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Seasonal Changes in Composition of Colonies of the Western Drywood Termite, *Incisitermes minor* (Hagen) (Isoptera: Kalotermitidae)

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Abstract

The entire contents of 38 naturally occurring colonies of the western drywood termite were examined over a period of 14 months in southern California. Emergence of alates from caged colonies was also observed. Large nymphs with wing buds (prealates) may be present from April through September. Alate emergence has been observed from early June through November and probably occurs over a longer period. There is no indication that colonies in the study area are strongly synchronized with respect to alate development and emergence. There is noticeable seasonal reduction in oviposition from October through April. More than two reproductives (primaries or secondaries) were never recovered from any colony, even the largest, suggesting that reports of supplementary reproductives in older colonies might be based on inadvertent mixing of colonies during extraction. The number and aggregate weight of soldiers was strongly correlated with colony size, supporting the hypothesis of a constant or optimal ratio of soldiers to other colony members. The average size of soldiers was weakly, but significantly correlated with colony size.

Despite its importance as a structural pest, our knowledge of the biology of the western drywood termite, *Incisitermes minor* (Hagen), is very limited. Most of the available information about this termite is based on work done nearly 60 years ago (Harvey 1934a, b). The future of drywood termite control in the United States will likely involve a shift away from structural fumigation towards increased use of local treatments. Factors driving this trend include cost, potential loss of registration of fumigant gases, and public fears of pesticides for which the standard fumigation tent is an all too visible symbol. The very success of fumigation has ironically contributed to the lack of recent information on drywood termites. Because current fumigants, when correctly applied, kill all stages within structures, questions about their biology have remained largely moot. The success of current and proposed local treatments, however, depends on a much greater knowledge of drywood termite biology and behavior.

Drywood termites, like other social insects, form complex social groups consisting of different terminal castes and immature individuals in different stages of development. The relative proportions of these stages and castes to each other are of considerable theoretical and practical interest. Colony composition is unlikely to be static. Differences would be expected relative to colony age and available resources and also due to seasonal fluctuations. The most notable of these is the swarming of reproductive forms. Careful reading of the tables given by Harvey (1934b) on the expected colony size and expected caste composition of colonies of different ages of *I. minor* reveals that these numbers are largely speculative and are not based on extensive observations of discrete colonies. Harvey (1934a) stated that *I. minor* swarms on hot days during the fall in coastal southern California. Nutting (1969) concluded that the swarming season for *I. minor* was between May and August in the vicinity of Tucson, Arizona . There is considerable anecdotal evidence that major flights may occur at any

time during the summer and early fall months and that some alates may be found during any month of the year.

Drywood termites, unlike subterranean termites, construct their tunnels completely within pieces of wood. Colonies contain many fewer individuals and are limited spatially. Consequently, the possibility exists of counting the majority, if not all, of the individuals in a single colony. During the process of extracting drywood termites from naturally-infested wood for studies requiring large numbers of individuals, records were kept on the composition of colonies collected over a 14 month period. Records have also been maintained over much of that period of swarming of alates from caged colonies.

Materials and Methods

Collection and Extraction of Termites. All termites were extracted from naturally infested wood collected in southern California. Most collections were made in the vicinity of Riverside, with some colonies taken from as far away as San Diego (150 km SW). Colonies were in logs, large branches, or scrap lumber in wood piles. In all cases it was clear that termites within a given piece of wood belonged to the same colony (data from ambiguous situations are not included here). Some of the colonies were probably derived from fragments of original colonies that had been separated at the time that infested trees had been cut down, while others had probably developed *in situ* from a pair of mated primary reproductives.

