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Eye size and behaviour of day- and night-flying leafcutting ant alates

John C. Moser[1], John D. Reeve[2]*, José Maurício S. Bento[3], Terezínha M. C. Della Lucia[4], R. Scott Cameron[5] and Natalie M. Heck[2]

[1] USDA Forest Service, Southern Research Station, 2500 Shreveport Hwy., Pineville, LA 71360, U.S.A.
[2] Department of Zoology, Southern Illinois University, Carbondale, IL 62901, U.S.A.
[3] Escola Superior de Agricutura Luiz de Queiroz, Departmento Entomologia, Fitopatologia e Zoologia Agrícola, 13418–900 Piracicaba SP, Brazil
[4] Departmeno de Biologia Animal da University Federal de Viçosa, 36570–000, Viçosa-MG, Brazil
[5] International Paper Co., Box 139, Savannah, GA 31402-1391, U.S.A.

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Abstract

The morphology of insect eyes often seems to be shaped by evolution to match their behaviour and lifestyle. Here the relationship between the nuptial flight behaviour of 10 *Atta* species (Hymenoptera: Formicidae) and the eye size of male and female alates, including the compound eyes, ommatidia facets, and ocelli were examined. These species can be divided into two distinct groups by nuptial flight behaviour: those that initiate the nuptial flight during the day and those that initiate it at night. The most striking difference between day- *vs* night-flying alates was in ocellus area, which was almost 50% larger in night-flying species. Night-flying species also had significantly larger ommatidia facets than day-flying species. A scaling relationship was also found between compound eye area, facet diameter, and ocellus area *vs* overall body size. Detailed observations are also presented on the nuptial flight behaviour of a night- *vs* day-flying species, *A. texana* and *A. sexdens*, respectively. The pattern in *A. texana* is for a single large and precisely timed nuptial flight before dawn, while flights of *A. sexdens* last for several hours, beginning at midday. Further observations suggest that the timing of the nuptial flight in *A. texana* is easily disrupted by light pollution.

Key words: *Atta*, leaf-cutting ants, nuptial flight, compound eye, ocelli, ommatidia

INTRODUCTION

The morphology of insect eyes often seems to be shaped by evolution to match their behaviour and lifestyle. Examples include the compound eyes in flies and butterflies, where mate location seems to select for increased size in males (Zeil, 1983; Rutkowski, 2000), and carabid beetles, where visual predators have larger compound eyes with more ommatidia and binocular overlap than predators using chemical or tactile cues (Bauer & Kredler, 1993). Insects that are active in low light conditions also tend to have larger ommatidia facets and compound eyes (Horridge, 1978; Land, 1989, 1997). This is also the general pattern with ocelli, consistent with their apparent function as light detectors (Goodman, 1981; Wehner, 1981). The ocelli are also believed to help stabilize insect flight, and vigorous fliers tend to have more prominent ocelli (Goodman, 1981; Simmons, 2002).

Bees and ants exemplify many of these general patterns. Jander & Jander (2002) found that nocturnal foraging bees have larger compound eyes and ommatidia facets than diurnal foragers, and also established that these quantities scale with overall body size. Essentially the same pattern was found with the ocelli of bees foraging at different times of day (Kerfoot, 1967). Coody & Watkins (1986) found that in army ants, the compound eyes and ocelli of night-flying male alates were larger than in day-flying species. Menzel & Wehner (1970) and Klotz, Reid & Gordon (1992) found a scaling relationship between the number and size of ommatidia and body or head size of worker ants. Klotz *et al.* (1992) also found that male and female alates of *Camponotus pennsylvanicus* DeGeer had more ommatidia and larger eyes than workers of comparable head size. This is presumably an adaptation for the visual demands posed by the nuptial flight in ants. In addition to these morphological differences, bees and ants may have other adaptations that improve the functioning of compound eyes at night, including structural changes within the ommatidia in response to varying light levels (Menzi, 1987) and neural

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*All correspondence to: J. D. Reeve.
E-mail: jreeve@zoology.siu.edu

summation of photons (Warrant, Porombka & Kirchner, 1996).

