Seasonal Production of Alates by Five Species of

Termites in an Arizona Desert Grassland[1]

by

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ABSTRACT

Production of winged termites was measured for two consecutive flight seasons on the Santa Rita Experimental Range, Pima County, Arizona. Five species (*Incisitermes banksi* (Snyder), *Paraneotermes simplicicornis* (Banks) (Kalotermitidae), *Heterotermes aureus* (Snyder) (Rhinotermitidae), *Amitermes pallidus* Light, and *Gnathamitermes perplexus* (Banks) (Termitidae)) produced 47,286 alates/ha with a dry weight of 174 g in 1974. *H. aureus* and *G. perplexus* produced alates at the rate of 0.04% and 0.11 to 0.13% of their total populations during the poorest and third poorest years for alate production since 1961.

Flights occur on or shortly after the first few evenings of "sufficient" rainfall. Later in the flight season "sufficient" rainfall may not result in flights, perhaps because all the alates have flown. Total rainfall for each flight season was very different; however, there was very little difference in the total number of alates produced each season. These relatively stable insect societies can thus produce a seasonally dependable, energy-rich food in the form of winged reproductives for a variety of predators.

INTRODUCTION

La Fage et al. (1973) detailed our methodology for studying foraging populations of subterranean termites in a desert ecosystem. Using data gathered by this method, Haverty et al. (1975) described the density of colonies and spatial distribution of foraging territories of one subterranean species. Following another method, Haverty and Nutting (1975) determined density and dispersion of foraging populations of five subterranean species. Here we present the results of a 2-year study to measure the rate of production of termite winged forms, or alates,

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along with some estimates of its relation to the total population and to seasonal rainfall.

The termites in the semiarid areas of southern Arizona have rather well-defined flight seasons which occur during either the summer or the winter rainy season. The flights of the subterranean species are strikingly associated with rainfall and presumably, the accompanying increase in soil moisture and relative humidity. Moisture has some apparent, but less obvious, influences on the flights of drywood termites. It is widely accepted that few pairs of reproductives survive their dispersal flights to establish new colonies in favorable unoccupied areas. While foraging termites are regularly sought out by certain ants, lizards, and birds, most of the energy-rich alates, during their brief debut, are opportunistically eaten by a wide variety of arthropods from scorpions to wasps, and vertebrates from fish to man (Nutting, 1969). To our knowledge no one has yet reported an alate production rate for any ecosystem which would show the total biomass that is essentially available to predators. Bouillon (1969) reviewed the few pertinent papers and gave production data on four African species. From his figures, production of these species could be related to total population. Lepage (1972) estimated alate production rates of two of the major species of termites on a Sahelian savanna in Senegal. Nineteen species occurred in his 1-km^2 reference quadrat. Nutting (1969) summarized the relationships between annual production of alates, colony size, and most environmental variables.

METHODS AND MATERIALS

This work was done on the site of our previous studies of subterranean termites 40 km south of Tucson, Arizona, on the Santa Rita Experimental Range at an elevation of 950 m (Haverty et al., 1974, 1975). The area is a shrub-invaded desert grassland, characterized by scattered trees, shrubs, and cacti. Seasonal activity patterns and surface foraging populations of two species were previously worked out on a 40X40-m plot of toilet paper rolls set out on a grid at 1-m intervals to serve as food (Haverty et al., 1974, 1976; La Fage, 1974).

For estimating the production of winged forms, two large walk-in cages, each containing an ultra-violet light trap, were installed on the baited grid described above, prior to the summer flight season (Fig. 1). During 1972, the cages were placed over areas known to have had high foraging densities of *Heterotermes aureus* (Snyder) (Rhinotermitidae) and *Gnathamitermes perplexus* (Banks) (Termitidae) (Haverty et al., 1976). They were made of Saran® screen (5.5X7.1 mesh/cm), supported by a frame of 2.5-cm conduit measuring 3.7X3.7X2.4 m, and each covered an area of 13.4 m^2 or ca. 0.0013 ha. The lower edges of the cages were banked with soil to prevent the exit or entrance of insects. One 15-watt, black-light insect trap (Ellisco, Inc., No. 110 103-PC) was placed in each cage. The two lights were powered by one storage battery (Goodyear Commercial D8D-SA; 12-volt, 200 amp/hr rating) and set to operate from ca. 15 minutes after sunset to ca. 15 minutes before sunrise by a photocell-actuated switch. Two batteries

