* species) and other birds, but they can usually escape by fast and erratic flight. *Magicicada* species do not have this ability. Thus, *Magicicada* and *Tibicen* display different morphological solutions, as well as different acoustic solutions (Oberdörster & Grant, 2006b), to two different levels of predation risk balanced against the common need to find mates. This common need is pursued with different tactics, and the different tactics are reflected in small intersexual differences in aspect ratios.

ACKNOWLEDGEMENTS

We thank the Princeton Environmental Institute for financial support granted through the Becky Colvin award to U.O., and the Department of Ecology and Evolutionary Biology for other research funding. Also, many thanks to all Oberdörsters who helped draw figures and gave especially helpful criticism and support. We thank Kathy Hill and David Marshall for catching some *Tibicen* individuals, Tom Doak, Rosemary Grant and Cassandra Nuñez for collecting extra specimens, Rosemary Grant for assistance in determining *Tibicen* flight speeds and for discussion, Michaela Hau for the use of a balance, and Ulla Norberg and three reviewers for helpful comments on the biomechanics of flight.

REFERENCES

Alexander DE. 2002. *Nature's flyers. Birds, insects, and the biomechanics of flight.* Baltimore, MD: The Johns Hopkins University Press.

Alexander RD, Moore TE. 1958. Studies on the acoustical behavior of seventeen-year cicadas. *Ohio Journal of Science* **58:** 107–127.

Alexander RD, Moore TE. 1962. The evolutionary relationships of 17-year and 13-year cicadas, and three new species (Homoptera: Cicadidae. *Magicicada*). *Miscellaneous Publications of the Museum of Zoology, University of Michigan* **121:** 1–59.

Beamer RH. 1931. Notes on the 17-year cicada in Kansas. *Journal of the Kansas Entomological Society* **4:** 53–58.

Becker WA. 1992. *Manual of quantitative genetics*, 5th edn. Pullman, WA: Academic Enterprises.

Behncke H. 2000. Periodical cicadas. *Journal of Mathematical Biology* **40:** 413–431.

Bulmer M. 1977. Periodical insects. *American Naturalist* **111:** 1099–1117.

Cooley JR. 2001. Long-range acoustical signals, phonotaxis, and risk in the sexual pair-forming behaviors of *Okanagana canadensis* and *O. rimosa* (Hemiptera: Cicadidae). *Annals of the Entomological Society of America* **94:** 755–760.

Cooley JR, Marshall DC. 2001. Sexual signaling in periodical cicadas, *Magicicada* spp. (Hemiptera: Cicadidae). *Behaviour* **138:** 827–855.

Cooley JR, Marshall DC. 2004. Thresholds or comparisons: mate choice criteria and sexual selection in a periodical cicada, *Magicicada septendecim* (Hemiptera: Cicadidae). *Behaviour* **141:** 647–673.

Cooley JR, Simon C, Marshall DC. 2003. Temporal separation and speciation in periodical cicadas. *Bioscience* **53:** 151–157.

Cooley JR, Simon C, Marshall DC, Slon K, Ehrhardt C. 2001. Allochronic speciation, secondary contact, and reproductive character displacement in periodical cicadas (Hemiptera: *Magicicada* spp.): genetic, morphological, and behavioral evidence. *Molecular Ecology* **10:** 661–671.

Cox RT, Carlton CE. 1988. Paleoclimatic influences in the evolution of periodical cicadas (Insecta: Homoptera: Cicadidae: *Magicicada* spp.). *American Midland Naturalist* **120:** 183–193.

Cox RT, Carlton CE. 1990. Evidence of genetic dominance of the 13-year life cycle in periodical cicadas (Homoptera: Cicadidae: *Magicicada* spp.). *American Midland Naturalist* **125:** 63–74.

Cox RT, Carlton CE. 1998. A commentary on prime numbers and life cycles of periodical cicadas. *American Naturalist* **152:** 162–164.

Dudley R. 2000. *The biomechanics of insect flight*. Princeton, NJ: Princeton University Press.

Dudley R, Srygley RB. 1994. Flight physiology of neotropical butterflies: allometry of airspeeds during natural free flight. *Journal of Experimental Biology* **191:** 125–139.

Dybas HS. 1969. The 17-year cicada: a four-year mistake? *Field Museum of Natural History Bulletin* **40:** 10–12.

Dybas HS, Davis DD. 1962. A population census of seventeen-year periodical cicadas (Homoptera: Cicadidae: *Magicicada*). *Ecology* **43:** 432–444.

Dybas HS, Lloyd M. 1974. The habitats of 17-year periodical cicadas (Homoptera: Cicadidae: *Magicicada* spp.). *Ecological Monographs* **44:** 279–324.

Grant PR. 2005. The priming of periodical cicada life cycles. *Trends in Ecology and Evolution* **20:** 169–174.

Grodnitsky DL. 1999. Form and function of insect wings. The evolution of biological structures. Baltimore, MD: The Johns Hopkins University Press.

Heliövaara K, Vaisinen RA, Simon C. 1994. Evolutionary ecology of periodical insects. *Trends in Ecology and Evolution* **9:** 475–480.

Hoppenstaedt FC, Keller JB. 1976. Synchronization of periodical cicada emergences. *Science* **194:** 335–337.

Itô Y, Nagamine M. 1981. Why a cicada, *Mogannia minuta* Matsumura, became a pest of sugarcane: an hypothesis based on the theory of 'escape'. *Ecological Entomology* **6:** 273–283.