The challenge in removing drywood termites from infested wood is that termites are soft and wood is hard. This problem was solved by extracting termites with berlese funnels. Infested wood was cut into pieces no longer than 10-12 cm. Termites that fell out the wood at this point were collected and held. Wood pieces were placed in berlese

funnels over hardware cloth under a 100 W bulb. Care was taken to ensure that the tunnels were oriented vertically so that the termites could escape the rising temperatures by moving downwards. Pieces of Kraft toweling were placed in the collection jars beneath the funnels so that the termites could hide and to reduce injury from milling about. In one test, infested wood was placed into the funnels in the afternoon at an ambient temperature of 22° C. Within 30 minutes the temperature above the top of the wood was well over 50° (the upper limits of the thermometer used) while the temperature below the wood and in the collection jar had scarcely risen. After 16 hours (the next morning) the temperature at the bottom of the wood had risen to 34° and that in the collecting jar to 25° C. In practice, the temperature changes depended on the amount of wood placed into the funnels, the degree to which it had been hollowed out by termites, and its moisture content. Most termites abandoned the wood within the first 4-5 hours. Occasionally termites clung to the bottom of one of the pieces and had to be brushed off with a paintbrush. Dissection of wood after extraction of several samples showed no live termites in the wood and no fresh cadavers, suggesting that all termites had abandoned the samples.

Some individuals were killed while sawing the wood into smaller pieces and in handling, but generally termites were collected in excellent condition, even extremely small nymphs. On many occasions eggs were found in the collection jars, apparently dislodged by the general exodus of the colony. Experience has shown that subsequent survival of termites after funnel extraction is very high by comparison with that of termites that have been extracted by splitting and dissecting infested wood. This is probably due to the combination of reduced trauma from jolting and banging, fewer individuals being inadvertently crushed while splitting the wood, and reduced handling.

Data were taken on the composition of colonies that were extracted from April, 1992 to June, 1993. The numbers of melanized reproductives, soldiers, nymphs (immatures without wing bud development), prealates (immatures with obvious wing

buds) and alates were noted. The presence or absence of eggs and "tiny nymphs" were noted. All soldiers, alates, prealates and nymphs were weighed in aggregate. All counting and weighing were done within 3 days of extraction to reduce bias from subsequent mortality.

Collection of Emerged Alates. Large, irregular pieces of infested wood that were too unwieldy for use in extracting colonies were placed inside 2 saran screen cages, 1.8 m on all sides. Cages were placed in areas exposed to afternoon sun on the Riverside campus.

Alate traps consisted of two 15-cm sections of 2.5 x 5.0 cm douglasfir lumber that were clamped together along their length with thumb screws. Ten to twelve holes (3.2 mm diam) were drilled to a depth of 12 mm along the union of the two blocks (Fig. 1). These traps are similar to those described by Su et al. (1989) for trapping alates of *Coptotermes formosanus* Shiraki. Thirty of these were hung from the top of each cage. Both in the field and in laboratory cages, alates would fly, mate, and use these entry holes to initiate copularia after de-alation. Typically, a pair would enter the hole and seal off the entry with carton, so that one could tell whether or not a given hole was occupied.

The two screen cages were set up in the first week of August, 1992 and left in place until January, 1993. They were put up again in the first week of June, 1993. Trap blocks were checked on an irregular basis.

Results

A total of 38 colonies were examined over a period of 14 months (Table 1). Ranges in weights of different stages are shown in Table 2. Reproductives were recovered in slightly less than one half of the colonies examined. It is very likely that reproductives were undercounted because only individuals that were collected while wood was being cut up prior to extraction or those that successfully emerged in the

funnels were counted. It is also possible that some replacement reproductives that had not yet become fully melanized were overlooked. Large nymphs can quickly become reproductively mature in the absence of functional reproductives (Harvey 1934a), but their coloration changes very slowly and they would be easy to overlook in a mass of several hundred nymphs and prealates. Primary reproductives (developed from alates) were not consistently distinguished from replacement, or neotenic reproductives because all of the latter that were observed were as large and as dark as the primaries and could only be distinguished under magnification by the absence of wing remnants. In laboratory tests it requires nearly a full year for a neotenic reproductive of *I. minor* to become fully darkened (Atkinson, unpublished). No brachypterous neotenics were observed (nor have any been observed in other colonies that have been examined that were not included in this study). In no case were more than one reproductive male or female recovered from any colony.

