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DENSITY, FECUNDITY, HOMOGENEITY, AND EMBRYONIC DEVELOPMENT OF GERMAN COCKROACH (*BLATTELLA GERMANICA* (L.)) POPULATIONS IN KITCHENS OF VARYING DEGREES OF SANITATION (DICTYOPTERA: BLATTELLIDAE)[1]

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Abstract.—Populations of the German cockroach, *Blattella germanica* (L.), were mass-collected on a seasonal basis in low-income apartments in Raleigh, North Carolina. Numbers of oothecae and each sex and instar were enumerated. Oothecae collected in June were examined for embryonic development.

Density showed a significant correlation with sanitation. However, certain kitchens had fewer cockroaches than expected at sanitation rating #6 (poorest sanitation) and others with good sanitation (rating #1) had more than expected. Possible explanations of these occurrences were based on analysis of age class frequencies. A structure apparently indicative of a stabilized population occurred at high density in sanitation 6 and low density at sanitation 1. Variability of age class structure stemmed from the individual kitchen infestation, nevertheless, there were several general characteristics. Adults and first-instars were usually the largest groups and nymphal mortality was highest among first-instars. The latter was a secondary factor in regulation of population growth, with primary control occurring at the level of oothecal production.

The German cockroach, *Blattella germanica* (L.), has been the subject of numerous biological studies (Cornwell, 1968). For example, *B. germanica*

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is known to shun light (Gunn, 1940), to prefer temperatures of 24–33°C (Gunn, 1935), and, indeed, to avoid unfavorable temperatures in choosing its habitat (Ogata, 1976). Water and humidity also affect habitat selection, as seen in a preference for both warm and steamy conditions (Gunn and Cosway, 1938; Cornwell, 1968). Less is known concerning factors that affect the growth of natural populations. Laboratory studies showed an increase of nymphal mortality with density (Chauvin, 1946). Under uncrowded conditions, Ross (1976) and Willis et al. (1958) found 83–85% of nymphs that hatched matured, although Ross (1929) reported mortalities of 5% for early molts and 40% for the last molt. An analysis of age class frequencies of collections from single family homes showed little decrease in numbers between first and last stage nymphs, suggesting low mortality (Ross and Wright, 1977). These collections were characterized by high proportions of non-productive females. It was suggested that failure to mate or produce egg cases, known results of insufficient food/water (Kunkel, 1966; Roth and Stay, 1962), were major factors in controlling growth of these populations. Moreover, it appeared that an adequate supply of water might be the most critical factor in the survival of early instars. High cockroach populations were correlated with poor sanitation (Wright, 1979).

This paper reports on a year long study of German cockroach populations in apartments characterized by six sanitation ratings. Selected data on cockroach age composition, density, fecundity, homogeneity and embryonic development, and temperature and relative humidity in apartments are presented. The data increase our understanding of free populations and provide information which can be used in the design of cockroach pest management systems and the evaluation of their success.

Materials and Methods

Four low-income apartment complexes in Raleigh, North Carolina, were used as research sites. Two factors determined apartment selection within each complex: 1) Presence, verified by visual inspection during the day, of numerous cockroaches in an apartment, and 2) permission of the tenants, since the apartments were sampled while the tenants occupied them. Inspection and response of tenants indicated that commercial pest control technicians had not recently disturbed the cockroach populations.

Three apartment complexes, designated A, B, and C, had almost identical construction and floor plans. Each complex was composed of brick and concrete, and contained a number of apartments with tiled concrete floors in the kitchen and bathroom and concrete floors elsewhere. Some apartments were interconnected by holes around stove fixtures, and some tenants spoke of spaces behind cabinets and sink areas. The fourth complex (D) had fewer apartments in each building and more distance between buildings. The floor plan was slightly different from complexes A, B, and C, with much less wall space between kitchens and living rooms and long, wall-sized glass doors on one side of the kitchen. All floors had tile on concrete. Apartments in all complexes had small bathrooms, two floor levels, and continuous stove and cabinet areas along three walls of the kitchen.

Collections in September and December of 1977 were made in apartments in one complex, while those in March and June of 1978 were from apartments in all four complexes where no previous collecting had occurred. Collecting during four months (Sept., Dec., Mar., June) provided seasonal information on German cockroach populations. Six apartments per complex were sites for September and December collections, while three apartments in each of the four complexes were sites for March and June collections. All collecting occurred during the early afternoon and on different days in the month.

Collections immediately followed crack-and-crevice treatments with a synthetic pyrethroid flushing agent, resmethrin. A modified vacuum cleaner (Wright, 1966) was used to collect the cockroaches. Extensive flushing and vacuuming were done where an initial, visual examination revealed abundant cockroaches which appeared evenly distributed throughout a room. In areas of spotty infestation, such as occurred in most bedrooms, crevices in furniture and closets were flushed. Cockroaches were separated immediately according to size of sieves of the USA Standard Sieve Series, numbers 7, 8, and 14. Specimens and oothecae were preserved in 70% ethanol for later classification.

