Dietrich, who collected the Mt. Desert Island material, informs me that he was unable to collect *S. tranquilla* in the field at that time. The writer had the same experience although he has collected this species in this area in previous years.

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POPULATION CHARACTERISTICS AMONG COLONIES OF THE ANT *FORMICA OPACIVENTRIS* EMERY[1] (HYMENOPTERA: FORMICIDAE)

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ABSTRACT

Population characteristics are described for approximately 400 mound nests of *Formica opaciventris* censused over a 3 year period in Wyoming. During this period of observation, density remained stable at 0.007 nests/sq. meter with a maximum density of 0.4 nests/sq. meter.

Mounds are categorized into size and activity classes and yearly changes are noted. Only a portion of the population releases sexuals, and on a statistical basis these fertile mounds are more likely to be found among the larger, more active segment of the population, and in the NW quadrant of this study area.

Mortality rate for the total population was 8%–9%, increasing regularly at lower activity levels. Nest birth rate was 5%–13% during the period of observation. These rates are compared with those of closely related species of *Formica*.

Population characteristics of social insects are of especial interest since these populations operate simultaneously at the level of

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the colony, the population of colonies, and the interspecies population of colonies, and can be investigated at each of these levels of integration. This report contains an examination and description of a population of the mound building ant *Formica opaciventris* Emery at the intraspecies population of colonies level, and it follows an earlier description of colony life history, nest structure and reproductive behavior in this species (Scherba, 1961).

Several different aspects of the population of colonies of ants have been investigated by zoologists over the years. Population of colonies densities have been measured, usually by a quadrat sampling technique, by Brian (1951, 1952), Headley (1949, 1952), and Talbot (1953). An interesting aerial estimate of *Pogonomyrmex* density is reported by Weber (1959). In general,

TABLE I

HIGH POPULATION OF COLONY DENSITIES FROM VARIOUS COMMUNITIES

Species	Nest per Square Meter	Square Meters Per Nest	Source
Ponera c. pennsylvanica	9.1	0.1	Headley (1952)
Myrmica rubra macrogyna	3.1	0.3	Brian (1951)
Aphaenogaster rudis	1.9	0.5	Talbot (1957)
Lasius niger neoniger	0.5	2.0	Talbot (1953)
Aphaenogaster fulva aquia	0.1	8.8	Headley (1949)
Formica opaciventris (maximum density)	0.04	24.4	Present study
Formica ulkei	0.02	47.2	Dreyer (1942)
Formica exsectoides	0.01	69.0	Andrews (1925)

species with high intranest densities seem to have lower population of colony densities in the habitats examined (Table I).

Measurements of density changes over a period of years have been reported for *Formica exsectoides* (Andrews, 1925, 1926; Cory and Haviland, 1938; Haviland, 1948), *Formica ulkei* (Dreyer and Park, 1932; Dreyer, 1942; Scherba, 1958; Talbot, 1961) and *Formica obscuripes* (King and Sallee, 1953, 1956). Some of the censuses span an impressive length of time: 9 years for the *F. obscuripes* population in Iowa, 15 years for the *F. exsectoides* population near Baltimore; 23 years for the *F. ulkei* population southwest of Chicago, and 48 years for the *F. exsectoides* population near Altoona, Pennsylvania.

Changes in the proportion of mound nests of different sizes with time have been included in some of the reports cited above. In each instance there was a definite trend toward the decrease in proportion of small mounds and corresponding increase in proportion of larger nests (Andrews, 1926; Dreyer, 1942; Scherba, 1958; Talbot, 1961).

Information about nest birth rate, the number of new colonies expressed as a proportion of existing colonies, has been reported for *F. ulkei* and *F. obscuripes.* The mean for two established populations was approximately 12.5%, while in a new and rapidly expanding population nest birth rate rose to 57.2% and then declined as the habitat stabilized (King and Sallee, 1953, 1956; Scherba, 1958; Talbot, 1961). Death rate, expressed here as the proportion of the population of a particular year which dies in each succeeding year, was 4.5% in the *F. exsectoides* population reported by Haviland (1948), approximately 9% in that reported by Andrews (1926), approximately 6% in the *F. ulkei* population reported by Dreyer (1942), approximately 9% for the same population at a later date (Scherba, 1958), and approximately 17% for the *F. obscuripes* population observed by King and Sallee (1953, 1956). Although both Scherba (1958) and Talbot (1961) report that death rate was higher among new nests than established nests, the opposite was reported for the *F. obscuripes* population followed by King and Sallee.