The largest female reproductives recovered weighed nearly twice as much as the smallest, which were similar in weight to alates. Both male and female reproductives gain weight slowly after establishing new colonies, although females gain weight faster (Atkinson, unpublished). Larger females had clearly distended abdomens, with pale inter segmental membranes showing between the darkened abdominal sclerites. Even the largest females were capable of moving quickly.

Eggs were not recovered in colonies from October through May (Table 1). Eggs were only recovered when they fell out of the pieces of wood in the funnels and their absence in the collection jars does not necessarily mean that they were not present. Nonetheless, these data do indicate that they were less abundant, even if not completely absent.

Large to medium-sized nymphs were present in all colonies. Miller (1969) and Nutting (1970) have advocated the use of the terms larvae and nymphs for immatures, the former being those without visible development of wing buds. This usage has not

been consistently followed by authors in the United States and is not followed here. I use the term nymph to refer to immatures without wing buds (larvae of Miller) and prealates to refer to those nymphs with visible development of wings (nymphs of Miller). Aggregate weights of nymphs ranged from 0.3 - 45.5 g. Nymphs were not counted individually, but an estimate of their numbers can be estimated using the median weight for large nymphs (12.0 mg, Table 2), which would tend to underestimate actual numbers. The estimated number of nymphs ranged from 25 to 3,660. Nymphs constituted more than 80% of the total colony weight in 33 of 36 colonies examined (47.2% to 99.6%, Table 3). In the 3 exceptions, most of the remainder consisted of alates or prealates. Kalotermitids do not have a true adult worker caste. In some termite species the largest nymphs remain in a state of suspended development, even though they may continue to molt. These are termed "pseudergates" (false workers) (Miller 1969). The presence of pseudergates has never been demonstrated in *I. minor* and I have observed no individuals that are clearly identifiable as such. Pseudergates, if present, would have been counted as large nymphs.

"Tiny nymphs" is a arbitrary category used to designate extremely small nymphs (probably instars 1-2). These were not weighed separately, but never represented more than about one tenth of the nymphs extracted. Tiny nymphs were found in most colonies, but were scarcest in the months of February to June. The seasonal patterns of occurrence of eggs and tiny nymphs suggests that egg production is lowest during the cooler months of the year, supporting the similar observation by Harvey (1934a).

Soldiers were present in all but three small colonies. Where present, soldiers constituted from 0.1 to 15.7 % of the total colony weight. Several authors have suggested that there is an "optimum" or "typical" ratio of soldiers to other colony members in mature or stable colonies. Haverty (1979) and Haverty & Howard (1981) have shown some experimental support for this premise with various species of subterranean termites (Rhinotermitidae). Nutting (1970) found some evidence of this in

several species of kalotermitids. Number of soldiers (Table 4, Fig. 2) and aggregate weight (Table 4) of soldiers were moderately correlated with total colony weight. Even though most authors have used number of individuals, rather than aggregate weights of individuals in different castes, the proportional trends, if any, should still be similar. These data support the hypothesis of a relatively constant proportion.

Average weights of soldiers varied widely from 10.7 to 32.9 mg. The average weight of soldiers of *I. minor* was not correlated with total colony weight (Table 4), but was weakly correlated with the logarithm of colony weight (Fig. 2, Table 4). These data suggest that any relationship between size of colony and size of soldiers is most pronounced in the case of smaller and/or younger colonies and tends to level off for medium to large colonies. Su & Scheffrahn (1988) suggested that there was a weak relation between colony size and worker size in colonies of *Coptotermes formosanus* in Florida. It is not clear whether this is because larger colonies are able to provide more or better food during immature development, or whether colonies (and constituent individuals) are larger because of access to higher quality food sources.