Here the relationship between the nuptial flight behaviour of 10 *Atta* species (Hymenoptera: Formicidae) and the eye size of male and female alates, including the compound eyes, ommatidia, and ocelli are examined. Alates of the leafcutting ant genus *Atta* seem to be either night- or day-fliers. Five species, *Atta cephalotes*, *A. colombica*, *A. mexicana*, *A. texana* and *A. vollenweiderii*, have been observed to fly at night (Moser, 1967; Dufour, 1987; A. Mintzer, pers. comm.; J. J. Howard, pers. comm.). Documented diurnal fliers are *A. bisphaerica*, *A. capiguara*, *A. laevigata*, *A. opaciceps*, and *A. sexdens rubripilosa* (Autuori, 1941; Geijskes, 1953; Mariconi, 1970; Amante, 1972; Dufour, 1987; Sales, 1998). These 10 species represent a closely related group (Borgmeier, 1959), and this presents an opportunity to evaluate the relationship between eye size and behaviour with less concern about phylogenetic inertia (Felsenstein, 1985). Whether there is a scaling relationship between eye size and overall body size in *Atta* alates is also determined. Detailed observations are also reported on the nuptial flight behaviour of a day- and night-flying species, *A. sexdens* and *A. texana*, respectively, and the two species are compared.

MATERIALS AND METHODS

Collection of specimens

Atta bispherica, *A. cephalotes*, *A. mexicana*, *A. sexdens* and *A. texana* alates were collected during the mating flights by the authors or cooperators (see Acknowledgements). Specimens of *Atta cephalotes* supplied by D. L. Dufour were collected by Amazon Indians as they gathered the alates for food at night (Dufour, 1987). The other species, graciously supplied by cooperators, were collected during or just after flights. Based on literature accounts or personal observations by the authors or cooperators, it was possible to classify the 10 species into distinct night- *vs* day-flying categories.

Measurements

An ocular micrometer was used to measure the length and width of *Atta* eyes and ocelli as well as head capsule width. Length measurements were taken along the longest axis of the eyes and ocelli, and head capsule measurements at the broadest part of the head. Both the left and right eyes were measured and these quantities averaged for each specimen, and the left and right ocelli were similarly treated. The middle ocellus was also measured for each specimen, but its dimensions were found to be highly correlated with the paired ocelli and so this variable was not included in later analyses. As a simple measure of eye and ocellus surface area, their cross-sectional area (at the base of the eye) was calculated using the formula for the area A of an ellipse with length L and width W ($A = \pi LW/4$). Thorax length was also recorded as an overall measure of body size.

The diameter of compound eye facets were measured using digital photographs. The centre of the compound eye was photographed for 10 specimens of each species (5 of each sex) and then the diameters of 10 facets on each eye measured using the software package ImageJ 1.30 (Rasband, 2003). A digital photo of a slide micrometer was used to calibrate these measurements. The 10 diameters were averaged to yield a single value for each specimen.

Statistical analyses

A mixed models analysis was used to compare eye and ocellus area, facet diameter, and head capsule width for day- *vs* night-flying species and male *vs* female alates. The square root of eye and ocellus area was used in our analyses, to place them on the same scale (linear) as head capsule width. Thorax length was used as a covariate in the analyses to control for differences in overall body size between species and the 2 sexes, and to determine if a scaling relationship exists between these variables and overall body size. While previous studies have sometimes found a non-linear relationship between eye and body size, in our data the relationship seemed to be linear over the range of body sizes observed, and so no transformations of the independent or dependent variables were used. The mixed model analysis treated the data as a split-plot design with species as plots. The time of nuptial flight (day *vs* night) and sex were regarded as the plot and sub-plot treatments, respectively, and species viewed as a random effect nested within time of flight. The mixed model analysis yielded F-tests for time of nuptial flight, sex, and a time × sex interaction, and χ^2 likelihood ratio tests for species and a species × sex interaction (Littell *et al.*, 1996). A similar split-plot analysis was conducted for thorax length itself. Least squares means from the mixed model analysis were used to judge the magnitude of the effects in the model. All analyses were carried out using SAS 8.02 (SAS, 2001).