Terminal sternum characters (Ross and Cochran, 1960) and the number of antennal doublets (Campbell and Priestly, 1970) were used for instar and sex determinations with a Wild-Heerbrugg M3 microscope at 40× magnification. With older nymphs, instar determinations were made by a judgement of their relative size after sexing, as breakage of antennae usually precluded use of doublets for instar determination. By combining fourth- and fifth-instars, the problem of classifying damaged, middle-sized nymphs was avoided.

At the time collections were made, an Atkins Thermistor Psychrometer, Model Number 3702B, was used to record ambient humidities and temperatures in each kitchen, living room, bathroom, and bedroom. A sanitation scale (Bennett, 1978; Table 1) was utilized to classify rooms in apartments according to sanitation.

The methods of Barr et al. (1976) were used to analyze information relative to the effects of humidity, temperature, and sanitation level on population density and age structure among German cockroaches. *F*-values were compared at the 0.05 level of significance.

Numbers of first-instar nymphs, oothecae, and adult females, and in the case of June collections, the numbers and progress of developing embryos, permitted fecundity comparisons among German cockroach populations.

Table 1. Sanitary rating scale (Bennett, 1978).

Scale	Sanitary Condition
1. Fairly clean, not cluttered	Floors not very dirty, shelves and cupboards not cluttered, except for normal amount of content, no obvious piles of trash.
2. Fairly clean and cluttered	Floors fairly clean but may be cluttered with trash, clothes, etc. (nongarbage); cupboard filled with nongarbage articles.
3. Generally dirty, not cluttered	Floors generally dirty and/or greasy; cupboards dirty and not washed out for some time.
4. Generally dirty and cluttered	Floors generally dirty and piled with nongarbage trash, clothing, or small amounts of garbage; cupboards not washed out, dirty, and filled with nongarbage articles.
5. Severely dirty, not cluttered	Very dirty with garbage obvious; area very greasy and uncleaned in a long time; dead cockroaches obvious and not swept up.
6. Severely dirty and cluttered	Very dirty with garbage obvious and piled around, greasy areas filled with articles, trash, papers, etc. (which make counting difficult); dead cockroaches obvious and not swept up.

The presence or absence of eye pigment was used to determine the extent of embryo development in oothecal chambers (Tanaka, 1976). In addition, various estimates of first-instar nymph production during selected months for each apartment complex and season aided productivity comparisons. It was assumed throughout that productivity did not vary within a complex during a month's time.

Estimates of monthly nymphal production were calculated three ways. The first method was based on the numbers of first-instar nymphs collected. The first nymphal stadium lasts about five days (Woodruff, 1938). Monthly hatch was considered to be composed of six equal "waves" of first-instar nymphs (30 days per month ÷ 5 days per first-instar = 6), giving rise to the following formula: No. of first-instar nymphs per month = (No. of first-instar nymphs counted in one wave) × (6 waves per month).

The second method was based on numbers of oothecae collected. Using a hatch estimate of 76% (Willis et al., 1958) and the mean of 37.6 embryos per ootheca (Table 2) the formula was: No. of first-instar nymphs per month = (No. of oothecae per month) × (28.6 nymphs emerging per ootheca).

The third method was based on the reproductive potential of all adult females collected. Assuming that a female German cockroach produces one egg case per month (Cornwell, 1968), and applying the hatch estimate of

Table 2. Estimates of numbers of first-instar nymphs hatching in a month per apartment complex, based on numbers of first-instar nymphs, oothecae, and adult females collected during each season.

		Method of Calculation		
		First-Instar Nymphs[a]	Oothecae[b]	Adult Females[c]
Month	Complex	Estimated Number		
September	A	9708	9667	22,451
December	B	16,728	19,191	40,869
March	A	5610	4919	11,268
	B	3246	5834	12,899
	C	8644	9381	22,222
	D	6258	16,645	34,063
	$\bar{x}$	5940	9195	20,113
June	A	5112	2889	7550
	B	3072	4004	10,096
	C	4512	9095	21,078
	D	11,094	7808	18,847
	$\bar{x}$	5948	5949	14,392

[a] Based on the formula: No. of first-instar nymphs per month = (No. of first-instar nymphs counted in one wave) × (6 waves per month).

[b] Based on the formula: No. of first-instar nymphs per month = (No. of oothecae) × (28.6 nymphs emerging per ootheca).

[c] Based on the formula: No. of first-instar nymphs per month = (No. of adult ♀) × (28.6 nymphs emerging per ootheca).

Willis et al. (1958), and the mean number of embryos per ootheca (Table 2), the formula was: No. of first-instar nymphs per month = (No. of adult ♀'s per month) × (28.6 nymphs emerging per ootheca).