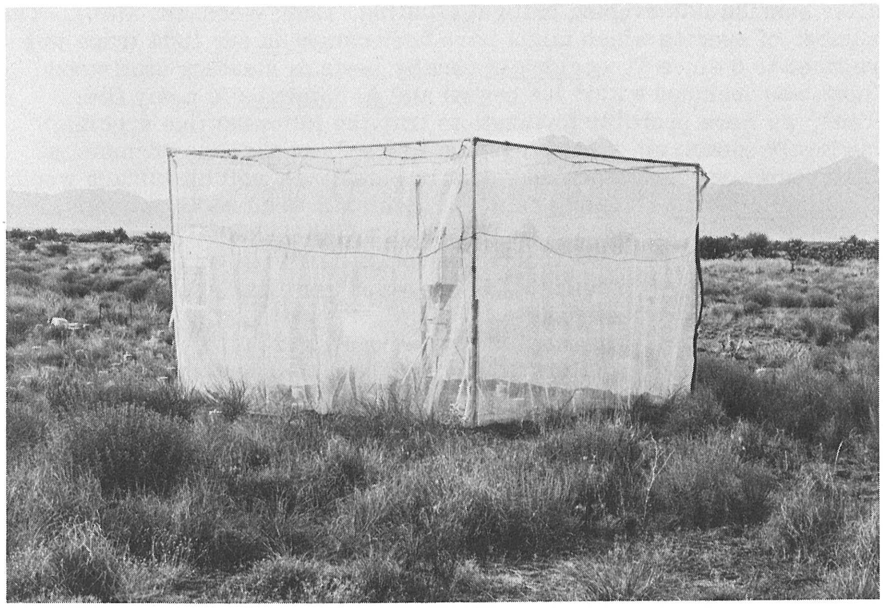

Fig. 1. Screened cage covering 0.0013 ha used to collect termite alates on the Santa Rita Experimental Range, Arizona.

were used, one being exchanged for recharging every 3-4 days.

An ethylene glycol-water mixture (1:1) was poured into the trap collection containers to a depth of 1-2 cm, sufficient to kill and preserve the insect catches for several days. The catches were emptied into plastic bags and returned to the laboratory for examination each time the batteries were exchanged. Winged termites were sorted out by species, counted, recorded, and preserved. Collections were continued from July 3 to September 3, 1973, and July 2 to September 2, 1974. The summer rainy season fell between the above dates each year. At each battery exchange, rainfall for the collection period was measured in two simple, wedge-shaped plastic rain gauges located ca. 25 m south of the traps.

Of 11 species known from the site, 10 fly during the summer rainy season; only Amitermes emersoni Light flies with the winter rains. Five of these fly at evening twilight: Incisitermes banksi (Snyder), Paraneotermes simplicicornis (Banks) (Kalotermitidae), H. aureus, Amitermes pallidus Light, and G. perplexus; two fly during the night: Pterotermes occidentis (Walker) (Kalotermitidae) and Tenuirostritermes tenuirostris (Desneux) (Termitidae); two at morning twilight: Amitermes silvestrianus Light and A. wheeleri (Desneux) (Termitidae); and another, A. minimus Light, flies on sunny days after rain. It should be noted that G. perplexus flies under a variety of conditions, sometimes during rainstorms but not always associated with rain, from shortly after sunrise into evening twilight (Nutting, 1969; Weesner, 1970). The number of species which might have been caught in our light traps was reduced to 8 since P. occidentis usually nests in standing dead wood (none was included within the cages) and A. minimus is a day flier. Thus, we were probably fortunate to trap the following five species, curiously enough all of them evening fliers; I. banksi, an uncommon, little known species which may nest in buried as well as surface wood; P. simplicicornis, a fairly common species in dead roots, stumps, and buried wood; H. aureus and G. perplexus, both extremely common foragers on surface dead wood and other plant material, and A. pallidus, a fairly common, (presumably) entirely subterranean species whose colonies have not yet been found.

The first author has observed alates of H. aureus, G. perplexus and some species of Amitermes leaving their colonies on many occasions. These termites typically open many small holes in the soil within one or two m^2 for the exit of their alates. They are closed immediately after flight. Behavior of the alates of P. simplicicornis and I. banksi is probably similar although there are no reports of it. The alates of I. banksi, H. aureus, and A. pallidus are small enough to penetrate the screen mesh of the cage we used. We must therefore, admit the possibility that a few individuals might have entered the cage from the outside; however, the fact that all except perhaps I. banksi generally lose their wings on or shortly after landing, even under lights, leads us to believe that most of those trapped did swarm within the cages.