Nuptial flight observations

Six nuptial flights of *A. sexdens* were observed from 1986 through 1991 near Viçosa, Minas Gerais, Brazil (20.45°S, 42.51°W), involving 12 nests ranging in size between 80 and 120 m^2. Seven flights of *A. texana* from 2 nests were observed in May 1992, in 2 locations near Nacogdoches, Texas, U.S.A. (32°N, 95°W). All colonies were monitored weekly from the time the ants began preparing for the nuptial flight. After the first significant rainfall (> 6 mm) beginning in September in Viçosa and in mid-April near Nacogdoches, the colonies were inspected daily until the day of the nuptial flight. On days that nuptial flights occurred, the following data were recorded: time when workers exhibiting increased aggressiveness arrived on the nest surface; time when the first alates emerged from the nest; time of initial take-off and termination of flight; number of flights for each colony. Weather data on nuptial

Table 1. Mean eye and ocellus area, facet diameter, head width, and thorax length (± SE) for 10 *Atta* species classified by time of nuptial flight and sex

Species	Time of flight	Sex	*n*	$\sqrt{\text{Eye area}}$ (mm)	$\sqrt{\text{Ocellus area}}$ (mm)	Facet diameter (μm)	Head capsule width (mm)	Thorax length (mm)
A. bisphaerica	Day	F	10	0.658 ± 0.003	0.201 ± 0.003	28.1 ± 0.6	5.50 ± 0.04	8.98 ± 0.09
		M	7	0.571 ± 0.009	0.174 ± 0.002	24.7 ± 0.5	2.47 ± 0.03	6.24 ± 0.08
A. capiguara	Day	F	4	0.668 ± 0.006	0.192 ± 0.004	29.6 ± 1.1	5.60 ± 0.04	8.93 ± 0.08
		M	9	0.545 ± 0.006	0.174 ± 0.002	25.1 ± 0.8	2.14 ± 0.03	5.18 ± 0.06
A. laevigata	Day	F	10	0.644 ± 0.005	0.191 ± 0.004	28.1 ± 0.5	4.98 ± 0.05	8.15 ± 0.08
		M	10	0.551 ± 0.005	0.185 ± 0.002	23.8 ± 0.5	2.22 ± 0.04	5.88 ± 0.12
A. opaciceps	Day	F	19	0.661 ± 0.004	0.208 ± 0.002	28.2 ± 0.6	4.97 ± 0.03	7.82 ± 0.06
		M	28	0.546 ± 0.004	0.190 ± 0.002	24.2 ± 0.6	2.15 ± 0.02	5.24 ± 0.03
A. sexdens	Day	F	8	0.645 ± 0.005	0.229 ± 0.004	29.3 ± 0.5	5.15 ± 0.04	8.36 ± 0.07
		M	6	0.563 ± 0.005	0.189 ± 0.005	24.7 ± 0.8	2.20 ± 0.04	5.42 ± 0.05
A. cephalotes	Night	F	52	0.659 ± 0.003	0.299 ± 0.001	28.1 ± 0.9	4.08 ± 0.01	7.29 ± 0.04
		M	30	0.522 ± 0.004	0.269 ± 0.003	24.9 ± 0.4	1.66 ± 0.03	4.96 ± 0.04
A. colombica	Night	F	15	0.740 ± 0.005	0.340 ± 0.003	30.0 ± 0.4	4.49 ± 0.02	8.05 ± 0.03
		M	8	0.692 ± 0.006	0.317 ± 0.002	30.9 ± 0.4	2.36 ± 0.04	6.49 ± 0.09
A. mexicanus	Night	F	12	0.661 ± 0.005	0.310 ± 0.004	29.0 ± 0.9	4.44 ± 0.06	8.29 ± 0.09
		M	17	0.569 ± 0.005	0.278 ± 0.003	25.6 ± 0.8	2.02 ± 0.02	5.77 ± 0.09
A. texana	Night	F	23	0.642 ± 0.005	0.318 ± 0.002	32.5 ± 0.7	4.02 ± 0.02	7.36 ± 0.03
		M	6	0.567 ± 0.009	0.286 ± 0.005	27.8 ± 0.5	2.15 ± 0.03	5.73 ± 0.07
A. vollenweideri	Night	F	6	0.676 ± 0.014	0.231 ± 0.007	30.1 ± 0.4	5.52 ± 0.07	8.4 ± 0.10
		M	13	0.545 ± 0.006	0.190 ± 0.003	24.5 ± 0.8	2.12 ± 0.02	5.36 ± 0.05