Prealates were found in many colonies from April through September, but not during other months. Alates were only recovered on two occasions, in July and August. Paired reproductives were collected in "alate traps" in cages with infested wood in late October and early November, 1992 (cages were in place from the beginning of August) and from mid June (cages were in place from the beginning of June) until the end of August, 1993 when observations ceased (Table 5). Trap blocks in the cages do not provide quantitative information on the relative numbers of swarming individuals, but are indicative of periods of major emergence.

Several points stand out from the patterns of occurrence of prealates and alates. The absence of prealates during most of the year suggests that any individual that develops visible wing buds will mature as an alate and emerge before the end of the season. There is no indication that alates "accumulate" in colonies awaiting a major

swarming period (Tables 1,3). Were this the case, alates would have been more frequently encountered and in ever greater proportions as such a swarming period approached. That major swarming can occur in summer is confirmed by the number of mated pairs found in alate traps in the cages.

Percentages of total colony weight represented by prealates or alates ranged from 0.99 to 49.1%. Alates recovered from within colonies generally weighed less than the largest prealates. This size difference was also perceptible visually. Fully formed alates tended to be slightly shorter and slimmer than the largest prealates. In several cases prealates or alates were found in relatively small colonies (less than 2 g total weight). These data do not allow an analysis of the proportion of a colonies' total resources that leave the colony as alates. All extractions of colonies only allow "instantaneous" views of the dynamic process of nymphal maturation and alate emergence. The total number of alates produced over the course of the entire swarming season would have to be tabulated and compared to colony members at the beginning and end of the process.

Discussion

Seasonal trends in colony composition are relatively weak in *Incisitermes minor* in inland areas of southern California. The major factor driving seasonal changes seems to be the reduction of oviposition and slower development rate of immatures during the cooler months of the year. This "slowdown" in oviposition seems to be primarily responsible for whatever unevenness of age structure is present in colonies. Swarming does not seem to be tightly synchronized among colonies present in a given area, but takes place over an extended period of at least 6 months. All or most alates within a given colony appear to emerge whenever suitable environmental conditions are present. There is no evidence for any process of "accumulation" of prealates or alates in colonies during the summer and fall.

Most of the literature on control of castes in termites focuses on mechanisms that suppress maturation of immatures to the terminal adult castes of soldiers or neotenic reproductives. Very little has been published on what controls development to alates, except for suggestions that alates do not appear in colonies below a certain size (Harvey 1934a, Miller 1969). It seems likely that all nymphs of *I. minor* will eventually complete the normal maturation sequence and become alates, except for a limited number of individuals that become soldiers or neotenic reproductives. Groups of large nymphs held in the laboratory at constant temperatures will develop wings at any time of year, depending mostly on initial body weight and the temperature at which held. Group size (from 10 to 100) does not seem to be a factor nor does the presence or absence of reproductives (Atkinson, unpublished). According to Harvey (1934a) immature development requires from 188-415 days. This would suggest that nymphs developing from eggs produced during the warmer months of the year will mature as alates and emerge during the following year. Time required for maturation and swarming may be determined by accumulation of day-degrees. The actual release of alates probably depends on other "triggering" events such as those discussed by Harvey (1934).

The data presented here support the hypothesis of a fixed ratio of soldiers to other caste members such as that suggested by Nutting (1970). Soldier size was only weakly related to colony size. In incipient colonies in the field or laboratory the first soldier is small, whether produced as part of a brood of primary alates or as a replacement from groups of orphaned nymphs (Castle 1934, Harvey 1934a, Miller 1969). None of the field colonies extracted in this study were small enough to fit that description. The most parsimonious explanation is that there is an "optimum" or "standard" size around which actual sizes will vary. This will be affected by the conditions in particular colonies such as genetic, nutritional (substrate quality) and environmental (temperature and humidity regimes).

