Journal of Insect Behavior, Vol. 19, No. 1, January 2006 (© 2006)
DOI: 10.1007/s10905-005-9012-1

Flight Speed of Tethered *Reticulitermes flavipes* (Kollar) (Isoptera: Rhinotermitidae) Alates

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Revised August 26, 2005; accepted September 29, 2005

Alates of the Eastern subterranean termite, Reticulitermes flavipes *(Kollar) were collected over two flight seasons (2002 and 2004) and flown on flight mills. Data were collected to test if alate mass, colony origin, or gender influenced flight speed. Flight speed ranged from 3.14 to 69.12 cm* s^{-1} *and the maximum distance flown by an alate was 458.3 m. Alate mass (*$P = 0.9406$*), gender (*$P = 0.3976$*), colony origin (*$P = 0.1244$*), and the interaction of gender and colony (*$P = 0.7093$*) did not significantly influence flight speed. Additionally, an electronic counting device was used to provide instantaneous flight speeds and allowed flight speed to be modeled during acceleration, cruising, and deceleration periods of flight. Mean (±SEM) flight speeds in 2004 were 20.64 (±2.21) cm* s^{-1} *(*$n = 13$*) for males and 17.76 cm* s^{-1} *(*$n = 1$*) for the single female flown, falling within the range of the 2002 values.*

KEY WORDS: insect flight; termites; *Reticulitermes flavipes*; flight speed; mass scaling; alate.

INTRODUCTION

It is thought that termite colonies are initiated mainly through the flight and eventual mating of alate primary reproductives from parent colonies

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(Kofoid, 1934; Thorne, 1996). This flight, eventual landing, tandem behavior, nuptial chamber construction, mating, and oviposition are all well–documented events in colony formation via alates (Kofoid, 1934; Nutting, 1969, 1979; Leong *et al.*, 1983). Some authors have claimed that neotenics (a non-alate supplemental reproductive form) are the most commonly found reproductive individuals in colonies of certain *Reticulitermes* Holmgren spp. (Lainé and Wright, 2003). However, this is likely the response of introduced species outside their native habitats. Vieau (2001) notes the low occurrence of swarming in colonies of *R. santonensis* Feytaud, which commonly uses budding in France. This particular species is suspected of synonymy with *R. flavipes* (Kollar), and may have resulted from an introduction into Europe (Jenkins *et al.*, 2001). There are other means of colony initiation in *Reticulitermes* spp. such as budding when supplemental reproductives are produced which fragments a colony (Nutting, 1969; Thorne, 1983, 1984; Atkinson and Adams, 1997; Thorne *et al.*, 1999; Husseneder and Grace, 2001a,b). Grace (1996) suggests that northern colonies of *R. flavipes* may resort to budding type expansion to a greater extent than termites found at the southern end of their range. Regardless of alternate modes of colony formation, swarming of *R. flavipes* in spring is a common event in its native habitat, the southeastern United States.

The role of flight in termite alate swarms is of ecological importance in terms of distribution patterns and dispersal capabilities. Flight behavior may vary among species or even indicate a sign of nascent speciation (Nutting, 1979; Haverty *et al.*, 2003). Understanding the phenology, physiology, and behavior of termite alate flights provides an insight into the dispersal capabilities of the species as well as demonstrates possible niches that may be exploited by individual groups among native subterranean species (*Reticulitermes* spp.; Haverty *et al.*, 2003). In addition to the natural means of colony expansion listed above, termites are often moved into new areas by alternate means. The most significant of these is the movement of infested materials by man (Kofoid, 1934). This is most important for the movement of invasive termite species; however, it is not generally a concern with the movement of native species within their native habitat, the forest.

This paper describes the results of several studies using the Eastern subterranean termite, *Reticulitermes flavipes*, a native termite to the southeastern United States as a model for termite alate flight. These studies were designed to answer several questions: Does flight speed and duration vary with gender, mass, or colony origin? To what extent does fatigue influence flight speed, and can alates of *R. flavipes* fly intermittently in the laboratory?