Johnson CG. 1969. *Migration and dispersal of insects by flight*. London: Methuen.

Karban R. 1981. Flight and dispersal of periodical cicadas. *Oecologia* **49:** 385–390.

Karban R. 1982. Increased reproductive success at high densities and predator satiation for periodical cicadas. *Ecology* **63:** 321–328.

Karban R. 1983. Sexual selection, body size, and sex-related mortality in the cicada *Magicicada cassini*. *American Midland Naturalist* **109:** 324–330.

Karban R. 1986. Prolonged development in periodical cicadas. In: Taylor F, Karban R, eds. *Evolution of insect life cycles.* New York: Springer-Verlag, 222–235.

Leonard DE. 1964. Biology and ecology of *Magicicada septendecim*. *Journal of the New York Entomological Society* **72:** 19–23.

Lessels CM, Boag PT. 1987. Unrepeatable repeatabilities: a common mistake. *Auk* **104:** 116–121.

Lewis T, Taylor LR. 1967. *Introduction to experimental ecology*. New York: Academic Press.

Lloyd M, Dybas HS. 1966a. The periodical cicada problem. I. Population ecology. *Evolution* **20:** 133–149.

Lloyd M, Dybas HS. 1966b. The periodical cicada problem. II. Evolution. *Evolution* **20:** 466–505.

Lloyd M, Kritsky G, Simon CM. 1983. A simple mendelian model for the 13- and 17-year life cycles of periodical cicadas, with evidence of hybridization between them. *Evolution* **37:** 1162–1180.

Lloyd M, White JA. 1976. Sympatry of periodical cicada broods and the hypothetical four-year acceleration. *Evolution* **30:** 786–801.

Marshall DC, Cooley JR. 2000. Reproductive character displacement and speciation in periodical cicadas, with description of a new species, 13-year *Magicicada neotredecim*. *Evolution* **54:** 1313–1325.

Marshall DC, Cooley JR, Simon C. 2003. Holocene shifts, life-cycle plasticity, and speciation in periodical cicadas: a reply. *Evolution* **57:** 433–437.

Martin A, Simon C. 1988. Temporal variation in insect life cycles. *Bioscience* **40:** 359–367.

Martin A, Simon C. 1990. Differing levels of among population divergence in the mitochondrial DNA of 13- and 17-year periodical cicadas. *Evolution* **44:** 1066–1080.

Nagamine M, Itô Y. 1980. 'Predator foolhardiness' in an epidemic cicada population. *Researches on Population Ecology* **22:** 89–92.

Norberg U. 1990. *Vertebrate flight*. New York: Springer-Verlag.

Norberg UM, Rayner JMV. 1987. Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London B* **316:** 335–427.

Oberdörster U, Grant PR. 2006a. Predicting emergence, chorusing and oviposition of periodical cicadas (*Magicicada* spp.). *Ecology* **87:** 409–418.

Oberdörster U, Grant PR. 2006b. Acoustic adaptations of periodical cicadas (Hemiptera: *Magicicada*). *Biological Journal of the Linnean Society* **90:** 15–24.

Pagel MD, Harvey PH. 1988. The taxon-level problem in the evolution of mammalian brain size: facts and artifacts. *American Naturalist* **132:** 344–359.

Rayner J. 1985. Linear relations in biomechanics: the statistics of scaling functions. *Journal of Zoology, London* **206:** 415–439.

Sanborn AF, Perez LM, Valdes CG, Seepersaud AK. 2001. Wing morphology and minimum flight temperature in cicadas (Insecta: Homoptera: Cicadoidea). *The FASEB Journal* **15:** A1106.

Simon CM. 1983. Morphological differentiation in wing venation among broods of 13- and 17-year periodical cicadas. *Evolution* **37:** 104–115.

Simon CM. 1992. Discriminant analysis of year classes of periodical cicada based on wing morphometric data enhanced by molecular information. In: Sorensen JT, Footit RG, eds. *Ordinations in the study of morphology, evolution and systematics of insects: applications and quantitative genetic rationales.* Amsterdam: Elsevier, 309–323.

Simon C, Tang J, Dalwadi S, Staley G, Deniega J, Unnasch TR. 2000. Genetic evidence for assortative mating between 13-year cicadas and sympatric '17-year cicadas with 13-year life cycles' provides support for allochronic speciation. *Evolution* **54:** 1326–1336.

Vogel S. 2003. Comparative biomechanics. *Life's physical world*. Princeton, NJ: Princeton University Press.

White JA, Ganter P, McFarland R, Stanton N, Lloyd M. 1983. Spontaneous, field tested and tethered flight in healthy and infected *Magicicada septendecim* L. *Oecologia* **57:** 281–286.

Wickman P-O. 1992. Sexual selection and butterfly design – a comparative study. *Evolution* **46:** 1525–1536.

Williams KS, Simon C. 1995. The ecology, behavior, and evolution of periodical cicadas. *Annual Review of Entomology* **40:** 269–295.

Williams KS, Smith KG, Stephen FM. 1993. Emergence of 13-yr periodical cicadas (Cicadidae: *Magicicadidae*): phenology, mortality, and predator satiation. *Ecology* **74:** 1143–1152.

Yoshimura J. 1997. The evolutionary origins of periodical cicadas during the ice ages. *American Naturalist* **149:** 112–124.