GENERIC DIVERSITY IN PHASE OF RHYTHM IN FORMICINE ANTS

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Ants are abroad through most of the day and night. But the species composition of this 24-hour patrol changes from one part of the day to the next (Talbot 1953; Wilson 1971). For example, in Michigan the maximum foraging activity of *Lasius neoniger* is at night, of *Myrmica americana* in the early morning and late afternoon, and of *Formica pallidefulva nitidiventris* in the middle of the day (Talbot 1946, 1953).

Likewise the mating flights of ants occur at different hours for different species (Kannowski 1963; Talbot 1945). The flight times may be similar for closely-related species (Kannowski 1959a).

If one were to look at many species of one genus, would he find them to be similar as to time of day of foraging or of mating flight? Or does each genus span the 24 hours in terms of its various species? The aim of this report is to quantitatively compare species diversity with generic diversity of such phase relationships in one tribe of ants, the Formicini. The biosystematics of much of this group, particularly of the genera *Lasius, Acanthomyops,* and *Formica,* is relatively well known on morphological and zoogeographic grounds (Wilson and Regnier 1971).

The comparisons are based on a compilation of literature records for as many species and genera as possible in this tribe (Figs. 1 and 2). A genus was included if there were records for three or more species. About a third of the species of *Acanthomyops,* of *Cataglyphis,* of *Lasius,* and of *Myrmecocystus* are represented in the records cited here, but a smaller fraction of the large genus *Formica.* These genera are all from North Temperate latitudes. (For a preliminary report see McCluskey, 1972.)

The workers could be classified as nocturnal, diurnal, etc. But in the absence of single or definite beginning points or midpoints of activity in most of the literature records, another method was used to reduce each rhythm to one point for comparison with other species: If the ants do not normally come above ground at all (e.g., *Acanthomyops* species), the species is plotted as an X at the extreme left (Fig. 1); if nocturnal only, one position farther to the right; if out as late as sunrise, another position to the right; etc. As far as possible, only summer records were used so as to make directly comparable.

It can be seen that the species in *Acanthomyops*, in *Formica*, and in *Cataglyphis* are closely grouped within each genus. The species in *Lasius* appear less so, but they barely overlap those of *Formica* or *Cataglyphis*.

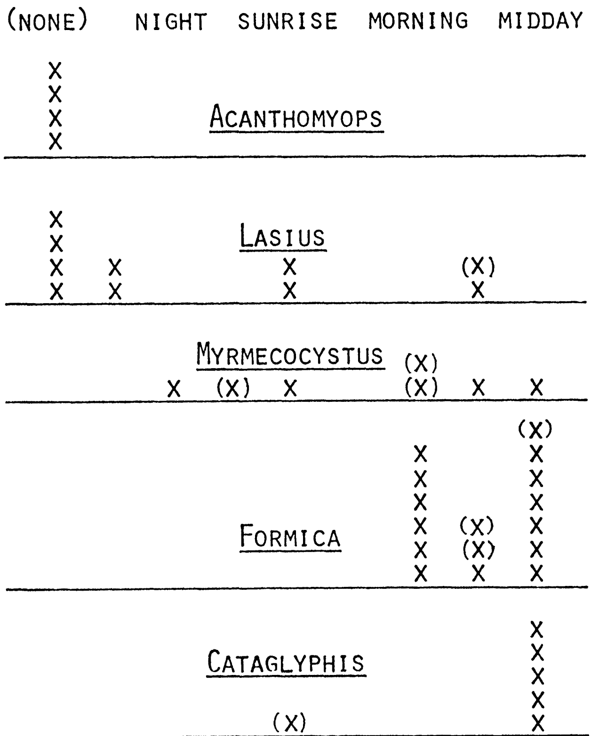

Figure 1

Scoring an X in the leftmost column of Fig. 1 as "1", next to the left ("night") as "2", and finally the rightmost column as "5", permits an analysis-of-variance comparison of the variation within a genus with the variation between the genera:

	SS	df	ms	F	P<
among genera	66.1	4	16.5	16.5	.001
within genera	36.9	37	1.0		

Thus the likeness within genera is greater than that between genera.

A different type of analysis confirms this conclusion. The "none" aboveground activity was now omitted, since that is not really a time character (thus eliminating *Acanthomyops* and some *Lasius* species); the "night" species were arbitrarily considered as (out until) 5 AM, "sunrise" 7 AM, "morning" 10 AM and "midday" 1 PM. These hours were treated as angles of a circular distribution, and the mean angles of the different samples (genera) were compared by Watson