MATERIALS AND METHODS

Termite Collection

Each of the two studies used slightly different methods for collecting termites. Termite alates were collected during the spring flight season for *Reticulitermes* Holmgren spp. During the 2002 study, three infested logs were collected on the campus of Auburn University (Lee County, AL) in discrete locations (separated by >1 km), wrapped in plastic bags and returned to the laboratory. Fully developed alates were collected for use on the flight mill (described later) as they emerged from the wood. For the 2004 study, an infested pine stump (*Pinus* Linn. spp.) was discovered on the Auburn University campus. *R. flavipes* alates were emerging and flying from the stump, so a plastic bag was wrapped around the stump. Small lengths (<10 cm) of infested wood containing alates were placed into a plastic box (32 cm × 19 cm × 11 cm) lined with moist paper toweling, the lid closed, and the entire box covered with black velvet. Alates were collected with forceps as the wood pieces were carefully pulled apart. For both studies, all termites were used within 3 days of original collection, and termites identified using morphological characters in the keys of Scheffrahn and Su (1994) and Hostettler *et al.* (1995).

2002 Study

From the three termite colonies, a total of 9 female and 12 male *R. flavipes* alates were tethered on a simple flight mill under ambient temperature of 25°C (Fig. 1). The flight mill is a simple device consisting of an acrylic upright cylinder with a pin set into the center, the crossbar consists of two lengths of metal attached to a plastic cap that fits over the pin and moves freely. The total length of the crossbar was 22 cm. Termites were tethered to thin silver wire using a drop of liquid bandage (New-Skin, Medtech, Jackson, WY) and fastened to the crossbar using modeling clay, with a matching piece of clay to balance on the opposite side (Fig. 1).

Once alates were tethered, flight was induced by either moving the crossbar downward swiftly to simulate "falling," or blowing gently on the alate from the anterior. As soon as flight began, a stopwatch was started to time the event, and the number of revolutions recorded using a hand counter. After each flight event concluded and the data were recorded, attempts were made to induce additional flight events. All alates were induced to make at least one additional flight event. All individual flight events were treated and recorded similarly, and were termed "bouts."

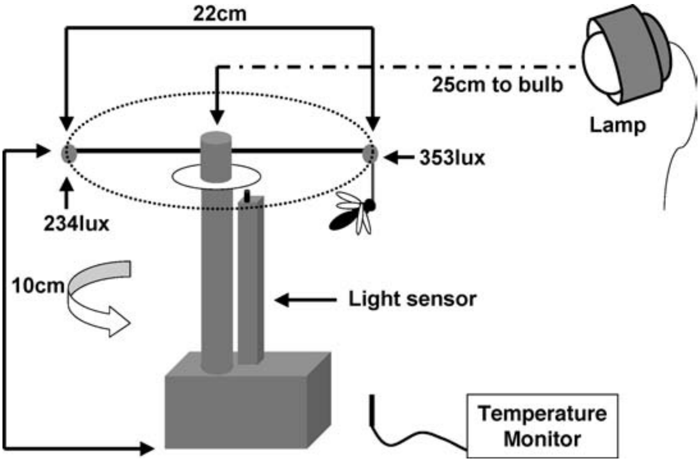

Fig. 1. Modified simple flight mill used in 2004 study. Flight mill used for the 2002 study did not have the light sensor apparatus, but was otherwise identical.

Statistical Analysis

Flight speed data for bouts in this experiment were analyzed independently from the 2004 data. Flight speed data in cm s^{-1} were subjected to a mixed procedure using alate gender and colony (and their interaction) as fixed effects, and considering the bouts as repeated measures (SAS Institute, 2001). Bout number was then used in estimates of the effect of flight fatigue on *R. flavipes* alates by linear regression. To counter the effects of unequal variance in this regression, the variance for each bout number was fit using simple linear regression (SAS Institute, 2001). The regression model relating flight speed to bout number was then weighted by the inverse of the predicted variance from the first model (Montgomery and Peck, 1982). Flight speeds for individual bouts were regressed on bout number to estimate the influence of fatigue on alate flight speed.

