

The left, anomalous ovary is greatly reduced, although it is well tracheated (as is usual for this organ). Its ovarioles are shorter and thicker than they are even in the pre-molt last-instar nymph. Only four ovarioles can be discerned with any certainty. These thicker fewer ovarioles could have been developed by fusion of the normal seven. The general appearance suggests an abortive ovary in which nevertheless some yolk-deposition has occurred (Fig. 1).

The connections of this anomalous ovary were lost in dissecting, but no recognizable left lateral oviduct is apparent. However, the left seminal receptacle is present, as an outpocketing of the *right* lateral oviduct. To my knowledge, no detailed description exists of the development in the Cimicidae of the internal female genitalia. Any such account should consider this significant relationship between lateral oviducts and seminal receptacles.

**SPECIES REPLACEMENT AS A FACTOR AFFECTING
DISTRIBUTION OF *FORMICA OPACIVENTRIS* EMERY¹
(HYMENOPTERA: FORMICIDAE)**

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Abstract The local distribution of a population of *Formica opaciventris* mounds in Wyoming is described.

At the study area *opaciventris* is restricted to a silver sage meadow and to the ecotones of that meadow with adjacent forests. Measurements of the spatial distribution of the mounds describe a tendency toward regular spacing, rather than a random or aggregated pattern.

F. opaciventris competes for constructed mound sites with *F. fusca* at those areas in which the distribution of the two species overlaps. Competition is evidenced by active species replacement, 93 instances of replacement are cited.

It is our purpose here to describe the ecological distribution of a single population of mound nests of *Formica opaciventris* and to identify some of the factors which appear to be influencing its density and distribution.

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We express appreciation to the National Park Service for permission to conduct these studies within the boundaries of Grand Teton National Park.

A particular factor, competition by active replacement of one species at the nest by another, is examined in detail.

Recent studies on ecological distribution of ants emphasize the effects on distribution not only of physical factors, e.g., temperature, rainfall, substrate, but also biotic influences, including relationships with vegetation, food, and other ant species present in a particular community or habitat (Bernard, 1958; Brian, 1956a; Hayashida, 1960; Wilson, 1961).

While Hayashida (1960) concludes that coexistence of ant species in a given habitat, such as forest margin, seems to correspond to the habitat preference of the individual species, the earlier studies of Brian (1952, 1952a, 1956a) using artificial nest sites clearly demonstrate the effect of one species of ant in a habitat on another species when both species are competing for the same nesting sites. Under the conditions of his experiments Brian found that both *Formica fusca* and *Myrmica scabrinodis* replaced *Myrmica rubra* colonies under stones, slate and banks of turf by direct aggression or occupation during temporary absences. Despite the clear-cut advantage of *M. scabrinodis* over *M. rubra* at the nest site, both species survived in a habitat by partitioning the available resources of the habitat (Brian, 1956a). Pontin (1961) described competition occurring between naturally coexisting colonies of *L. flavus* and *L. niger* and demonstrated that a decrease in density of *L. flavus* occurred as a result of this coexistence.

The population under discussion is located on Moose Island, in the Snake River, one mile east of the town site of Moran, in Jackson County, Wyoming. The island is at an altitude of 2065 meters. The number and distribution of *opaciventris* nests on the island have been determined by census during the summers of 1957-1959 and 1962-1964. There are numbered survey stakes erected at each mound and individual records are maintained on the size, activity and species at each nest site (Scherba, 1961, 1963).

Distribution of *F. opaciventris*. *F. opaciventris* is confined to western North America and has been collected in North Dakota, Montana, Wyoming, Colorado and New Mexico (Creighton, 1950, Wheeler, 1963). Gregg (1963) records this species from 9 localities in central Colorado, ranging from 1572 meters to 3201 meters in elevation, and inhabiting montane meadows, forest margin, plains meadows and sagebrush desert. Nest construction types include masonry dome, thatched nest and detritus dome (Gregg, 1963; Cole, 1954).