The re-entry of fecundated females into established nests in several species of *Formica* would be expected to render these colonies immortal, but this appears to be not the case, although data on longevity of colonies is scanty. Dreyer (1942) has estimated the longevity of *F. ulkei* at 20–25 years, and King and Sallee (1953, 1956) have calculated the half-life, that point in time on a modified survivorship curve at which the mixed-age population of a particular year has declined by one-half, for the populations mentioned.

Regulation of colony density, where investigated, involves interaction of physical environmental factors (Cole, 1934) with competition for food and nesting sites (Brian, 1952, 1952a, 1956; Pontin, 1961) and territoriality (Brian, 1955).

It is important to note that most of the longer-term population of colonies investigations have been conducted upon the long-lived, conspicuous mound nests of *Formica* species, especially those of the *exsecta* group. This has the advantage of permitting comparisons among the several populations examined, but also invites caution in extending expectations to other groups of ants.

THE POPULATION

The population examined in this report is located on Moose Island, a small island in the Snake River, one mile east of Jackson Lake, in western Wyoming. The site is at an elevation of 6775 feet. The conspicuous mound nests of this population occupy the central Silver Sagebrush (*Artemisia cana*) meadow and are entirely restricted to this meadow.

Formica opaciventris is one of three North American species in the *exsecta* group of *Formica*, together with *ulkei* and *exsectoides*, mentioned above. Characteristics of this population with respect to density, composition, birth rate, and death rate are described below.

METHODS

A total census of the number of *opaciventris* mounds on Moose Island was recorded during July and August, 1957, 1958, and 1959. After the meadow was carefully mapped and its boundaries delineated, the location of each *opaciventris* mound was noted on the map and a numbered survey stake was erected next to each mound.

At each mound, the length of the longest basal diameter, in inches, was measured in 1957 and 1959, as an index of mound size. For purposes of tabulation, mounds are classified into three size groups, following the scheme of Dreyer and Park (1932); small mounds < 24 inches; medium mounds 24 to 47 inches; large mounds > 48 inches. The size of a small number of mounds was not measured because of indefinite boundaries in certain incipient and moribund nests, and because of oversight in others. These mounds are listed as unclassified (Table 2).

In 1957, 1958, and 1959, an estimate of the level of activity of the inhabitants of each mound was recorded by reference to the following criteria: level 4—workers abundant and active, mound surface soil freshly mined overall, vegetation absent from apical area of mound; level 3—workers abundant and active, mound surface soil freshly mined overall but with some vegetation on apical mound area; level 2—workers active, mound surface with little freshly mined soil, vegetation present on apical mound area as well as on other portions of mound surface; level 1

—workers sparse, mound surface dried, cracked, with little or no mined soil, vegetation abundant on surface. The activity classes so defined are assumed to be correlated with the density and vigor of the worker population inhabiting each mound. Although there is no difficulty in assigning activity levels consistently to active mounds, it has not been possible to consistently state with certainty that a formerly inhabited mound is now

TABLE II

FORMICA OPACIVENTRIS, NESTS CLASSIFIED BY SIZE AND ACTIVITY, JULY–AUGUST 1957, 1958 AND 1959

Activity Level*	Activity Classes					
	1957		1958		1959	
	n	%	n	%	n	%
0	11	2.57	15	3.77	10	2.39
1	69	16.12	49	12.31	41	9.79
2	82	19.16	84	21.11	117	27.92
3	115	26.87	120	30.15	174	41.53
4	140	32.71	126	31.66	75	17.90
unclassified	11	2.57	4	1.00	2	0.48
	428		398		419	

Size Classes**	Size Classes					
	1957		1958		1959	
	n	%	n	%	n	%
Unclassified	58	13.55	not		126	30.07
Small	315	73.60	measured		244	58.23
Medium	44	10.28			44	10.50
Large	11	2.57			5	1.19
	428				419	

* See text for explanation of categories.