flight days were obtained from a weather station located 1 km from the colonies in Viçosa and from thermometers and a rain gauge placed in the vicinity of nests near Nacogdoches.

RESULTS

Measurements

Table 1 summarizes eye and ocellus area, facet diameter, head capsule width, thorax length, and sample sizes for each of the 10 *Atta* species. There was no significant effect of time of flight on compound eye area, but ocellus area was significantly larger in night-flying alates (Table 2, Fig. 1). Least squares means from the mixed model analysis indicate that night-flying alates have ocellus areas 47% larger than day-flying alates (0.28 *vs* 0.19 mm). There was no significant difference between male and female alates for these variables. Facet diameter was also significantly larger in night-flying alates, although the magnitude of this effect was small (Table 2, Fig. 2). The least squares means for facet diameter were 8% larger for night- *vs* day-flying alates (28.5 *vs* 26.4 μm). There was also a modest effect of time of nuptial flight on head capsule width (Fig. 2, Table 2), with night-flying alates being 11% smaller than day-flying alates (3.28 *vs* 3.68 mm). There was a highly significant effect of sex on both head capsule width and thorax length, with males having head capsules 48% smaller (2.37 *vs* 4.59 mm) and thorax lengths 31% smaller (5.63 *vs* 8.16 mm) than females (Fig. 2, Table 2). Thorax length was a highly significant covariate for eye and ocellus area, facet diameter and head capsule width, suggesting that the dimensions of these organs scale with overall body size (Table 2, Figs 1 & 2). There were also highly significant differences across species for all the morphological variables, as well as significant species × sex interactions (Table 2). These findings suggest that there are many idiosyncratic differences in eye, head capsule and body size across the different species and sexes.

Comparison of nuptial flight behaviour between a day-flyer, *A. sexdens*, and night-flying *A. texana*

Pre-nuptial flight behaviour observed for both species included: (1) workers cleaning the nest surface; (2) excavation and enlargement of the nest exit holes; (3) increased aggressiveness of the worker ants. The time when workers and alates first came to the nest surface, time of flight initiation, flight duration and number of flights were the most distinctive features of the nuptial flights of *A. sexdens* vs *A. texana* (Table 3). For both species, workers were the first to leave the nest on the day of the nuptial flight. *Atta texana* workers appeared on the nest surface > 4 h before take-off, whereas workers appeared on *A. sexdens* nests only 30 min before flight. Large numbers of *A. texana* workers also appeared on the nest surface on several nights when nuptial flights did not materialize. *Atta texana* alates steadily emerged to the nest surface 4 h before take-off, which occurred just before dawn (Table 3). In contrast, *A. sexdens* alates came to the nest surface only 15–30 min before take-off. They arose almost individually and gradually so that there was peak take-off at 45 min after swarming started and a typical flight lasted 3–5 h (Table 3). Whereas *A. sexdens* flew between 11:00 and 15:00 depending on temperature and wind conditions, *A. texana* always initiated its nuptial flight precisely 15 min

Table 2. Mixed model analysis of eye and ocellus area, facet diameter, head capsule width, and thorax length. Shown are F-tests for the fixed and χ^2 likelihood ratio tests for the random effects in the model (see text for further details)