Results and Discussion

Ambient relative humidity of rooms was variable, ranging from 25–83%, with an average of 54.5%. Means were lower in December (52.5) and March (42.6) and higher in June (64.7) and September (63.3). The humidity in cracks and crevices is assumed to have varied similarly on a seasonal basis. Preliminary measurements under the kitchen sinks in September were nearly identical to the ambient values for kitchens. Neither relative humidity nor the related factor of temperature showed a correlation with either the density or age structure of the populations at the 0.05 level of significance. It is doubtful if either of these factors exerted much effect on the populations. The mean temperature of 26.1°C and range of 21–30° were close to the optimal temperature of about 25° (Gould, 1941) and the optimal range of 24–33° (Gunn, 1935), respectively. Providing the cockroach has water to drink, its response to humidity is weak (Gunn and Cosway, 1938).

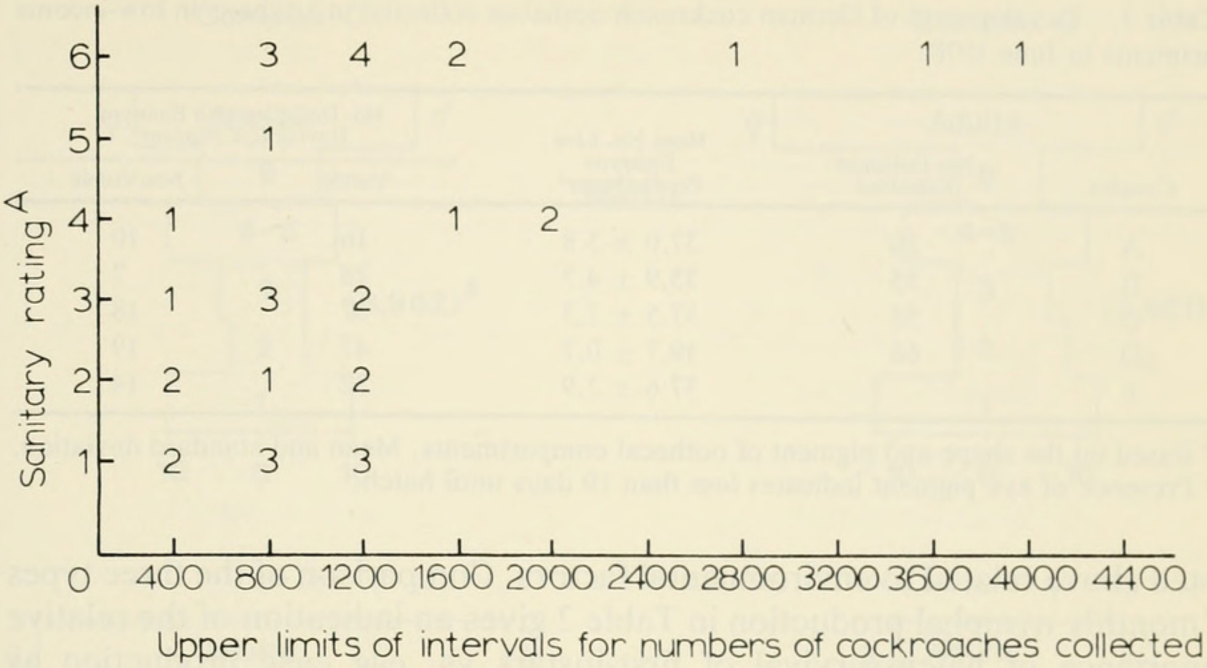

Fig. 1. Numbers of German cockroach samples collected in kitchens in 36 low-income apartments arranged by class size and sanitary rating. The numbers 1, 2, 3, and 4 refer to the total number of kitchens where samples were collected with a specific sanitary rating and a designated range of cockroaches. For example, there were 3 kitchens where samples were collected which had a sanitary rating of 3 and the number of observed cockroaches was over 400, but less than 800. A, Based on a sanitation scale developed by Bennett (1978). B, For example, an upper limit of 400 includes an interval of 1–400 cockroaches.

Sanitation had a significant effect (0.05) on population density in kitchens. In apartments rated poor in sanitation, greater populations of cockroaches were present (Fig. 1). One-third of the kitchens had the poorest possible sanitation rating (rating of 6). Three of these kitchens with poor sanitation contained cockroach populations exceeding 2400 cockroaches. The German cockroach is typically active in darkness (Gunn, 1940), yet kitchens with large cockroach populations had many individuals active in the day. Crowding in shelter areas could make this unusual behavior necessary. Productivity in kitchen populations was not affected by sanitation as rated on Bennett's sanitary scale (see Table 1). Cockroach populations in kitchens with sanitary ratings of 4–6 produced an estimated average of 22.9 first-instar nymphs emerging per ootheca, while populations in kitchens with sanitary ratings of 1–3 produced an estimated average of 23.5 nymphs emerging per ootheca, based on the number of oothecae and first-instar nymphs collected in the kitchens. Populations in apartments with unsanitary conditions (4–6 on the sanitary rating scale) averaged 36.7 developing embryos per ootheca, while those in apartments with better sanitation (1–3 on the sanitary rating scale) averaged 38.2 embryos per ootheca.