** Size Classes: Small = $<$ 24 inches; Medium = 24–47 inches; Large = $>$ 48 inches.

abandoned and a dead nest. For these cases of apparently moribund mounds, which may actually be dead nests, level 0 is assigned. A small number of mounds were not classified as to activity level for the reasons stated above and these nests are tabulated as Unclassified (Table II).

POPULATION STRUCTURE

Density In 1957 there were 428 mound nests of *F. opaciventris* distributed on the silver sage meadow with an overall density of one mound/147.2 square meters (0.007 nest/square meter), and a maximum density of one mound/23.7 square meters (Table I). Size of the mound population remained at approximately 400 nests during the three seasons of observation and varied by less than 10% from year to year (Table II and Fig. 1).

Size class changes In both 1957 and 1959 medium mounds were the most abundant, large mounds the least (Fig. 2). Between 1957 and 1959 changes in mound size and the founding of new, small nests resulted in an increased proportion of small and a decreased proportion of medium mounds. Rate of change from one size class to another was approximately 18% for me-

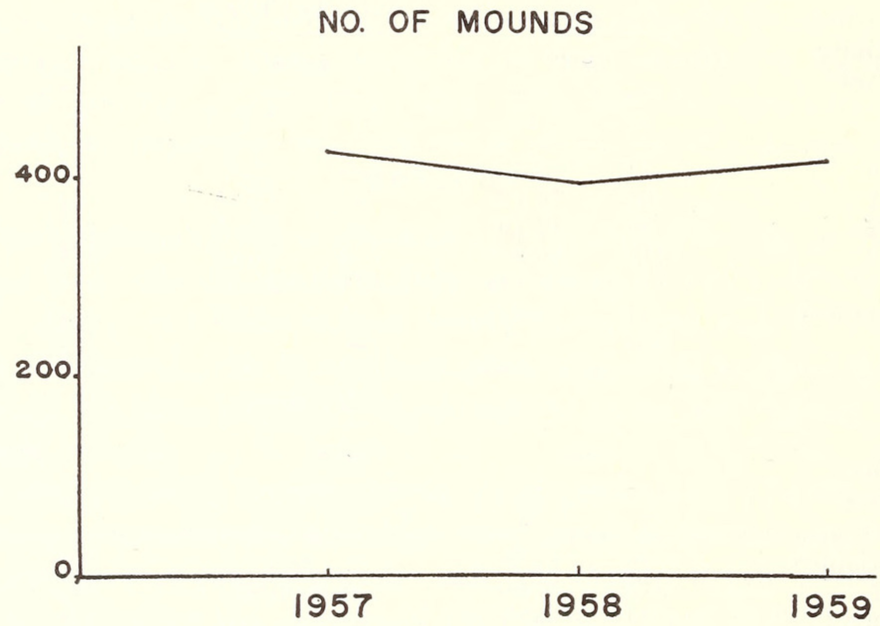

Figure 1 Change in total size of population of colonies during the 3 year period of census.

dium and large mounds, 9% for small mounds. Of the 70 size class changes recorded from classified mounds, 16 increased in size class and 54 decreased in size class over the two-year period.

Activity level The proportion of mounds at each activity level was similar in 1957 and 1958, then changed markedly in 1959. During 1957 and 1958, the population of mounds comprised 31%–33% level 4; 27%–30% level 3; 19%–21% level 2; 12%–16% level 1, and 2%–4% level 0 mounds (Fig. 3).

Changes in activity level from one level to another occurred among 48.4% of the 1957 population and 44.2% of the 1958 population. These changes did not occur with equal frequency at each activity level; instead there appears to be a gradation in stability such that a larger proportion of the level 0 mounds changed levels each year, with the proportion decreasing at each level to level 4, with the exception of the level 4 changes in 1959 (Table III).