On Moose Island *opaciventris* builds conspicuous mound nests of soil overlain with a thin covering of thatch. These mounds are distributed over a silver sagebrush (*Artemisia cana*) meadow and also occur at the margins of the meadow.

The meadow is rectangular in shape, elongate in the N-S direction and occupies an area approximately 280 meters by 160 meters. The meadow

occupies the largest portion of Moose Island and dips very gradually to the north, with a steeper northfacing slope at the northern end of the meadow. The southeast portion of the meadow contains a low moist area, often with standing water in June, covered by a stand of sedge (*Carex* sp.) and bordered by willow (*Salix* sp.). The sod in this area is broken due to heavy trampling by elk and moose. The higher portion of the meadow, the southwestern edge, contains a stand of big sagebrush (*Artemisia tridentata*). There are no mounds of *F. opaciventris* on the northern slope, the southwestern tip, or among the moist sedges. Over the years individual nests have been observed in the moist sedge stand; in all cases these have failed to persist.

The meadow is bordered to the west by a stand of Lodgepole pine (*Pinus contorta*); to the north by a thick stand of willow (*Salix* sp.); to the east by a mixed aspen (*Populus tremuloides*) lodgepole-pine stand; on the southeast tip by a willow thicket, and to the south by the shore line. There are no mounds of *F. opaciventris* within the lodgepole stand, or in clearings within the stand, and there are no *opaciventris* mounds within the willow thickets or the aspen-lodgepole stand, both of which are dense and shaded.

Presumably dense shade and shade-related factors, and high moisture levels, are among the factors limiting the ecological distribution of *opaciventris* on Moose Island. These observations accord well with the habitat distribution of the species in Colorado (Gregg, 1963).

Approximately 400 mound nests of *opaciventris* are distributed throughout the meadow except as noted, including along the ecotones of the lodgepole and the aspen-lodgepole stands. Large dead mounds are abundant in the southeastern sector of the meadow and large, active mounds are abundant in the central and northwestern portions of the meadow, perhaps indicative of a gradual microgeographic shift of this population to the northwest portion of the meadow.

Spatial distribution. The pattern of spatial distribution has been determined using the distance-to-nearest-neighbor method of Clarke and Evans (1954). This method was suggested to the author by Professor Joseph Connell of the University of California at Santa Barbara. In determining the spatial distribution pattern, the boundaries of the meadow were mapped, eliminating from the calculation those portions of the meadow, such as the wet area, and certain portions of the ecotone which obviously contained no nests. Distance to the center of the nearest nest was measured for 349 mounds, 89.7% of the population.

Under this technique, the pattern of spatial distribution, R , is equal to 1 in a randomly spaced population, <1 in aggregated population, and >1 , to a maximum of 2.15 for a population that is regularly spaced.

For the population under discussion, $R = 1.3076$, indicating that the population tends to be regularly spaced. The average distance-to-nearest-neighbor, 5.8 meters, is one-third farther apart than would be expected in a randomly distributed population. The distribution pattern found here differs significantly from random, $p < .001$.