Dependent variable	Source	d.f.	F	χ^2	P
$\sqrt{\text{Eye area}}$	Time (day *vs* night)	1, 8.02	2.44	–	0.1569
	Sex	1, 56	3.13	–	0.0823
	Time × sex	1, 9.14	1.12	–	0.3162
	Thorax length	1, 251	46.40	–	< 0.0001
	Species[time]	1	–	177.8	< 0.0001
	Sex × species[time]	1	–	63.7	< 0.0001
$\sqrt{\text{Ocellus area}}$	Time	1, 8	20.53	–	0.0019
	Sex	1, 52.3	0.37	–	0.5439
	Time × sex	1, 6.62	8.08	–	0.0265
	Thorax length	1, 135	14.01	–	0.0003
	Species[time]	1	–	479.3	< 0.0001
	Sex × species[time]	1	–	5.3	0.0107
Facet diameter	Time	1, 7.96	5.73	–	0.0430
	Sex	1, 40.6	0.08	–	0.7822
	Time × sex	1, 8.54	0.00	–	0.9513
	Thorax length	1, 58.4	9.54	–	0.0031
	Species[time]	1	–	25.9	< 0.0001
	Sex × species[time]	1	–	8.3	0.0020
Head capsule width	Time	1, 7.95	7.38	–	0.0266
	Sex	1, 14.4	295.17	–	< 0.0001
	Time × sex	1, 7.87	3.75	–	0.0894
	Thorax length	1, 285	56.81	–	< 0.0001
	Species[time]	1	–	135.8	< 0.0001
	Sex × species[time]	1	–	149.6	< 0.0001
Thorax length	Time	1, 8.07	0.89	–	0.3731
	Sex	1, 7.87	187.28	–	< 0.0001
	Time × sex	1, 7.87	2.95	–	0.1246
	Species[time]	1	–	236.6	< 0.0001
	Sex × species[time]	1	–	119.6	< 0.0001

Table 3. Comparison of nuptial flight features of *Atta sexdens rubropilosa* near Viçosa, Minas Gerais, Brazil and *A. texana* near Nacogdoches, Texas, U.S.A.

Flight features	*A. sexdens*	*A. texana*
Worker appearance on nest surface (min before flight)	20–40	> 240
Alate appearance on nest surface (min before flight)	15–30	240–300
Time of take-off	11:00 to 15:00	15 min before dawn
Duration of flights (min)	180–300	2–15
No. of flights per nest	1	> 4

Table 4. Weather features on the days of six *Atta sexdens* nuptial flights in three localities near Viçosa, Minas Gerais, Brazil (1986–91) and seven *A. texana* nuptial flights in two localities near Nacogdoches, Texas, U.S.A. (1992)

Weather features	*A. sexdens*	*A. texana*
Minimum rainfall (mm)	> 19.4	> 12.7
Minimum temperature (°C)	20.1–22.2	16.1–19.4
Maximum temperature (°C)	24.3–29.4	16.1–19.4
Relative humidity (%)	71.5–81.7	~ 100
Wind (m/s)	0.9–2.7	Little or absent
Light	Bright	Dim
Weather conditions	Cloudy to clear	Cloudy

before the initiation of nautical twilight. In this study, all colonies of *A. texana* and *A. sexdens* observed in a given area swarmed simultaneously.

During this study, *Atta texana* nuptial flights occurred with less pre-flight rainfall, lower temperatures, and higher relative humidity than those of *A. sexdens* (see Table 4). Little or no wind occurred during the nuptial flights of both species.

DISCUSSION

Overall, the most striking differences between day *vs* night-flying alates was in ocellus area, which was almost 50% larger in night-flying species. Night-flying species also had significantly larger ommatidia facets than day-flying species, although the magnitude of this effect was small. These results are consistent with patterns found in a number of insect taxa (see Introduction), and suggest that larger ocelli and ommatidia have evolved in *Atta* to ensure successful nuptial flights under low-light conditions. These morphological differences may be only the most obvious adaptations to varying light intensities in these species. For example, there may be changes in ommatidial structure that improve light sensitivity in night-flying species, such as those found in *Camponotus* ants (Menzi, 1987).