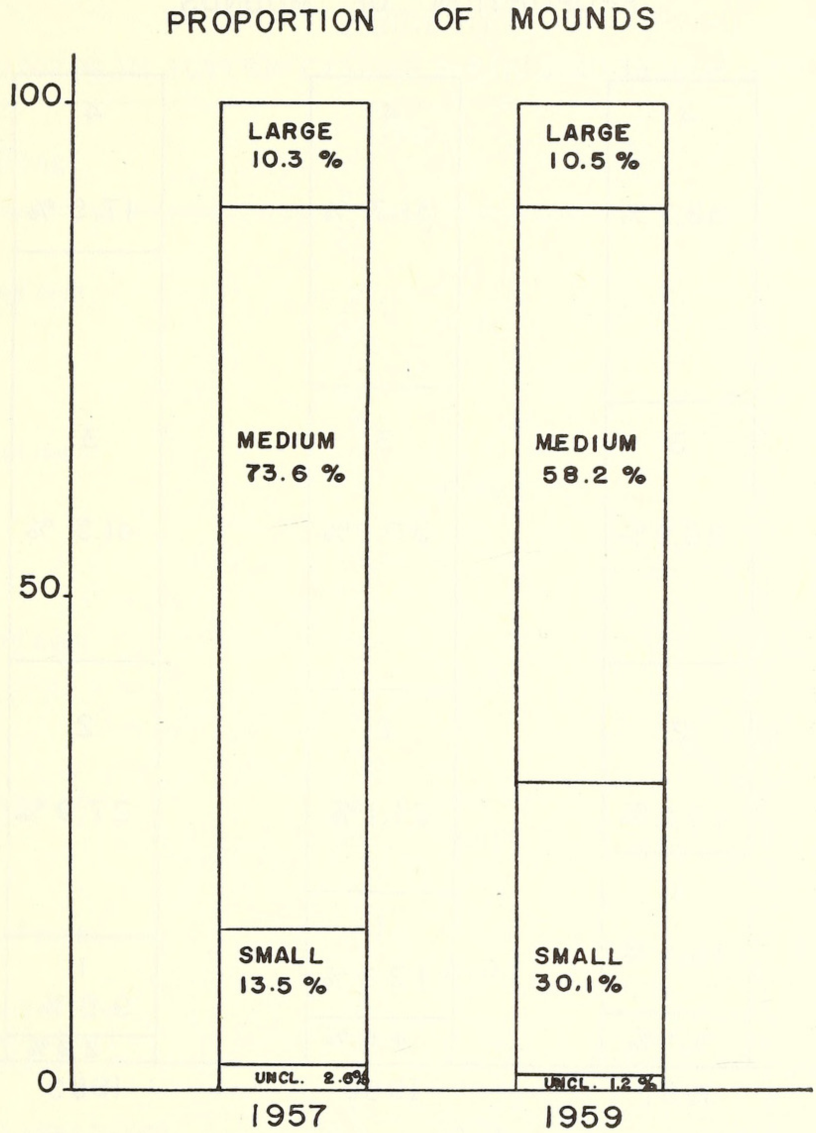

Figure 2 Proportion of mounds in percent at each size class in 1957 and 1959.

The following changes in the proportion of mounds at each activity level occurred between 1957 and 1959. A gradual decrease in level 1 mounds from 16.0% to 9.7%; an increase in level 2 mounds from 19.2% to 27.9%; a marked increase in level

3 mounds from 26.9% to 41.5%; a marked decrease in level 4 mounds from 32.7% to 17.9%.