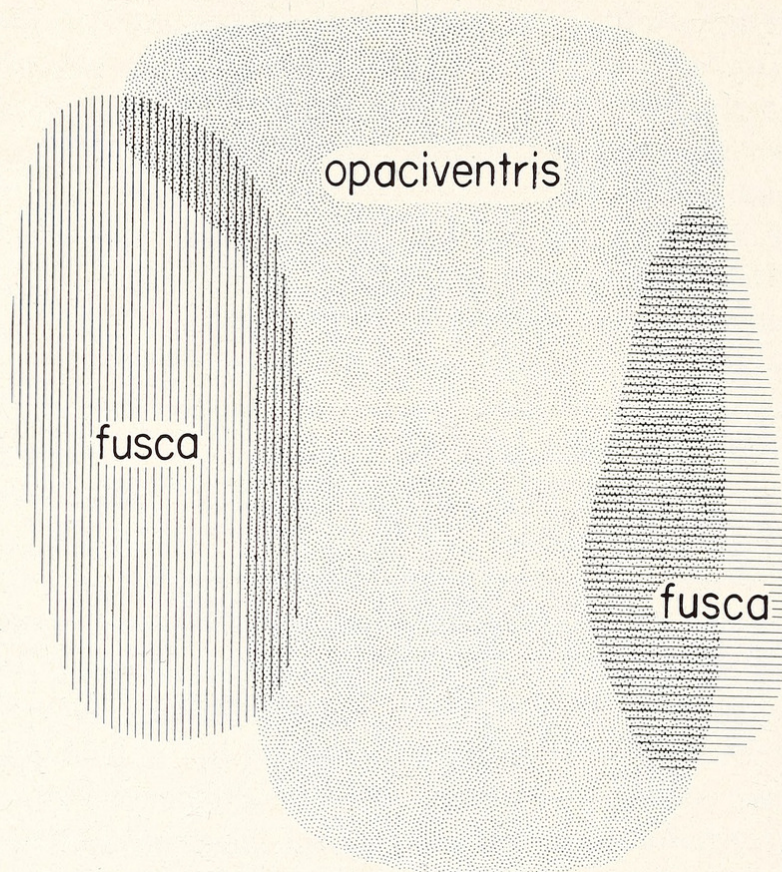


Figure 1 Local distribution of populations of *Formica opaciventris* and *Formica fusca* on Moose Island showing the areas of overlap which occur at margins of the silver sage meadow with forests to the west (left) and east (right). Species replacements at nest sites occur at these areas of overlap.

It is, of course, not evident whether this spacing is due to spacing of suitable, or preferred nesting sites or to a tendency to locate bud nests at a distance from parental nests, an expression of territoriality.

Species replacement. Mound nests of other species of *Formica*, especially *F. fusca*, are abundantly distributed throughout the open portions of the lodgepole pine stand to the west and in clearings in the aspen-lodgepole stand to the east of the silver sage meadow. With one exception, a nest in the northern portion where *opaciventris* is scarce, *F. fusca* nests are not found in the open meadow, despite their widespread occurrence in open fields and meadows elsewhere.

However, mounds of both *F. fusca* and *F. opaciventris* coexist at the ecotones of the meadow with these forests (Fig. 1). Nests of the social

parasite *F. puberula* with its host, *F. fusca*, also occur occasionally along the ecotone.

Annual census of all of these mounds indicate that the species of ant occupying an ecotone mound has often been replaced the following year by another species. In three of the cases cited in Table I replacement of *fusca* by *opaciventris* has followed the observation of active siege by *opaciventris*. Siege was evidenced by the finding of numbers of recently killed *fusca* workers, *opaciventris* workers entering the *fusca* nest and carrying away brood, and fighting between *fusca* and *opaciventris* workers. We infer that such aggression is a major, though not the sole cause of species replacement at the ecotone. In some cases the nest site was abandoned before replacement occurred.

All of the nests listed in Table I occur at ecotones. At 54 nests

TABLE I

Species Replacement at Marked Nest Sites, 1957-1964

1. <i>F. opaciventris</i> replaces <i>F. fusca</i>	54
2. <i>F. fusca</i> replaces <i>F. opaciventris</i>	13
3. <i>F. opaciventris</i> replaces <i>F. puberula</i> + <i>F. fusca</i>	3
4. <i>F. fusca</i> replaces <i>F. opaciventris</i> which replaced <i>F. fusca</i>	10
5. <i>F. opaciventris</i> replaces <i>F. fusca</i> which replaced <i>F. opaciventris</i>	5
6. <i>F. opaciventris</i> replaces <i>F. puberula</i> + <i>F. fusca</i> which replaced <i>F. fusca</i>	3
7. <i>F. puberula</i> + <i>F. lasioides</i> replaces <i>F. opaciventris</i>	2
8. <i>F. opaciventris</i> replaces <i>F. fusca</i> which replaced <i>F. puberula</i> + <i>F. fusca</i>	2
9. <i>F. puberula</i> + <i>F. fusca</i> replaces <i>F. opaciventris</i> which replaced <i>F. fusca</i>	1
	<hr/> 93

opaciventris has replaced *fusca*; at 13 nests *fusca* has replaced *opaciventris*. At 21 nests, two replacements have occurred, as: *opaciventris*, then *fusca*, then *opaciventris*.