2004 Study

Prior to use on the flight mill, each alate was placed into a single microcentrifuge tube (Fisherbrand, Fisher Scientific, Fair Lawn, NJ) and weighed to the nearest 0.01 mg using a digital balance (model AX205 Delta Range, Mettler-Toledo GmbH, Greifensee, Switzerland). In addition to the overall flight number of revolutions and time which were recorded manually using a stopwatch and hand counter, this study recorded the instantaneous flight speed data using a computer. The flight mill used in the 2002 study was modified to use an infrared light sensor that detected changes in a pattern printed on a circle of paper mounted on the base of the crossbar of the flight mill (Fig. 1). The light sensor sends data to a computer which recorded the data in Hz once per second. This system is a custom modification of a Sable Systems Tach-2 (Sable Systems, Henderson, NV). Immediately below the flight path of the tethered alate, temperature was recorded using a digital temperature probe (Humidity/Temperature monitor model 4082, Fisher Scientific International, Inc., Hampton, NH) (Fig. 1), temperature during the flight was recorded as a single value upon completion of the flight. Data were acquired and analyzed using the Datacan software package (Sable Systems). All recordings contained at least 30 s of baseline data after the flight recording. Baseline data were collected to ensure that the device does not record events when the flight mill is stationary. After baseline conversion the data were converted to cm s^{-1} using the following equation:

$$\text{Flight speed}\,(\mathrm{cm\,s^{-1}}) = [C/P] \times X \qquad (1)$$

where C is the flight path circumference in cm, P is the number of changes in the pattern per circumference (each change from light to dark or vice versa is a cycle recorded by the machine), and X (in Hz, i.e. cycles s^{-1}) is the data recorded by the computer. Once the data were baseline corrected and converted to flight speed, the recordings were separated into sections and analyzed separately as acceleration, cruising, and deceleration sections. It is recognized that the deceleration sections of the data include both the actual deceleration of the animal and the momentum of the flight mill itself. This flaw is inherent in the use of flight mills, and may not be distinguished from the effects of the animal until the alate's wings cease movement.

Statistical Analysis

Alate mass was used as a predictor of flight speed, and duration of flight (both as time and distance flown) using linear regression (SAS Institute, 2001). Only male data were used in these analyses ($n = 13$), due to the low number of female flights ($n = 1$). To determine if these flight sections followed a linear relationship, the sectional data for acceleration, cruising, and deceleration for each alate were regressed separately against time (Minitab, Inc., 2003).

RESULTS

2002 Study

Mean (±SEM) flight speeds separated by gender and colony are presented in Fig. 2. Male alate flight speeds of individual bouts ranged from 3.14 cm s^{-1} (colony A alate) to 69.12 cm s^{-1} (colony A alate). Flight speeds of individual bouts for female alates ranged from 4.32 cm s^{-1} (colony B alate) to 69.12 cm s^{-1} (colony C alate). During this study, the maximum distance flown by a male alate was 265.4 m, and 458.3 m by a female alate. There was no significant influence of gender (df = 1, 15; $F = 0.76$; $P = 0.3976$), colony origin (df = 2, 15; $F = 2.40$; $P = 0.1244$), or their interaction (df = 2, 15; $F = 0.35$; $P = 0.7093$) on flight speed.

Fatigue, as measured by bout number, had a significant effect on the flight speed of *R. flavipes* alates (df = 1, 283; $F = 20.63$; $P < 0.0001$; $r^2 = 0.054$) as illustrated in Fig. 3. The equation relating flight speed to bout is

$$\text{Flight speed (cm s}^{-1}) = 25.5\,(\pm 1.48) - 0.19\,(\pm 0.04) \times \text{bout} \tag{2}$$