At present, we are unable to account for most of the observed changes on the basis of external environmental factors. A pos-

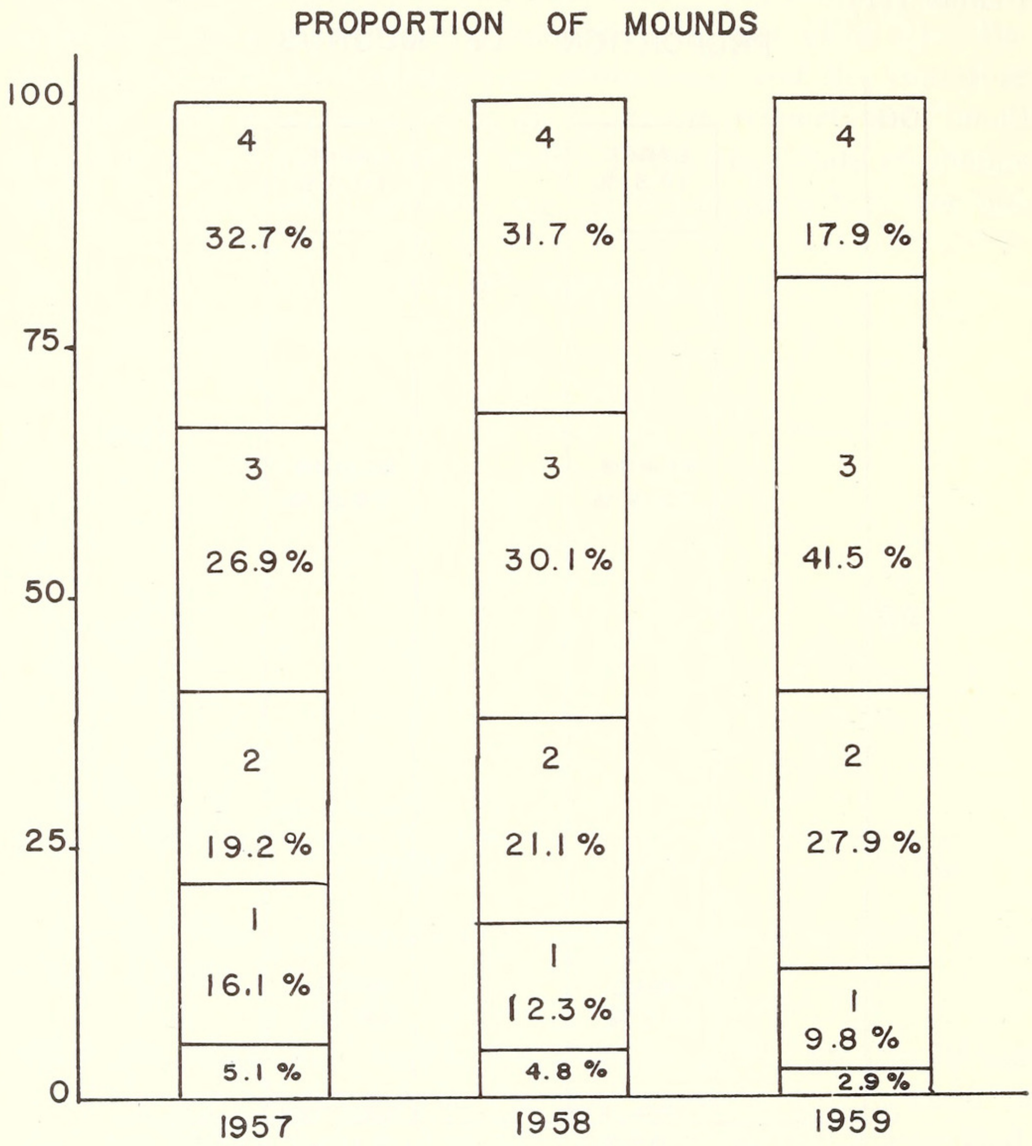

Figure 3 Proportion of mounds in percent at each activity class, during census in 1957, 1958 and 1959. The lowest group in each column denotes the proportion of level 0 and Unclassified mounds.

sible exception is the increase in number of 1958 level 4 mounds which became level 3 in 1959, and the corresponding decrease in the number of 1958 level 3 mounds which became level 4 in 1959 (Table III). These changes, which involve decreased surface nest building activity, occurred during a period of extremely low rainfall, the dry spell of July, 1959. Mean precipitation for that month is 0.97 inches. During the period of observation the rainfall in July totaled 1.49 inches in 1957, 1.16 inches in 1958, and 0.13 inches in 1959 (data kindly furnished by Mr. James