The data have implications for population dynamics in addition to those

Table 3. Development of German cockroach oothecae collected in kitchens in low-income apartments in June 1978.

Complex	No. Oothecae Examined	Mean No. Live Embryos Per Oothecae[a]	No. Oothecae with Embryos Having Eye Pigment[b]	
			Visible	Not Visible
A	26	37.0 ± 3.8	16	10
B	35	35.9 ± 4.7	28	7
C	55	37.5 ± 2.3	37	18
D	66	39.7 ± 0.7	47	19
$\bar{x}$		37.6 ± 2.9	32	14

[a] Based on the shape and pigment of oothecal compartments. Mean and standard deviation.
[b] Presence of eye pigment indicates less than 10 days until hatch.

noted above related to environmental factors. Comparison of the three types of monthly nymphal production in Table 2 gives an indication of the relative importance of hatch-survival of first-instars vs. egg case production as mechanisms that limit population growth. Estimates of monthly hatch based on observed numbers of first-instars are shown in column 3. These estimates tended to be lower than those based on the total number of oothecae × the average number of nymphs emerging from an ootheca in the laboratory (column 4). However, the magnitude of the difference was frequently small, especially in lower density apartments in complexes A and B. Apparently neither hatch nor immediate post-hatch survival were drastically reduced in these apartments. In contrast, March data from complex D and June data from complex C suggest a greater hatch reduction and/or post-hatch mortality. In these instances monthly hatch as estimated from observed numbers of first-instars (column 3) was less than half that expected from estimates based on the number of oothecae (column 4). Surprisingly, June results from complex D showed the reverse situation. In complex D, it appears that populations were growing very little in March, but did increase in growth in June. If collections were made at a time of first egg case hatch of a large proportion of the females, overall monthly hatch would be over-estimated. The one "wave" would be larger than the others. Alternatively, it would be difficult to account for a higher hatch from estimates based on observed numbers of first-instars than those from laboratory hatch. The large number and low variability of egg cases of June collections (Table 3, complex D) support this hypothesis of high input from first egg case hatch. Whether these differences between population structure-growth in complex D and the other three complexes are related to structural differences noted earlier is unknown.

The hatch estimates shown in Table 2 (column 5) are based on an assumption that all adult females were reproductively active. The disparity between these data and the estimates based on numbers of oothecae (column