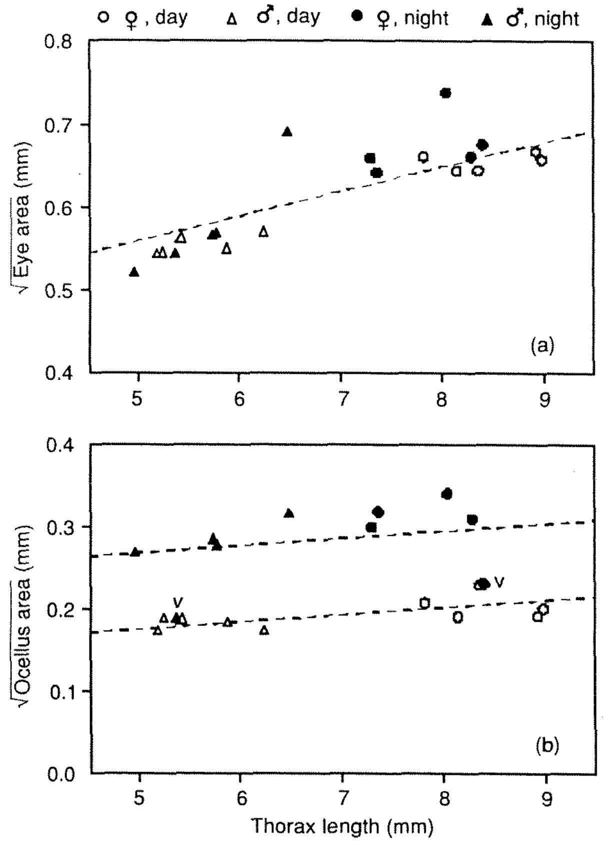

Fig. 1. Eye area (a) or ocellus area (b) *vs* thorax length for day and night-flying *Atta* species, males and females. Each point represents a mean for each species and sex. Dashed lines, fitted relationships between eye or ocellus area and thorax length estimated obtained from a mixed models analysis (see Materials and methods). For eye area in (a), there is only a single common line ($y = 0.4101 + 0.0299x$) because no significant difference was found between day- and night-flying or male and female alates (see Table 2). For ocellus area in (b), two lines were drawn corresponding to day- and night-flying alates ($y = 0.1315 + 0.0088x$, $y = 0.2240 + 0.0088x$) because our analysis found a significant difference between these two groups. The points labelled with the letter 'v' correspond to *A. vollenweideri* (see Discussion for further details).