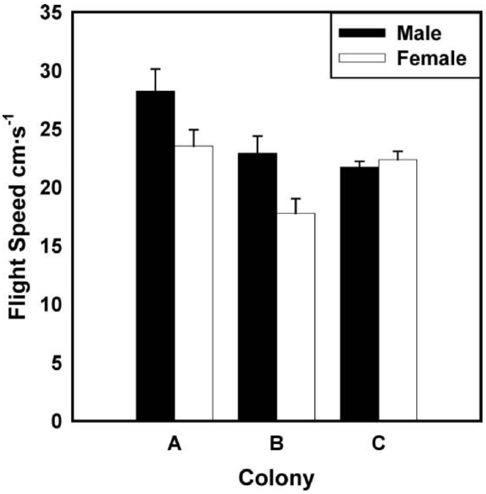

Fig. 2. Mean flight speed of male and female alates from each of three colonies. Flight speeds were not significantly influenced by either colony or gender, 2002 data.

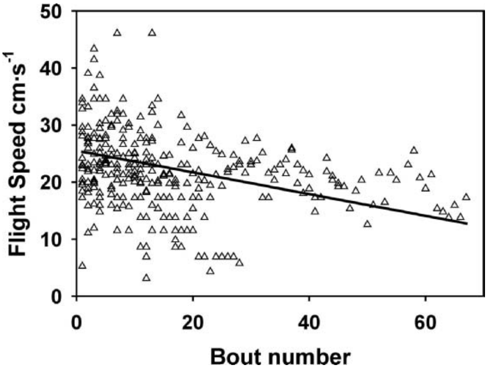

Fig. 3. Fatigue when flying: influence of bout number on speed, 2002 data.

2004 Study

The gender of alates obtained from this colony was skewed toward males. Of the 67 alates collected, only three were females (4.5%) and only one female could be induced to fly. Of the remaining 64 male alates, only 13 (20.3%) could be induced to fly for more than 5 s. Termites flying for less than 5 s were removed from the data set. For male alates the mean (±SEM) temperature during flight was 26.68°C (±0.17), and for the single female flight the temperature was 27.4°C.

Mean (±SEM) masses for these alates were the single female 4.34 mg ($n = 1$), and the males 4.21 (±0.10) mg ($n = 13$). Overall mean flight speeds (using the hand-counter and timer) from both genders fell within the range of the 2002 data set. Mean (±SEM) male flight speed was 20.64 (±2.21) cm s^{-1}, and the speed for the single female was 17.76 cm s^{-1}. Alate body mass did not significantly influence overall flight speed (df = 1, 12; $F = 0.01$; $P = 0.9406$). Alate mass also did not significantly influence overall duration of flight in these alates when measured as distance flown (in revolutions; df = 1, 12; $F = 0.01$; $P = 0.9423$) or as time flown (in s; df = 1, 12; $F = 0.01$; $P = 0.9423$).

To demonstrate the importance of using alates for behavioral and physiological work immediately after collection, the influence of age since collection on the mass of *R. flavipes* alates was examined using linear regression (genders combined). Alate mass (in g) declined significantly over time (in h) since field collection (df = 1, 65; $F = 9.90$; $P = 0.003$; adjusted $r^2 = 0.12$) as illustrated in Fig. 4. The equation representing this influence is

$$\text{Mass (in mg)} = 4.24\,(\pm 0.062) - 0.0052\,(\pm 0.0017) \times \text{age (in h)} \qquad (3)$$