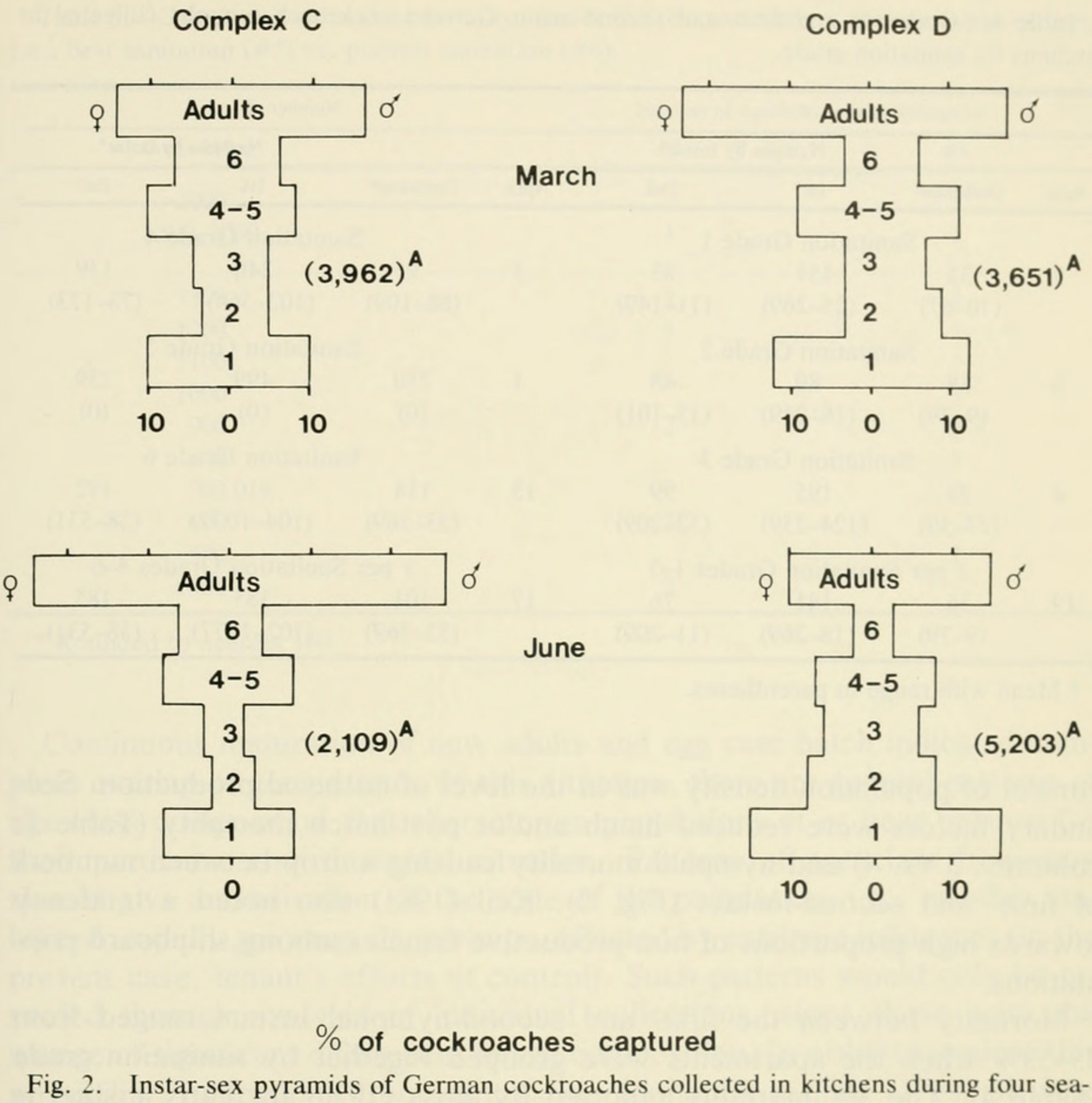

Fig. 2. Instar-sex pyramids of German cockroaches collected in kitchens during four seasons of 1977–1978. Numbers in parentheses (A) next to the pyramids are the total numbers of captured cockroaches.

4) indicates that less than one-half of the adult females were producing viable oothecae. In this species, limited availability of food causes failure to mate (Roth and Stay, 1962) and failure of mated females to produce oothecae (Kunkel, 1966). Either limited food and/or water in relatively sanitary conditions or limited access to these resources due to crowding in unsanitary conditions could account for the heavy proportion of reproductively inactive females. A few may have been past the productive part of their life span (Willis and Lewis, 1957; Willis et al., 1958), although death, rather than failure to produce viable oothecae, is the major age-related cause of reproductive failure among females of this species (Cochran and Ross, unpublished data). The present data provide strong evidence that major

Table 4. Oothecae and first- and second-instar German cockroach nymphs collected in kitchens by sanitation grade.

	Number of				Number of		
		Nymphs by Instar[a]				Nymphs by instar[a]	
Apts.	Oothecae[a]	1st	2nd	Apts.	Oothecae[a]	1st	2nd
	Sanitation Grade 1				Sanitation Grade 4		
9	33	151	83	3	95	240	139
	(10–67)	(25–269)	(11–149)		(88–109)	(102–364)	(73–173)
	Sanitation Grade 2				Sanitation Grade 5		
6	38	89	48	1	230	499	239
	(9–79)	(18–219)	(15–101)		(0)	(0)	(0)
	Sanitation Grade 3				Sanitation Grade 6		
4	39	195	99	13	114	410	192
	(27–59)	(124–239)	(52–209)		(33–369)	(104–1077)	(38–531)
	$\bar{x}$ per Sanitation Grades 1–3				$\bar{x}$ per Sanitation Grades 4–6		
19	36	141	76	17	101	385	185
	(9–79)	(18–269)	(11–209)		(33–369)	(102–1077)	(38–531)

[a] Mean with range in parentheses.

control of population density was at the level of oothecal production. Secondary factors were reduced hatch and/or post-hatch mortality (Table 2, columns, 3 vs. 4) and nymphal mortality causing a drop between numbers of first- and second-instars (Fig. 2). Keil (1981) also noted a tendency towards high proportions of non-productive females among shipboard populations.

Mortality between the first- and second-nymphal instars ranged from 45–53% when the apartments were grouped together by sanitation grade (Table 4). The 5% mortality reported by Ross (1920) for early instars is much less than that observed in these complexes. There was no significant difference in the percent of nymphal mortality between the first- and second-nymphal instars when compared by kitchens grouped into the sanitary grades 1–3 and 4–6. Mortality was 45.2% and 47.9% respectively. However, there was extensive variation among individual collections (see below). The number of oothecae collected in apartments grouped by sanitation grade also varied widely, but more oothecae were collected in apartments with sanitation grades of 4–6 than in those with grades of 1–3 (Table 4).

Examination of oothecae collected in June from apartments in the four complexes showed consistency in the number of live embryos per ootheca, with an average of 37.6 live embryos per ootheca (Table 3), which is less than the 45 embryos reported by Tanaka (1976). Eye pigment, indicating nymphal emergence from the oothecae would occur in 10 or fewer days, was visible in 70% of the oothecae examined.