RESULTS AND DISCUSSION

The data resulting from the two seasons of trapping are given in Table 1. We have tried to give truer estimates for the numbers and biomass of the alates of Heterotermes and Gnathamitermes by adjusting the trap catches according to the proportion between estimates of the average foraging populations on the entire 40X40-m grid and those on the caged area. Using data from previous studies (Haverty et al., 1976) we have determined the average foraging populations/m^2 for the entire grid and the caged areas to be 3.8:28.1 for Heterotermes and 7.0:9.6 for Gnathamitermes. As a result we have reduced the estimates of numbers and biomass/ha for Heterotermes by multiplying by 3.8/28.1 and for Gnathamitermes by 7.0/9.6 (see Table 1). Lack of comparable population estimates prevented correction of the figures for I. banksi, P. simplicicornis, and A. pallidus. Our corrected estimate of 9,224 alates/ha for G. perplexus compares very favorably with estimates for three abundant African termitids: Macrotermes bellicosus (Smeathman) (as Bellicositermes bellicosus (Smeathman)) at 10,000-20,000/ha, Trinervitermes trinervius (Rambur) at 15,000/ha (Lepage, 1972), and Apicotermes gurgulifex Emerson at 5,000/ha (Bouillon, 1969). However, it is considerably less than estimates for three additional African termitids: Trinervitermes geminatus (Wasmann) at 190,000/ha, Apicotermes desneuxi Emerson at 400,000/ha, and Cubitermes exiguus Mathot at 566,000/ha (Bouillon, 1969).

The total numbers of alates produced by all five species are estima-

Table 1. Number of alates trapped and estimated numbers and biomass of alates produced/hectare during 1973 and 1974 summer flight seasons, Santa Rita Experimental Range, Arizona.

Species	1973			1974		
	No.	Est. No. Alates/ha.	Biomass g/ha	No.	Est. No. Alates/ha.	Biomass g/ha
Amitermes pallidus	2	748 1/	0.98	4	1,495 1/	1.96
Gnathamitermes perplexus	34	9,224 2/ (12,707 1/)	32.14	41	11,123 2/ (15,324 1/)	38.75
Heterotermes aureus	36	1,808 2/ (13,455 1/)	1.85	37	1,858 2/) (13,830 1/)	1.91
Incisitermes banksi	38	14,202 1/	35.36 3/	71	26,536 1/	66.07 3/
Paraneotermes simplicicornis	57	21,304 1/	53.11	70	26,162 1/	65.22
Totals	167	47,286	123.44	223	67,174	173.91

1/ Estimates within cages not adjusted according to average population for the entire study area (estimates probably high).

2/ Estimates within cages adjusted according to average population figures for the entire study area.

3/ Dry weight of similar-sized Paraneotermes alate used for biomass estimate.

mated at 47,286 and 67,174/ha with biomass of 123.44 and 173.91 g/ha for the 1973 and 1974 summer flight seasons. Although these figures may not be particularly impressive when considered on an annual basis, the intermittent nature of the flights insures a succession of energy-rich meals for a variety of predators during a 2- or 3- month season. Termite alates have a very high fat content; for example, nymphs of P. simplicicornis with long wing pads contain 45.5 percent fat on a dry-weight basis (LaFage, Haverty and Nutting, unpublished). Dealated reproductives of G. perplexus contain 56.3% fat and 6.87 kcal/g-dry weight (Dimmitt, 1975).

Most predators, whether arthropod or vertebrate, appear to be opportunistic with regard to this food supply (Nutting, 1969). Dimmitt (1975), however, reported that spade-foot toads, e.g. Scaphiopus couchi Baird, utilize termite alates almost exclusively and can collect sufficient numbers during 2 or 3 nights in the rainy season to meet their energy requirements for an entire year. Indeed, these toads seem to cue on the same environmental variables (most likely a certain minimum rainfall at an appropriate time of day) which trigger termite flights (Dimmitt, 1975).