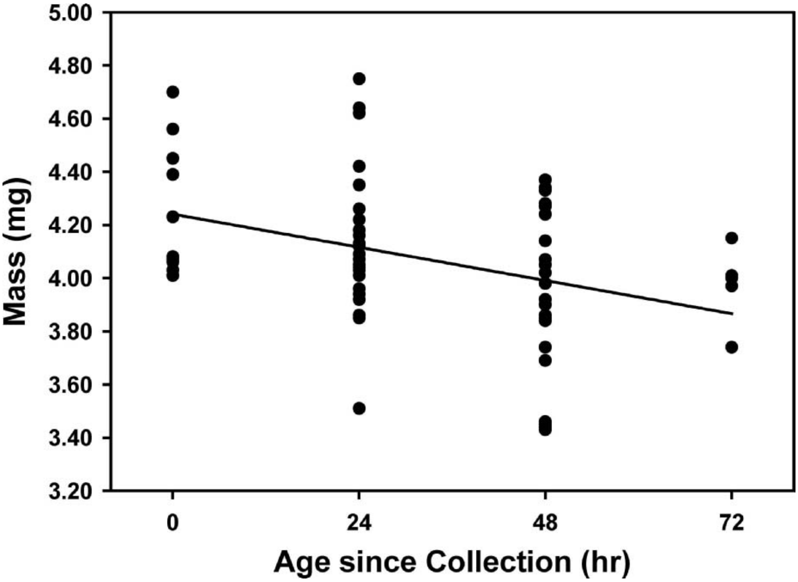

Fig. 4. Influence of age since collection on alate mass, 2004 data.

Linear regressions of the various sections of instantaneous flight speed data were divided into those that had a significant linear relationship with time, and then into those that were either positively (speeds increase) or negatively (speeds decrease) associated with time (Fig. 5). For all sections, only ten recordings were usable, from nine males and the single female. Of

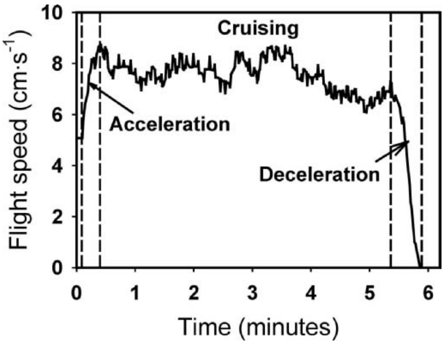

Fig. 5. Instantaneous flight speed in a male *R. flavipes* alate, 2004 data. Acceleration, cruising, and deceleration sections indicated by arrows.

Table I. Linear Regression Results for Individual Alate Instantaneous Flight Speed Sections Using Time as the Predictive Variable

Alate	Acceleration P^a	Cruising P^a	Deceleration P^a	Acceleration $r^{2\ b}$	Cruising $r^{2\ b}$	Deceleration $r^{2\ b}$
♂ 1	0.005 (+)	<0.0001 (−)	<0.0001 (−)	0.484	0.900	0.980
♂ 2	<0.0001 (+)	<0.0001 (−)	<0.0001 (−)	0.933	0.704	0.837
♂ 3	<0.0001 (+)	<0.0001 (−)	<0.0001 (−)	0.980	0.923	0.983
♂ 4	<0.0001 (+)	0.002 (+)	<0.0001 (−)	0.990	0.227	0.901
♂ 5	<0.0001 (+)	0.024 (+)	<0.0001 (−)	0.957	0.212	0.988
♂ 6	0.002 (+)	0.830 (ns)	<0.0001 (−)	0.557	0.000	0.924
♂ 7	<0.0001 (+)	0.517 (ns)	<0.0001 (−)	0.503	0.000	0.909
♂ 8	<0.0001 (+)	<0.0001 (−)	<0.0001 (−)	0.888	0.289	0.949
♂ 9	<0.0001 (+)	<0.0001 (−)	<0.0001 (−)	0.740	0.422	0.992
♀ 1	0.142 (ns)	<0.0001 (−)	<0.0001 (−)	0.421	0.697	0.985

[a] (+) indicates flight speed positively associated with time; (−) indicates flight speed negatively associated with time.

[b] Adjusted r^2 reported.

the acceleration sections, flight speed for all male alates increased significantly with time, but flight speed of the single female alate did not (Table I). For cruising flight speed sections, all but two (both males) were significantly associated with time (Table I). However, all cruising sections except two (male alates 4 and 5; Table I) were negatively associated with time. Finally, the deceleration sections were all significantly negatively associated with time (Table I). Individual alate models describing significant relationships between flight speed and time are presented in Table II.