TABLE III

CHANGES IN ACTIVITY CLASS MEASURED IN 1958 AND 1959

Class Change	1958 n	1958 %	1959 n	1959 %*
4 to 3	33		55	
4 to 2	5		1	
4 to dead nest	0		1	
Total	38	27.14	57	45.23
3 to 4	22		4	
3 to 2	24		25	
3 to 1	6		2	
3 to dead nest	5		1	
Total	57	49.56	32	26.66
2 to 4	1		1	
2 to 3	16		19	
2 to 1	18		9	
2 to 0	3		0	
2 to dead nest	9		5	
Total	47	57.31	34	40.47
1 to 3	2		3	
1 to 2	8		10	
1 to 0	11		5	
1 to dead nest	28		18	
Total	49	71.01	36	73.46
0 to 2	1		3	
0 to 1	2		2	
0 to dead nest	6		8	
Total	9	81.81	13	86.66
Unclassified to 3	4		1	
Unclassified to 2	2		1	
Unclassified to 1	1		2	
	7		4	
TOTAL CHANGES	207	48.36	176	44.22

* Percentages are based on the total number of mounds at that level during the previous census.

Braman, U.S. Bureau of Reclamation, Moran, Wyo.). Experimental results indicate that we might expect just this kind of decrease in nest building during periods of low rainfall (Scherba, 1961), and is therefore a possible explanation of the marked change in activity level proportions observed in 1959.

Mound fertility An earlier report noted that 20%–25% of a large sample of the population of mounds released winged sexuals during the days of mating flights in 1957 and 1959. We have called such nests fertile mounds and we now wish to inquire whether relationships exist between mound fertility and size, activity level and location within the population.

We have compared the proportion of fertile mounds at each size class and activity level with the proportion of mounds at each size class and activity level in the total sample of mounds examined. This comparison indicates that there were significantly fewer fertile small mounds in 1959 ($\chi^2 = 4.31$; $p < .05$) significantly fewer fertile level 1 and level 2 mounds ($\chi^2 = 8.05$; $p < .01$) and, correspondingly, significantly more fertile level 3 and 4 mounds ($\chi^2 = 7.4$; $p < .01$) in 1959, than would be expected if fertility were equally distributed among the size classes and activity levels.

For purposes of mapping the location of mounds, the study area has been subdivided into quadrants, NE, NW, SE and SW, and the proportion of fertile mounds in each area has been compared to the number of mounds sampled in that area. In both 1957 and 1959 the proportion of fertile mounds was significantly greater in the NW quadrant ($\chi^2{}_{1957} = 13.34$; $p < .001$: $\chi^2{}_{1959} = 5.11$; $p < .025$). Of the total of 17 mounds which liberated females during the period of census, 10 were located in the NW quadrant.

On the basis of these comparisons we conclude that fertile mounds are more likely to be found among the larger, more active segments of the population of colonies and in the NW quadrant of this study area.

Mortality Of the 428 colonies censused in 1957, 48 died in 1958 and 26 in 1959, a mortality rate of 9.0%. For the 398 mounds of the 1958 population, 32 colonies died in 1959, a mortality rate of 8.04%. However, the frequency of dead nests was not distributed equally throughout the study area, but was highest in the SE quadrant. Both in 1958 and in 1959 the mortality rate decreased at each activity level from 0 through 4 (Table IV). Further, the mortality rate was very high among newly established mounds. Of 20 colonies founded in 1958, 7 were dead in 1959, a mortality rate of 35%.

A total of 81 colonies died during the period of observation from 1957 through 1959. Factors which contributed to this mortality are obscure; however, in 13 cases the colonies were replaced by other species of mound-building ants.