We have previously estimated total population of H. aureus (4.31X 10^6/ha) and G. perplexus (7.97X10^6/ha) in this area (Haverty et al., 1975, 1976). Using these estimates we might speculate further that these species are producing alates at a rate of about 0.04% of the total population for Heterotermes and from 0.11 to 0.13% for Gnathamitermes. These rates are extremely low when compared with equivalent literature values for other rhinotermitids and termitids. Nutting (1969) and Bouillon (1969) provide the most recent reviews of such data: Coptotermes lacteus (Froggatt), 6.0% (Rhinotermitidae); Nasutitermes exitiosus (Hill), 2.4%; Odontotermes obesus (Rambur), 23-43% (nymphs); Trinervitermes geminatus (Wasmann), 3.9% (maximum); Apicotermes desneuxi Emerson, 6.1% (approximate); A. gurgulifex Emerson, 1.2% (approximate); and C. exiguus, 10.9% (mean) (Termitidae).

The comparatively low productions of alates during the 2 years which we have sampled is probably best explained by the fact that the months preceding the flight season in both years were generally unfavorable for alate development. Having observed the number and size of flights in Tucson (only ca. 40 km north and 200 m lower than our study site) since 1961, Nutting (unpublished data) has determined that 1973 was the poorest and 1974 the third poorest year for alate production for both Heterotermes and Gnathamitermes. Since extensive meteorological data are available it may eventually be possible to sort out the environmental parameters responsible for the low numbers. Alate production rates for G. perplexus might be low because some daylight flights were not trapped, or they might simply appear to be low for both species because our total population estimates are too high. Since alates of all of these species are attracted by UV light, we feel it is unlikely that many escaped the traps when they were operating.

The two flight seasons were very different with respect to rainfall. In 1973 (July 3-September 3) the site received only 78.0 mm of rain while 166.0 mm fell in 1974 (July 2-September 2). (The July-August rainfall at the Santa Rita Experimental Range averages ca. 200 mm.) However, total numbers of alates of P. simplicicornis, H. aureus, and G. perplexus differ very little from one season to the next (Table 1). This suggests that flights may be triggered by individual storms, but that the total number of alates which emerge during the flight season is not dependend upon, or correlated with, the total amount of rain falling during that time. This assumption is further borne out by the observation that alates are commonly matured and waiting for the proper conditions to release them (Nutting, 1969). Table 2 presents the records for the 3- or 4-day collection intervals during both flight seasons. Flights of G. perplexus and H. aureus in general occur on the same day as, or within a few days after, rainfall greater than 3.0 mm. Paraneotermes flights appear (here) to follow storms of more than 18 mm, and several flights occurred over a period of 10 days in 1974 after an extremely large storm (78.1 mm).

Although the cues for the flight of these species (Table 2) are unknown, it cannot be rainfall acting alone since flights of all three species are sometimes staged on rainless evenings. However, rather close synchrony with rainfall must make it possible for recently flown alates of the subterranean species to penetrate the moistened soil; otherwise the desert soils are often hard-packed and extremely dry to a depth of 1 m or more (Nutting, 1966, 1969). Flight cues may also include one or more of the following: changing temperature, light intensity or barometric pressure, and atmospheric electricity (Nutting, 1969). On the other hand, examination of Table 2 shows that there are cases where flight did not follow "sufficient" rain (July 27-29, July 30-August 2, 1973, for P. simplicicornis; August 17-19, 20-22, 1973; July 26-28, 29-31, 1974, for H. aureus). With conditions otherwise suitable, P. simplicicornis and many other species will not fly if it is

Table 2. Rainfall and numbers of alates trapped during collection intervals, 1973 and 1974 flight seasons, Santa Rita Experiment Range, Arizona, USA

1973						1974					
Collection Interval		Rain for Interval (mm)	Alates collected			Collection Interval		Rain for Interval (mm)	Alates collected		
			Gnaper[1/]	Hetaur[1/]	Parsim[1/]				Gnaper	Hetaur	Parsim
07	03/04	0	0	0	0	07	01	3.6	0	0	0
	05/08	19.8	0	0	17		02/04	3.8	0	0	1
	09/11	0	0	0	1		05/07	78.1	31	16	57
	12/15	18.3	18	7	10		08/10	0	4	7	9
	16/19	0	1	7	25		11/14	3.7	1	0	3
	20/22	0	0	0	0		15/17	7.2	4	6	0
	23/26	0	0	0	0		18/21	12.7	0	1	0
	27/29	18.8	15	16	0		22/25	8.1	1	2	0
07/08	30/02	0	0	0	4		26/28	10.7	0	0	0
	03/05	0	0	0	0		29/31	1.0	0	3	0
	06/09	0	0	0	0	08	01/04	27.2	0	2	0
	10/12	2.2	0	0	0		05/07	3.8	0	0	0
	13/16	0	0	0	0		08/11	0	0	0	0
	17/19	3.9	0	0	0		12/14	0	0	0	0
	20/22	0	0	6	0		15/18	0	0	0	0
	23/26	7.6	0	0	0		19/22	2.0	0	0	0
	27/30	0	0	0	0		23/27	0	0	0	0
08/09	31/03	7.9	0	0	0	08/09	28/02	4.3	0	0	0