Table 5. Comparative densities in collections at the two extremes of the sanitation ratings, i.e., best sanitation (#1) vs. poorest sanitation (#6).

Cockroaches[a]	Number of Apartments With Ratings of: #1	#6
>2000		3
1500–2000	1	1
1300	1	1
1200	1	1
1100		
1000		2
900	2	3
800		1
700		2
600	3	
500		1
<500	2	

[a] Rounded to nearest 100.

Continuous maturation of new adults and egg case hatch indicated complete overlap of generations. In this situation, there are general patterns of age class composition that characterize populations at or near balance for their particular environmental situation. Patterns of age class frequency should give an indication of the state of the population, i.e., whether stabilized, rapidly growing, or, perhaps, affected by extrinsic influences (in the present case, tenant's efforts at control). Such patterns would only be revealed through analysis of individual collections, since these were the source of significant differences in age composition. In order to explore this possibility, collections from contrasting sanitation ratings (1 vs. 6) were compared. It was assumed those with maximum numbers for the particular environment would give the best indication of the age composition of a stabilized population.

Collections ranging from 300–900 predominated at sanitation 1 (Table 5). In contrast, at sanitation 6 most fell within a range of 900–4000, with 900 apparently on the low side for poor sanitation. Age composition of the higher density collections differed from that of the smaller collections. Among the former, at least 25% were first-instars (Fig. 3A). A drop of over 12% occurred between first- and second-instars and, in all except one collection, first-instars outnumbered adults (difference ranging from 6–16%). In contrast, first-instars formed less than 25% of sanitation 6, low density collections. The drop between first- and second-instars was smaller (<12%), except in one intermediate density collection (Fig. 3A–952), and adults outnumbered first-instars consistently. The unifying feature found at sani-