We conclude that within the forest, conditions are such that *opaciventris* is excluded; in the meadow *opaciventris* can exclude *fusca*. At the ecotones conditions are such that neither species can exclude the other despite active replacement at nest sites, and hence both coexist; a field situation reminiscent of the laboratory findings of Park (1954).

DISCUSSION

Species replacement appears as the kind of interaction that may suitably be termed competition as that term is defined by Milne (1961). Under Milne's definition competition is "the endeavour of two (or more) animals to gain the same particular thing, or to gain the measure each wants from the supply of a thing when that supply is not sufficient for both (or all)."

It can be argued that the data do not include a measure of the availability of nesting sites along the ecotone. However, the existence of aggressive replacement of species is itself sufficient indication that constructed nests are a resource in short supply along the ecotones of the meadow.

Competition for nesting sites presumably alters the densities of each of the competing species, although the extent of the effect is not apparent.

From the results of Brian (1952), Pontin, (1961) and the present study, it would appear that competition, as defined, is probably not uncommon as one of the interactions structuring the composition and relative abundance of the ant fauna of a particular ecological community. Andrewartha (1961) has suggested that "... no sort of competition is very commonplace in nature." Further studies of these interactions may suggest a revision of this point of view, at least for ant populations.

In attempting to account for the kind of distribution of *F. opaciventris* that is seen on Moose Island, we must evidently recognize: exclusion from wet or shaded areas, a limitation of density due to spaced, non-random nest distribution, and the existence of competition for constructed nest sites at the margins of the distribution.

CONCLUSIONS

At the study site *F. opaciventris* is restricted to large portions of a montane meadow, and excluded from areas of dense shade or marsh. Pattern of spatial distribution is neither random, nor aggregated, but tends toward regular spacing.

At the ecotones of the meadow with adjacent forests, *F. opaciventris* competes with *F. fusca* for constructed nest sites, as evidenced by species replacement, and it is suggested that competition is one of the interactions structuring ant populations in ecological communities.

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NOTES ON SOME AFRICAN THECLINAE (LEPIDOPTERA: LYCAENIDAE)¹

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Abstract Locality records of the West African sibling species *Dapidodigma hymen* Fabricius and *D. demeter* Clench are given and the distributions mapped and discussed, showing an area of sympatry from Ghana to Nigeria. The distribution, subspecies and characters of another two sibling species are given: *Iolaus* (*Iolaus*) *eurisus* Cramer (Sierra Leone to Nigeria) and *I. vexillarius* (Senegal to Gabon). *Iolaus* (*Iolaus*) *bolissus* Hewitson is divided into three subspecies: *bolissus* (western Congo), *azureus* (Cameroun, Liberia) and *aurora* (Uganda). *Iolaus* (*Epamera*) *aphnaeoides aethes* is described from Cameroun (the species previously was known only from eastern Africa).

THE DISTRIBUTION OF *Dapidodigma hymen* F. AND *demeter* CLENCH

When I recently discriminated these two species (Clench 1961, Ann. Carnegie Museum 36: 49-62, pl. 1) material was available from only a few localities: several in Liberia, representing *hymen* Fabricius; two in southern Cameroun, representing nominate *demeter* Clench; and one in Katanga, representing *demeter nuptus* Clench. As pointed out in that paper, *demeter* was considered specifically distinct from *hymen* chiefly because of the dif-

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Scherba, Gerald. 1964. "Species Replacement as a Factor Affecting Distribution of *Formica opaciventris* Emery (Hymenoptera: Formicidae)." *Journal of the New York Entomological Society* 72, 231–237.

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