1/ Termite species: Gnaper, Gnathamitermes perplexus; Hetaur, Heterotermes aureus; Parsim, Paraneotermes simplicicornis

windy or rainy at flight time (Nutting, 1966). This sufficient rainfall thus might have come at dusk when termites normally fly and would have effectively eliminated any flights. G. perplexus, of course, flies under a wide variety of conditions (see Methods and Materials).

These three species ordinarily stage flights throughout the rainy season, generally July-September, but P. simplicicornis sometimes sends out a few flights in June or even late May, well in advance of the rains (Nutting, 1966, 1969). The data in Table 2 suggest that in poor years such as these, a colony may release all or most of its alaes as soon as suitable conditions occur early in the season. After these initial flurries there may simply be no more alates in the colonies to fly.

In the face of widely varying weather conditions, it is evident that these relatively stable insect societies can produce a seasonally dependable, energy-rich food (their own reproductives) for a variety of predators. While most predators of swarming termites are probably opportunistic, a few such as the spade-foot toad, Scaphiopus couchi, appear to depend upon the alates as their major food for the entire year. When we consider the unpredictability of the seasonal flights, however, the success of these predators requires that their appetites be tuned to the same environmental cues as the flights of their prey. There are records of years in certain areas where the proper cues were never given; the termites did not fly (Nutting, 1969; Lepage, 1974). One wonders about the fate of "obligate" predators in such times.

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REFERENCES

Bouillon, A. 1969. Les études des populations des termites ethiopiens. Rev. Ecol. Biol. Sol 6: 469-482.

Dimmitt, M. A. 1975. Terrestrial ecology of spadefoot toads (Scaphiopus): Emergence cues, nutrition, and burrowing habits. Ph. D. Dissertation, Univ. Calif. Riverside, Calif. 92507, USA.

Haverty, M. I., La Fage, J. P., and Nutting. W. L. 1974. Seasonal activity and environmental control of foraging of the subterranean termite, Heterotermes aureus (Snyder), in a desert grassland. Life Sciences 15: 1091-1101.

Haverty M. I. and Nutting, W. L. 1975. Density, dispersion, and composition of the desert termite foraging populations and their relationship to superficial dead wood. Environ. Entomol. 4: 480-486.

Haverty, M. I., Nutting, W. L., and La Fage, J. P. 1975. Density of colonies and spatial distribution of foraging territories of the desert subterranean termite, Heterotermes aureus (Snyder). Environ. Entomol. 4: 105-109.

Haverty, M. I., Nutting, W. L., and La Fage, J. P. 1976. A comparison of two techniques for sampling abundance of subterranean termites in an Arizona desert grassland. Insectes Sociaux (In Press).

La Fage, J. P. 1974. Environmental factors controlling the foraging behavior of a desert subterranean termite, Gnathamitermes perplexus (Banks). M. S. Thesis, Univ. Arizona, Tucson, Arizona 85721, USA.

La Fage, J. P., Nutting, W. L., and Haverty, M. I. 1973. Desert subterranean termites: A method for studying foraging behavior. Environ. Entomol. 2: 954-956.

Lepage, M. 1972. Recherches écologiques sur une savane sahélienne du Ferlo Septentrional, Sénégal: Données preliminaires sur l'écologie des termites. La Terre et la Vie 26: 383-409.

Lepage, M. 1974. Recherches écologiques sur une savane sahelienne du Ferlo Septentrional, Sénégal: Influence de la sécheresse sur le peuplement en termites. La Terre et la Vie 28: 76-94.

Nutting, W. L. 1966. Colonizing flights and associated activities of termites. I. The desert damp-wood termite Paraneotermes simplicicornis (Kalotermitidae). Psyche 73: 131-149.

Nutting, W. L. 1969. Flight and colony foundation. In "Biology of Termites" (Ed. K. Krishna and F. M. Weesner) 1: 233-282. Academic Press, New York.

Weesner, F. M. 1970. Termites of the Nearctic Region. In "Biology of Termites" (Ed. K. Krishna and F. M. Weesner) 2: 477-525. Academic Press, New York.