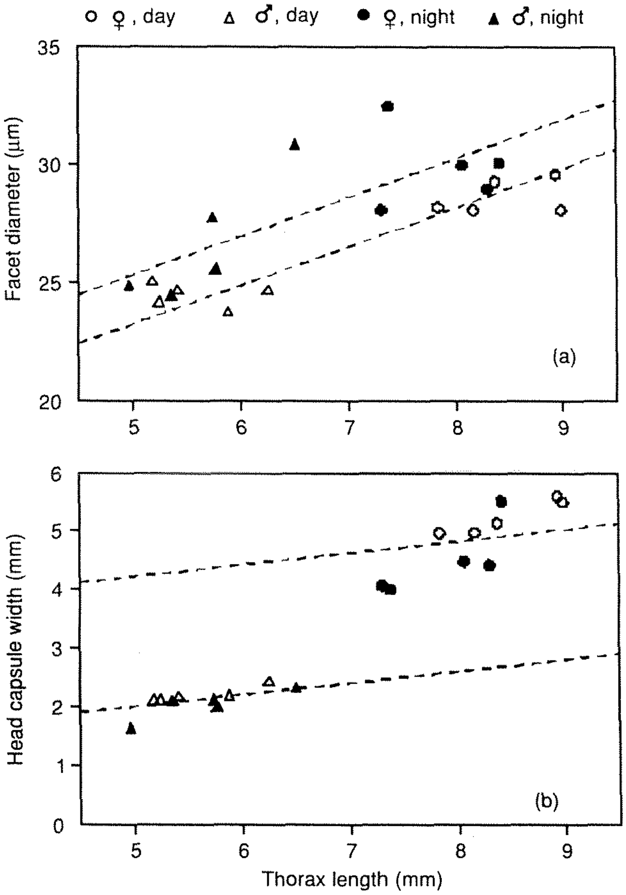

Fig. 2. Facet diameter (a) or head capsule width (b) *vs* thorax length for day- and night-flying *Atta* species, males and females. Each point represents a mean for each species and sex. Dashed lines, fitted relationships between facet diameter or head capsule width and thorax length obtained from a mixed models analysis (see Materials and methods). For facet diameter in (a), two lines were drawn corresponding to day- and night-flying alates ($y = 14.992 + 1.653x$, $y = 17.078 + 1.653x$) because our analysis found a significant difference between these groups (see Table 2). For head capsule width in (b), the two lines corresponding to male and female alates ($y = 1.020 + 0.201x$, $y = 3.235 + 0.201x$), were also found to be significantly different.

Compound eye area, ocellus area and facet diameter were also found to scale clearly with overall body size, as measured by thorax length. Although inspection of Figs 2 & 3 suggests that there are sexual differences in these variables, thorax length seems to account for these differences better than sex itself (in our statistical analyses, the effect of sex was non-significant while thorax length was always highly significant). Thus, sexual differences in these variables can be accounted for by differences in the overall body size of male and female alates. The exception is head capsule width, where males seem to have disproportionately small heads for their body size, a common feature of male ants (Smith, 1943).

Our analyses suggest that *A. vollenweideri* may be an outlier among night-flying *Atta*, because its ocellus area falls close to day-flying species (see Table 1, Fig. 1b). This raises the intriguing possibility that night-flying is a recently evolved trait in this species, and ocellus size has not been selected to match behaviour.

Observations of nuptial flight behaviour suggest two different strategies in *A. sexdens* vs *A. texana*. The pattern in *A. texana* is for a single large and precisely timed nuptial flight on a given day (although there may be multiple flights per nest), while the opposite seems to be true for *A. sexdens*. Precisely timed swarming among *Atta* is probably an adaptation for coordinating flights with the best possible weather and soil conditions and for avoidance of high mortality by predators (Wilson, 1975). Synchronized nuptial flights across an area (as occurs in both species) may reduce predation rates by swamping the local predators with prey, and also assures a thorough mixing of genes among nests. However, the pre-dawn behaviour of *A. texana* is a less obvious strategy to reduce predation, because armadillos, bats, birds and other ants (such as *Solenopsis* spp.) still actively feed on *A. texana* alates and mated females (Warter, Moser & Blum, 1962; Moser, 1967; Mintzer & Vinson, 1985). There is no information available on the predation rates of alates at different times of day, but it may be that the relative risk of predation in *A. texana* is actually lower before dawn, or perhaps there are environmental variables key to the survival of the alates after flight that select night-flying behaviour. A study of the gut contents of predators active at different times of day, and their densities, would provide some insight on predation risk.

Light pollution may also have a disruptive effect on the timing of *Atta* behaviour. In this study, the alates from the seven *A. texana* nests observed in Texas all flew in complete darkness, about 15 min before dawn. More recently, flights from two large colonies, which occurred 15 min after dawn, have been observed in an area where extraneous light could be seen all night from man-made sources. Most of this light originates from 'night lights' which are now placed on tops of long poles in front of most rural homes and businesses. These lights are also extremely attractive to both male and female alates, and because of this, the number of new fertile queens may be substantially lowered due to reduced insemination and to predation by *Solenopsis* species (fire ants) and birds. Thus, artificial light sources apparently disrupt both the timing of nuptial flight, and probably also the mating success of alates and their ability to escape predation.