DISCUSSION

The flight speed data collected in 2002 did not support the hypothesis that gender influenced flight speed (Fig. 2). This is not surprising as a difference in flight speed between genders would result in disproportionate mixtures of alate sexes in flight swarms, decreasing the possibility of finding appropriate partners for founding colonies. Prior to collecting these data, a difference in flight might have been reasonable if one of the sexes (the slower one) flew earlier than the other, allowing the faster sex to meet the other in mid-air. However, the data reported here do not support this hypothesis. Since *R. flavipes* colonies are commonly the result of monogamous outbred pairings (Vargo, 2003), it might be argued that colonies synchronize their alate releases at least on a local basis probably dictated by weather (Nutting, 1969), however data on direct observation of the timing of alate releases from colonies is currently lacking. Other basic

Table II. Linear Regression Models Describing Various Sections of *R. flavipes* Alate Flight

Alate	Acceleration model	Cruising model	Deceleration model
♂ 1	FS = 7.88 (±0.17) + 5.12 (±1.46) × T	FS = 9.07 (±0.06) − 0.91 (±0.02) × T	FS = 3.26 (±0.07) − 10.7 (±0.35) × T
♂ 2	FS = 7.69 (±0.06) + 3.55 (±0.15) × T	FS = 9.55 (±0.04) − 0.39 (±0.02) × T	FS = 7.97 (±0.11) − 2.04 (±0.07) × T
♂ 3	FS = 10.2 (±0.13) + 26.1 (±1.07) × T	FS = 14.2 (±0.06) − 1.02 (±0.01) × T	FS = 5.97 (±0.10) − 15.4 (±0.40) × T
♂ 4	FS = 4.78 (±0.07) + 17.1 (±0.40) × T	FS = 10.2 (±0.13) + 1.27 (±0.37) × T	FS = 8.11 (±0.30) − 13.7 (±0.71) × T
♂ 5	FS = 2.81 (±0.06) + 7.45 (±0.41) × T	FS = 4.45 (±0.07) + 0.96 (±0.39) × T	FS = 4.21 (±0.06) − 11.2 (±0.25) × T
♂ 6	FS = 11.8 (±0.16) + 5.52 (±1.38) × T	Not significant	FS = 11.1 (±0.33) − 18.8 (±0.83) × T
♂ 7	FS = 0.17 (±0.19) + 1.91 (±0.18) × T	Not significant	FS = 2.85 (±0.08) − 4.17 (±0.21) × T
♂ 8	FS = 5.65 (±0.16) + 10.3 (±0.80) × T	FS = 8.13 (±0.06) − 0.02 (±0.02) × T	FS = 7.81 (±0.20) − 17.1 (±0.76) × T
♂ 9	FS = 10.8 (±0.08) + 1.58 (±0.11) × T	FS = 13.9 (±0.09) − 0.52 (±0.04) × T	FS = 11.1 (±0.04) − 3.77 (±0.02) × T
♀ 1	Not significant	FS = 7.06 (±0.07) − 0.70 (±0.03) × T	FS = 4.60 (±0.07) − 11.0 (±0.27) × T

Note. In the models, flight speed (FS) is in cm s^{-1}, and time (T) is in s.

physiological parameters do not differ significantly between the sexes in *R. flavipes* alates, such as lipid content (Shelton and Appel, 2001a), perhaps due to the termite need for maintaining males within a colony (unlike other eusocial insects; Kofoid, 1934). Flight fuel (lipids; Beenakkers, 1969; Sacktor, 1974) should be similar given both sexes fly similarly. Unlike ants, where males are not retained during colony initiation, male alates of termites must contain enough lipids to ensure survival after mating and colony founding, another reason for similarity in lipid contents between the sexes. Although it is almost certainly a statistical anomaly, it is interesting to note that the maximum flight speeds measured for both sexes in 2002 were identical (69.12 cm s^{-1}).

The hypothesis that colony origin influenced flight speed was also not supported by the 2002 data set (Fig. 2). This result supports a growing body of knowledge indicating that while members of termite colonies may vary in other ways such as behavior (Su and Haverty, 1991; Thorne and Haverty, 1991; Shelton and Grace, 1996; Husseneder and Grace 2001a; Campora and Grace, 2004) and responses to toxicants (Osbrink and Lax, 2002), basic physiological parameters remain similar among colonies within species. Colonies of both *Coptotermes formosanus* Shiraki and *C. vastator* Light did not have significantly different cuticular permeability values in intraspecific comparisons (Shelton and Grace, 2003). Other physiological values, such as CO_2 release rates also do not differ among colonies of *R. flavipes* (Shelton and Appel, 2001b).