Both Harvey (1934a) and Nutting (1970) observed multiple reproductives of the same sex (i.e. supplementaries) in some colonies of *I. minor* and other kalotermitids. None were observed in the 38 colonies examined. It is possible that these observations in which supplementary reproductives were found actually consisted of functionally separate colonies that had developed from fragmentation of a larger original colony within a large system of tunnels. Close examination of the tables presented by Harvey (1934a) reveals that he was unsure in many cases of how many separate colonies were actually involved. Nutting (1970) noted that in several of the cases where he found more than a single pair of reproductives in a colony that these pairs were widely separated from each other. None of the pieces of wood examined in this study were longer than 2 m long, and it may be that the volume of wood was not sufficient for colony fragmentation to occur.

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Table 1. Presence of castes or stages in drywood termite colonies extracted from infested wood in southern California.

year	month	no. colonies	Number of colonies in which stage present					
			reproductives[a]	eggs	"tiny" nymphs	soldiers	prealates	alates
1992	Apr.	2	1	?[b]	?[b]	2	0	0
	May							
	June	3	0	?[b]	3	2	3	0
	July	2	1	?[b]	2	2	2	0
	Aug.	5	2	5	5	5	4	1
	Sept.	1	0	1	1	1	1	0
	Oct.	5	4	0	5	5	0	0
	Nov.	1	1	0	1	1	0	0
	Dec.							
1993	Jan.	3	3	0	3	3	0	0
	Feb.	2	0	0	1	2	0	0
	Mar.	3	0	0	3	3	0	0
	Apr.	5	2	0	3	4	4	0
	May	1	1	0	1	0	0	0
	June	5	3	2	2	5	2	0
	Totals	38	17	6[c]	30[d]	35	16	1

[a] At least one obvious melanized reproductive.
[b] Presence not noted in early samples.
[c] Based on 31 colonies for which presence of eggs was noted.
[d] Based on 36 colonies for which presence of tiny nymphs was noted.

Table 2. Weight ranges for castes or stages found in naturally infested wood samples (mg).

Caste / Stage	No. of Samples	Minimum	Maximum
Soldier	34[b]	10.7	32.9
Prealates	10[b]	12.7	23.4
Alates	2[b]	11	13.7
Large nymphs[a]	22[b]	7.7	16.2
Eggs	1	0.23	0.23
Female reproductives	7[c]	11.5	29.4
Male reproductives	4[c]	11	15.4

[a] Largest nymphs without external development of wing buds.
[b] Based on composite groups.
[c] Based on individuals found in colonies at time of extraction.

Table 3. Aggregate weight and percentage of total colony weight of castes and stages in 36 drywood termite colonies collected in southern California.