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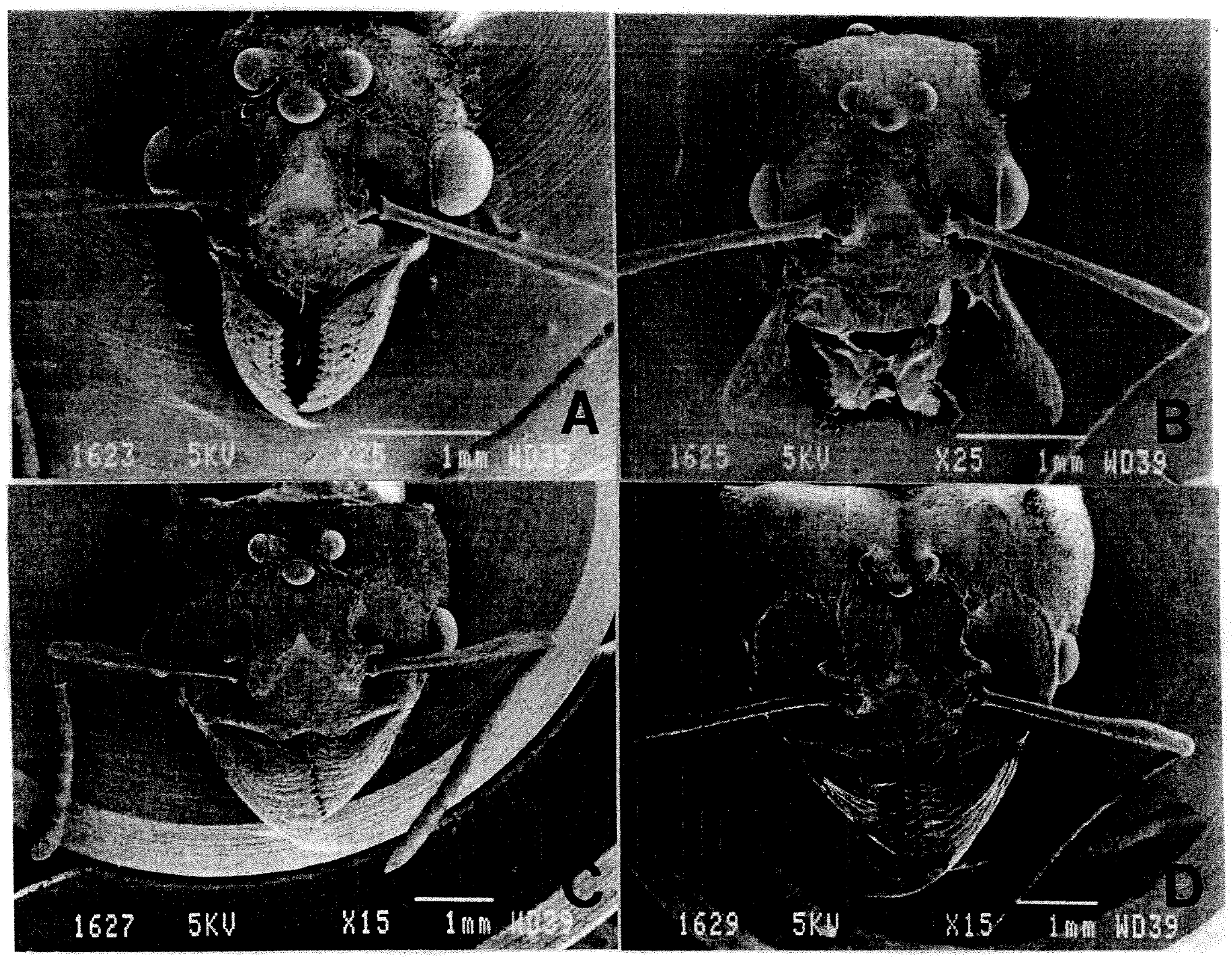

Figure 1. Heads of *Atta texana* and *Atta sexdens rubropilosa*, males (A and B, respectively) and females (C and D, respectively), showing the ocelli and compound eyes.