A model of flight speed is an important goal in understanding subterranean termite expansion capabilities both as beneficial insects within forest habitats and in urban areas where these animals can be pests. Flight speed is obviously an important part of such a model along with the abiotic variables that can influence flight speed, such as temperature, humidity, wind speed, and other weather-related variables (Nutting, 1969; Leong *et al.*, 1983). Biotic factors also play a role in estimating distance traveled by termite alates. In the 2002 study, an estimation of the influence of fatigue on the overall flight speed of *R. flavipes* was determined. The influence was statistically significant, but had a small effect on the flight speed of the alates, only ~5% of the variability was explained in this way. The maximum flight distance made in an individual bout of flying was 458.3 m by a female alate. Because there is no evidence of intermittent termite flight occurring in nature, the ability to restart flight may be an artifact of the flight mill method, restricting our maximum flight distance estimate to the single bout value above. However, the presence of such intermittent flight has never been directly tested. If flight were intermittent, the maximum distances presented here would be greatly increased when combining all bouts of flight.

The 2004 data did not support the hypothesis that mass influenced flight speed in *R. flavipes* alates. The lack of a mass scaling of flight speed is surprising, even when assuming that an increase in mass necessarily equates to an increase in flight muscle mass. However, variability in lipid content and total body water do occur among individual *R. flavipes* alates (Shelton and Appel, 2001a). While an increase in body mass could certainly represent an increase in flight muscle mass, body mass also includes lipid content, water content, non-flight musculature, and other variables such as the amount of food being digested. Variation in any of these latter variables would constitute a mass difference that does not relate to flight muscle mass in any way (although both are required for flight muscle metabolism), thus the assumption above is incorrect.

The instantaneous flight speed measurements provided interesting information on the flight behavior of these termites. Much of the results were intuitive given the nature of the data. In general, acceleration sections of flight speed increased over time, while deceleration sections decreased over time (Table I). The single female alate flight recording suggests that there may be some differences among the sexes in acceleration models (Tables I and II), but the single female replicate makes this information anecdotal. The most interesting observation is that *R. flavipes* alates do not maintain a constant cruising speed. In most cases these cruising sections of flight speed decreased over time (Table I), indicating a constant slowing of flight by the alates prior to a sharp decline (Fig. 5). Perhaps this is evidence that termite alates require another cue for releasing further flight, perhaps wind speed, or temperature variation (note that temperature in these studies was kept constant), or perhaps even a chemical cue indicating the presence of other alates nearby. Wind speed seems a likely candidate considering the capacity for restarting flight indicated in the 2002 study.

The studies presented in this paper have provided basic information regarding termite alate flight in the Eastern subterranean termite. While these data were produced under laboratory conditions, they are appropriate estimates given that the environmental conditions under which *Reticulitermes* spp. alates are reported to fly (calm wind, warm, bright midday conditions) (Kofoid, 1934; Nutting, 1969) were matched in the laboratory (no wind, ∼26.7°C, 353 lux). Further studies of flight in this species will build upon the data presented here toward a goal of modeling the flight capabilities of this species under natural conditions.

ACKNOWLEDGMENTS

The authors thank M. J. Tanley and Yongyu Xu for expert technical assistance during the course of these studies. Thanks are also given to Dunlun Song and Xueyou Hu for their assistance in alate collections during the 2004 studies. The assistance of J. R. B. Lighton, B. Joos, and R. Turner in constructing the flight mill speed device is greatly appreciated. The input of two anonymous reviewers, as well as J. K. Grace (University of Hawaii), P. D. Gerard (Mississippi State University), and J. E. Mulrooney (USDA Forest Service) in improving earlier drafts of this manuscript is appreciated. These studies were supported in part by USDA Forest Service agreement SRS 02-CR-11330130-212 with the Department of Entomology & Plant Pathology at Auburn University.

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