Date sample extracted	Nymphs		Soldiers		Prealates		Alates		Total
	wt. (g)	% col. wt.	wt. (g)	% col. wt.	wt. (g)	% col. wt.	wt. (g)	% col. wt.	col. wt.
6/19/92	3.58	100.0[a]	-	-	+[a]		-	-	3.58
6/23/92	6.61	99.4[a]	0.04	0.6	+[a]		-	-	6.65
6/25/92	4.47	87.8[a]	0.62	12.2	+[a]		-	-	5.09
7/8/92	37.57	92.1	0.66	1.6	2.43	5.94	0.15	0.4	40.81
7/30/92	13.1	98.4[a]	0.22	1.6	+[a]		-	-	13.36
8/18/92	1.61	79.2	0.27	13.4	0.15	7.41	-	-	2.04
8/18/92	14.6	47.2	1.09	3.5	6.59	21.32	8.643	27.9	30.93
8/24/92	3.58	97.4	0.06	1.6	0.04	0.99	-	-	3.67
8/25/92	0.9	91.2	0.09	8.8	-	-	-	-	0.98
8/27/92	22.8	89.7	1.88	7.4	0.73	2.87	-	-	25.38
9/19/92	1.2	94.1	0.04	2.8	0.04	3.05	-	-	1.28
10/8/92	9.7	84.3	1.81	15.7	-	-	-	-	11.51
10/8/92	8.22	87.7	1.15	12.3	-	-	-	-	9.37
10/13/92	6.95	97.6	0.17	2.4	-	-	-	-	7.12
10/13/92	7.94	96.4	0.29	3.6	-	-	-	-	8.23
10/19/92	6.08	98.5	0.09	1.5	-	-	-	-	6.17
11/19/92	9.58	91.0	0.95	9.0	-	-	-	-	10.52
1/12/93	8.8	92.0	0.77	8.0	-	-	-	-	9.56
1/13/93	43	95.4	2.06	4.6	-	-	-	-	45.05
1/29/93	3.03	86.4	0.48	13.6	-	-	-	-	3.50
2/19/93	6.55	89.6	0.76	10.4	-	-	-	-	7.30
2/19/93	5.99	94.4	0.36	5.6	-	-	-	-	6.35
3/2/93	7.42	94.7	0.42	5.3	-	-	-	-	7.84
3/2/93	2.54	95.3	0.13	4.7	-	-	-	-	2.67
3/2/93	3.37	96.3	0.13	3.7	-	-	-	-	3.50
4/5/93	10.1	96.3	0.39	3.7	-	-	-	-	10.52
4/22/93	1.52	68.9	-	-	0.69	31.13	-	-	2.21
4/22/93	8.46	52.6	0.02	0.1	7.60	47.27	-	-	16.07
4/26/93	1.1	84.9	0.02	1.4	0.18	13.71	-	-	1.30
4/26/93	1.77	91.7	0.12	6.4	0.04	1.88	-	-	1.93
5/10/93	0.3	93.1[b]	0	-	-	-	-	-	0.33
6/1/93	1.55	94.8	0.06	3.8	0.02	1.43	-	-	1.64
6/1/93	4.52	95.2	0.23	4.8	-	-	-	-	4.74
6/2/93	12.7	99.6	0.05	0.4	-	-	-	-	12.76
6/3/93	1.55	93.5[c]	0.11	6.5	-	-	-	-	1.65
6/3/93	18.1	89.3	2.18	10.7	-	-	-	-	20.31

[a] Prealates not weighed separately from nymphs.
[b] Weights of reproductives constituted 6.9% of the total colony weight.
[c] Weights of reproductives constituted 2.7% of the total colony weight.

Table 4. Summary of regression statistics for soldier characteristics and colony size (weight)

Dependent Variable	Independent Variable	F	prob. > F	r^2	slope	intercept
Number of soldiers	Colony weight	28.46	0.0001	0.4556	1.62	6.10
Aggregate weight of soldiers	Colony weight	27.58	0.0001	0.4479	0.04	0.12
Average weight of soldiers	Colony weight	3.80	0.06	0.1006	0.23	16.78
Average weight of soldiers	Log (N) Colony weight	12.50	0.0012	0.2688	3.58	12.78

Table 5. Number of alate pairs captured in cages containing infested wood. Traps (described in text) were checked irregularly.

Date checked	No. Pairs	Observations
Aug. 15, 1992	-	cages set up
Oct. 13	63	
Oct. 19	4	
Nov. 20	14	
Nov. 25	12	
Jan. 10, 1993	0	cages removed
June 1, 1993	-	cages set up
June 30	177	
July 7	185	
July 9	8	
July 12	27	
July 16	2	
July 20	3	
Aug. 4	103	
Aug. 9	0	
Aug. 13	0	
Aug. 25	192	

Figure 1. Trap used for collecting mated alates. Two halves of opened unit on right, assembled unit on left.