Natality New mounds are formed by budding from established nests during the summer months of ant activity. At present, there is no evidence that fertile queens found colonies independently, or by temporary social parasitism of *F. fusca.*

TABLE IV
RELATIONSHIP BETWEEN ACTIVITY CLASS AND MORTALITY

Activity Level	1958		1959	
	Number of Dead Nests	% of 1957 Nests	Number of Dead Nests	% of 1958 Nests
0	6	54.55	8	53.33
1	28	40.58	18	36.73
2	9	10.97	5	5.95
3	5	4.35	1	0.83
4	0	0.00	1	0.79

TABLE V
COMPARISON OF POPULATION CHARACTERISTICS OF MOUNDS

	1958			*1959*		
	NW	SE	In the Total Population	NW	SE	In the Total Population
Birth rate[1]	4.96%	1.15%	4.67%	15.52%	8.45%	12.81%
Death rate[1]	6.61	20.69	11.21	8.62	12.68	8.29
Activity Level 4 Mounds	42.24	12.68	31.66	24.41	8.82	17.90
Large Mounds	7.44[2]	18.39[2]	10.28[2]	8.66	19.12	10.50

[1] Expressed as a percent of the mound population of the preceding year.
[2] 1957 data.

In 1958, 20 new colonies were founded, nest birth rate, 4.7% and in 1959, 51 colonies were founded, nest birth rate 12.8%. Expressed as the number of established nests per new nest, there was 21.4:1 in 1958 and 7.8:1 in 1959. Nest birth rate was not uniform in all areas; the SE quadrant had the lowest rate, 1.15% in 1958 and the NW the highest, 15.5% in 1959.

New colonies are founded in abandoned mounds of *F. opaciventris,* in mound nests occupied by *F. fusca,* in ant-mined soil at the base of sagebrush, in soil clumps mined by pocket gopher digging, and, rarely, in soil that was not already worked.

DISCUSSION

Comparison of the population characteristics now available for the North American *exsecta* species shows substantial agreement in order of magnitude of maximum density, nest birth rate, and death rate among these species (Table VI). These characteristics would appear to result from certain specialized features found in this group of ants; return of fecundated females to established nests, polygyny, high worker density and the formation of new nests by budding.

Although data are not available from other ant species, it is

TABLE VI

COMPARISON OF POPULATION CHARACTERISTICS AMONG *EXSECTA* SPECIES

Species	Maximum Density (colonies/ sq. meter)	Nest Birth* Rate in %	Death Rate* in %	Source
F. exsectoides	0.015	....	4.5% – 9%	Andrews (1926)
F. ulkei	0.020	9% – 16%	6% – 9%	Dreyer (1942)
				Scherba (1958)
F. opaciventris	0.041	5% – 13%	8% – 9%	Present study

* See text for explanation of these terms, as used here.

instructive to contrast the *exsecta* situation with the observations of Wildermuth and Davis (1931) who estimated that in an 80 acre alfalfa field in Arizona, 80,000 to 100,000 *Pogonomyrmex* queens were released per acre, in the Fall. The following year there were no new nests, although unsuccessful incipient colonies were abundant.

One of the surprising characteristics of the population under discussion is the release of sexuals from the mound. This involves only about one quarter of the population of mounds each year, probably on a rotating basis. Thus none of the mounds which released females in 1957 did so in 1959, and half of the sample mounds fertile in 1957 were sterile in 1959.

A mechanism which could account for this situation is suggested by the work of Brian (1953, 1954) who has demonstrated that production of sexuals is related to the worker/larva ratio in the colony. Lange (1956) has, also, related the production of fertile offspring to the size of the worker population in *F. rufa*. Differential sex ratios, such as those reported here, have been explained on the basis of temperature differences between mounds of different size, smaller mounds tending to have lower temperatures and more males (Lindauer, 1962).

SUMMARY

Population characteristics are described for approximately 400 mound nests of *Formica opaciventris* censused over a 3 year period in Wyoming. During this period of observation, density remained stable at 0.007 nests/sq. meter with a maximum density of 0.04 nests/sq. meter.

Mounds are categorized into size and activity classes and yearly changes are noted. Only a portion of the population releases sexuals, and on a statistical basis these fertile mounds are more likely to be found among the larger, more active segment of the population, and in the NW quadrant of this study area.

Mortality rate for the total population was 8%–9%, increasing regularly at lower activity levels. Nest birth rate was 5%–13% during the period of observation. These rates are compared with those of closely related species of *Formica*.

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