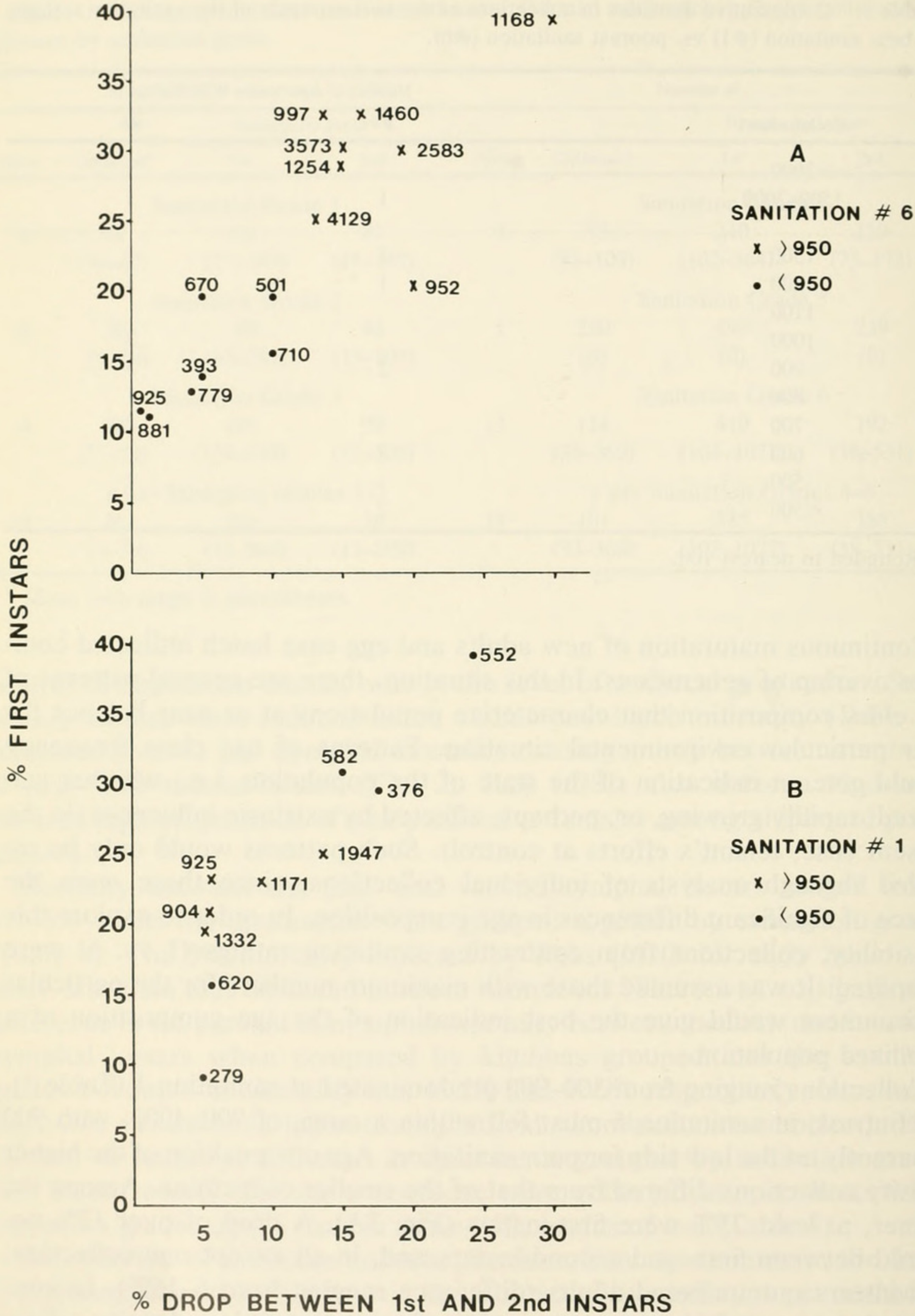

Fig. 3. Comparison of the proportion of first-instar German cockroaches and first-instar mortality at sanitation 6 vs. 1 for low and high density groups. A, Differences between high and low density groups at sanitation 6; characteristics of high density (x) presumably are those of a stabilized population. B, Characteristics of presumed stabilized populations which occur among low density groups at sanitation 1 (first-instars >25%).