Figure 2. Relationship between number of soldiers and colony size.
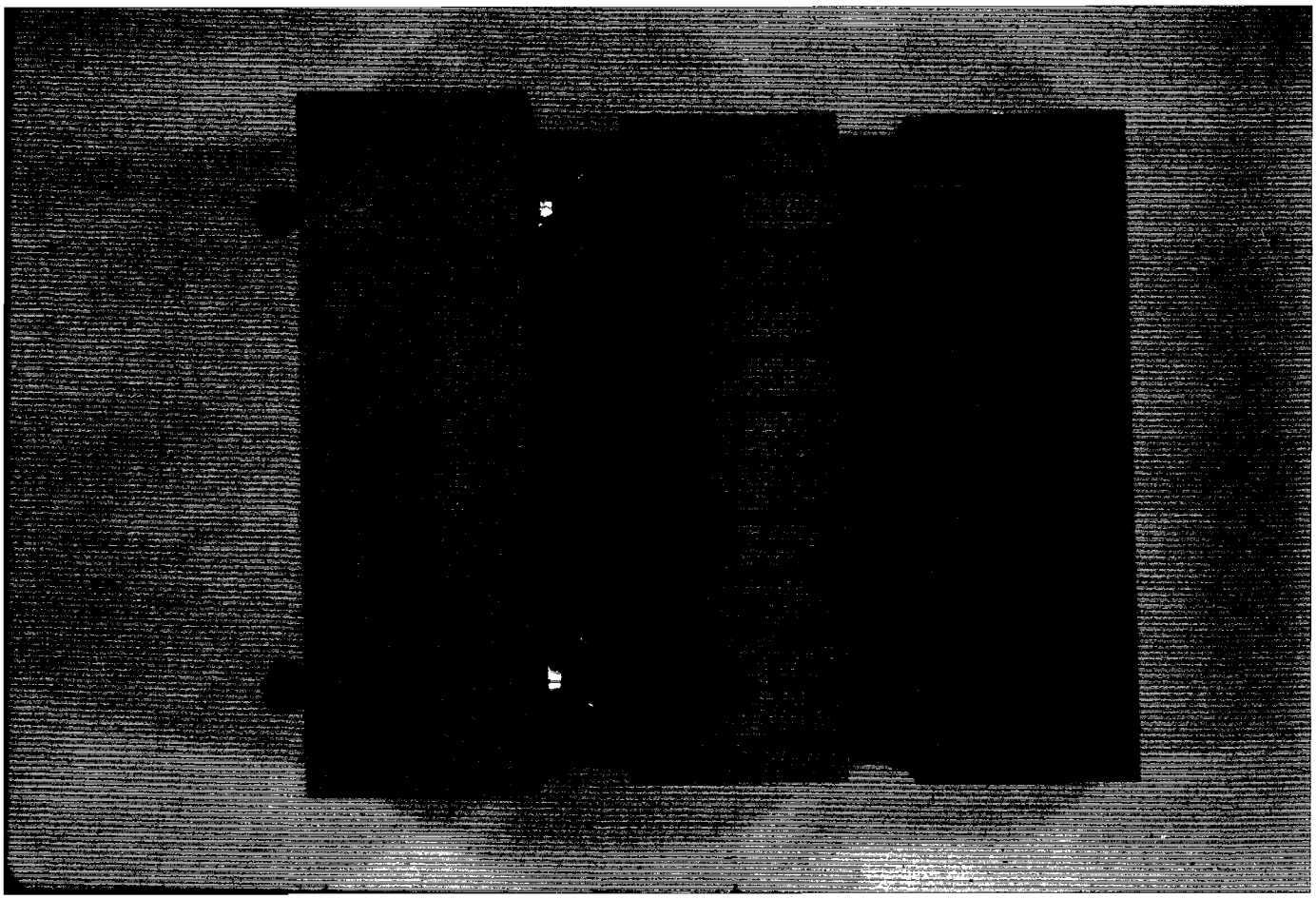
Figure 3. Relationship between average soldier size and colony size.