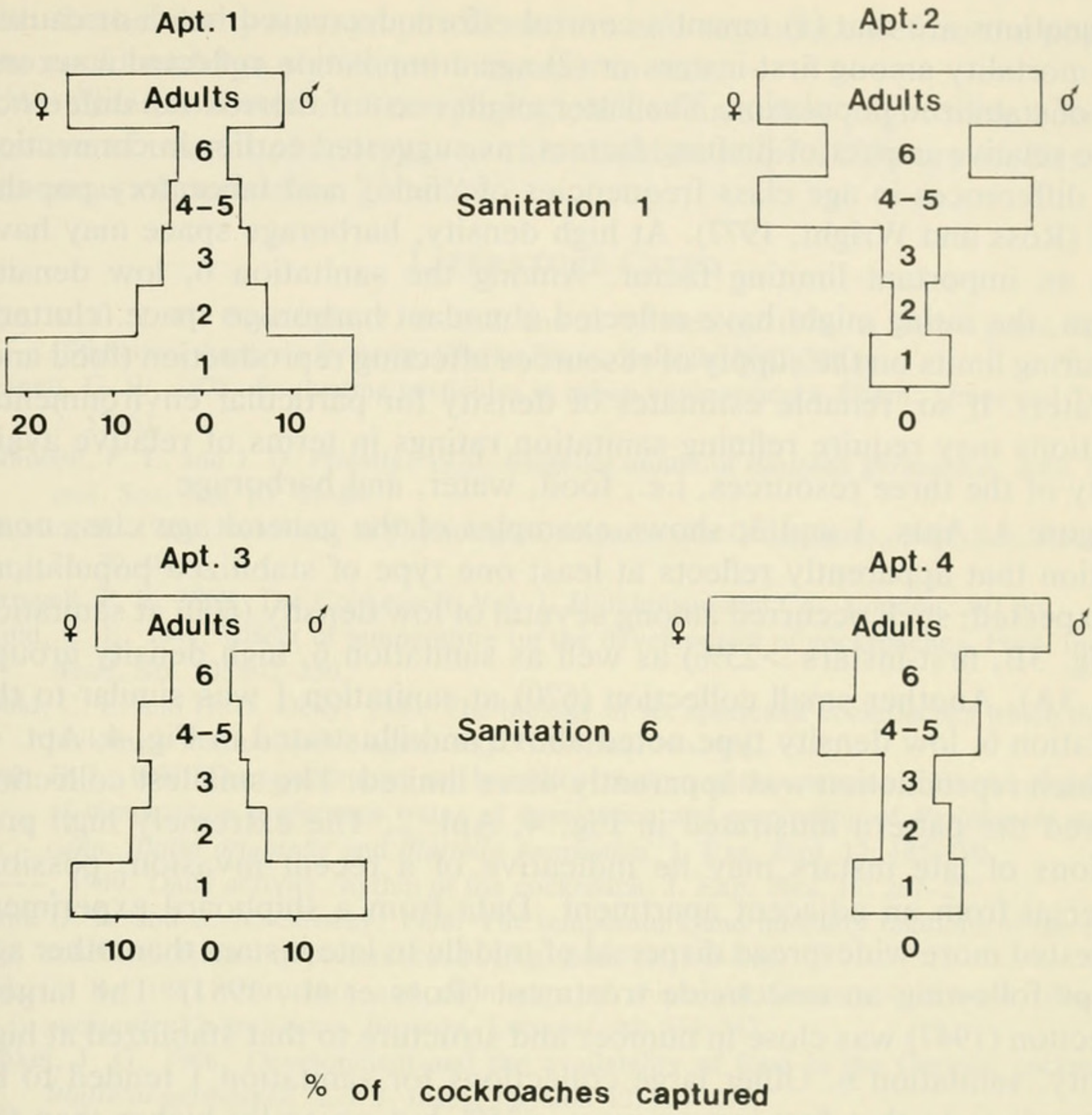

Fig. 4. Examples of German cockroach age class frequencies from single apartments. Apts. 1 and 3 are typical of presumed stabilized type as seen at sanitation 1 and 6, respectively. Apt. 2 shows a composition that may be indicative of a recent immigration. Apt. 4 illustrates the structure typical of low density, sanitation 6 groups, as well as some at sanitation 1, in which reproduction was apparently more limited than in the type shown in apts. 1 and 3.

tation 6 was that high density apparently characterizes populations that are essentially stabilized for their particular environmental situation. Therefore the age composition of the low density collections was examined for clues as to why they were smaller than expected and whether they might provide insight into situations where sanitation and density do not show a close correlation. Recent introductions would represent expanding populations, with higher proportions of immatures than in stabilized groups. This possibility was ruled out since none of the low density groups had higher proportions of nymphs than the high density groups. Rather, age class frequencies suggested a more limited reproduction. The proportion of first-instars was smaller, as in the example shown in Fig. 4, Apt. 4. Possible explanations are that (1) tenant's control efforts decreased hatch or caused high mortality among first-instars or (2) age composition reflected a second type of stabilized population. The latter might occur if there was a difference in the relative impact of limiting factors, as suggested earlier in connection with differences in age class frequencies of "field" and laboratory populations (Ross and Wright, 1977). At high density, harborage space may have been an important limiting factor. Among the sanitation 6, low density groups, the rating might have reflected abundant harborage space (clutter), obscuring limits on the supply of resources affecting reproduction (food and/or water). If so, reliable estimates of density for particular environmental situations may require refining sanitation ratings in terms of relative availability of the three resources, i.e., food, water, and harborage.

Figure 4, Apts. 1 and 3, shows examples of the general age class composition that apparently reflects at least one type of stabilized population. As expected, such occurred among several of low density (600) at sanitation 1 (Fig. 3B, first-instars >25%) as well as sanitation 6, high density groups (Fig. 3A). Another small collection (620) at sanitation 1 was similar to the sanitation 6, low density type noted above and illustrated in Fig. 4, Apt. 4, in which reproduction was apparently more limited. The smallest collection showed the pattern illustrated in Fig. 4, Apt. 2. The extremely high proportions of late instars may be indicative of a recent invasion, possibly dispersal from an adjacent apartment. Data from a shipboard experiment suggested more widespread dispersal of middle to late instars than other age groups following an insecticide treatment (Ross et al., 1981). The largest collection (1947) was close in number and structure to that stabilized at high density, sanitation 6. Other large collections for sanitation 1 tended to be intermediate in that first-instars were <25% but generally higher than the 11–20% range typical of those with apparent limited reproduction. A possible explanation of both unusually high densities for sanitation 1 and incipient limits on reproduction is a recent change for the better in house-keeping habits.

The data presented here and those published earlier (Ross and Wright, 1977) provide some of the first evaluations of the effects of density-independent factors (temperature and humidity) and density-dependent factors (food/water) on density and age class structure. We suggest that the latter, when considered in conjunction with an evaluation of the environmental resources, may prove to be a useful tool in evaluating the state of the population (stable, growing, new introduction, decreasing) and, possibly, assessing the effects of control measures. The evidence of population control at the level of oothecal production is primarily important in respect to recovery potential. Lowered density would stimulate reproduction among an increased proportion of the adult females. This would engender far more rapid growth than if expansion depended on decreased nymphal mortality, with the necessity for nymphs to mature and reproduce before the population could undergo significant increases in size.

We note an absence of morphological deviants that might have been indicative of mutant phenotypes as this could be helpful if future studies lead into areas of population genetics.

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Note

A 2000+-Year-Old Beetle (Coleoptera: Dermestidae)

Robert Brier, Philosophy Department, Long Island University, Greenvale, N.Y., recently submitted for identification nine adult specimens of a dermestid beetle found inside a wrapped, mummified cat. I identified them as *Dermestes frischii* Kugelann, a widely distributed species in Europe, Asia, Africa, and North America. The larvae of this species feed on carcasses, bones, dried fish, and a number of other substrates, usually dead animal matter, and have been found in mummies (Hope. 1834. Proc. Entomol. Soc. Lond. 1834: 11–13; Lesne. 1930. Bull. Soc. Entomol. Egypte 1930: 21–24).

The exact origin of the mummified cat is not known, but Brier placed the date at 332 BC to 30 BC based on the wrapping which he regards as characteristic of the Ptolemaic dynasty in Egypt. The beetle specimens would thus be 2011 to 2313 years old.

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