Fig. 1. Worker surface activity (limited mainly to summer records, for most direct comparison of species). Each X represents one species and shows its nearest approach to midday; those based on the most limited cited records are enclosed in (). The leftmost column "NONE" indicates that the species does not usually come above ground at all. Following are species and literature sources represented: *FORMICA: bradleyi* (Wheeler and Wheeler 1963), *dakotensis* (Talbot 1971), *exsectoides* (Andrews 1927, 1929; McCook 1877), *fusca* (Morisita 1939), *fusca lemani* (Brian 1955), *lasioides* (Wheeler and Wheeler 1970), *neogagates* (Talbot 1953), *obscuripes* (Weber 1935), *pallidefulva nitidiventris* (Talbot 1946, 1953, 1965), *polyctena* (Bruns 1954; Chauvin 1965a,b), *pratensis* (Stebaev 1971; Stebaev and Reznikova 1972), *sibylla* (Wheeler 1917), *subintegra* (Talbot and Kennedy 1940), *subnitens* (Ayre 1958, 1959), *subpilosa* (Stebaev 1971; Stebaev and Reznikova 1972), *subpolita* (Mallis 1941), *ulkei* (Holmquist 1928). *LASIUS: emarginatus* (Tohmé 1969), *flavus* (Bernard 1968; Odum and Pontin 1961; Talbot 1965; Wilson 1955), *fuliginosus* (Wilson 1955), *minutus* (Kannowski 1959b; Talbot 1965), *neoniger* (Talbot 1946, 1953, 1965), *niger* (Eidmann 1926; Morisita 1939), *sitiens* (Wilson 1955), *sitkaensis* (now *pallitarsis*) (Talbot 1965; Wilson 1955), *speculiventris* (Talbot 1965), *umbratus* (Stärcke 1937; Talbot 1965; Wilson 1955). *ACANTHOMYOPS: claviger, interjectus, latipes,* and *murphyi* (Talbot 1963; Wheeler and Wheeler 1963). *MYRMECOCYSTUS:* lugubris (Cole 1966), *melliger orbiceps* (now *placodops*) (Wheeler 1908b), *mexicanus* (Cole 1966; LaRivers 1968), *mexicanus hortideorum* (McCook 1882), *mimicus* (Cazier and Statham 1962; Leonard 1911), *mojave* (Cole 1966; LaRivers 1968; Leonard 1911), *pyramicus* (Smith 1951), *wheeleri* (Snelling 1971). *CATAGLYPHIS: albicans* (Délye 1968), *albicans viaticoides* (Tohmé 1969), *altisquamis* (Tohmé 1969), *bicolor* (Délye 1968; Pickles 1944; Tohmé 1969; Wehner and Duelli 1971), *bicolor setipes* (Gupta 1970), *bombycina* (Délye 1968), *frigida* (Tohmé 1969), *lucasi* (Baroni Urbani 1969; Délye 1964). An annotated table giving the details of support for Figs. 1 and 2 is available from the author.

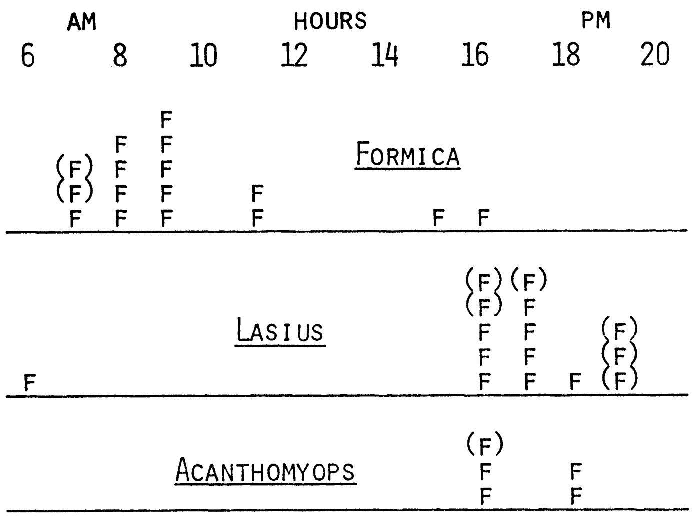

Fig. 2. Flight hours. Each F represents for one species the halfway point between the earliest and latest literature records of flight; ( ) indicate the most fragmentary records. The following are represented: *FORMICA: dakotensis* (Talbot 1971), *fusca* (Kannowski 1959a; Talbot 1965), *montana* (Kannowski 1963; Kannowski and Johnson 1969), *neogagates* (Talbot 1966), *obscuripes* (Clark and Comanor 1972; Talbot 1971), *obscuriventris* (Talbot 1964), *opaciventris* (Scherba 1961), *pallidefulva nitidiventris* (Talbot 1948), *pergandei* (Kannowski and Johnson 1969), *pratensis* (Eidmann 1928; Wheeler 1908a), *rufa* (Donisthorpe 1927; Standen 1909), *rufibarbis* (Forel 1874a), *sanguinea* (Forel 1874b), *subintegra* (Kannowski 1963; Talbot and Kennedy 1940), *subnitens* (Ayre 1957), *ulkei* (Scherba 1958; Talbot 1959). *LASIUS: alienus* (Gösswald 1932; Hall 1887), *brunneus* (Forel 1874b; Schenck 1852), *carniolicus* (Kutter 1946), *emarginatus* (Forel 1874b, 1928), *flavus* (Donisthorpe 1927; Forel 1874b; Talbot 1965; Wilson 1955), *fuliginosus* (Wilson 1955), *minutus* (Kannowski 1959a; Talbot 1965), *nearcticus* (Wilson 1955), *neoniger* (Kannowski 1963; Talbot 1945, 1965; Wilson and Hunt 1966), *nevadensis* (Cole 1956), *niger* (Donisthorpe 1927; Forel 1874b), *pallitarsis* (Medler 1958; Talbot 1965), *speculiventris* (Kannowski 1959a; Talbot 1965), *subumbratus* (Kannowski 1971), *umbratus* (Crawley 1913; Forel 1874a, 1875; Kannowski 1963; Rau 1934)*. *ACANTHOMYOPS: claviger* (Talbot 1963, 1973), *interjectus* (Talbot 1963), *latipes* (Gregg 1963; Talbot 1963, 1973), *murphyi* (Talbot 1963), *subglaber* (Talbot 1973).

*The morning record (Rau 1934) is most unusual for this species (Kannowski 1963) and I omitted it in plotting the midpoint in the graph. Crawley (1913) and Forel (1874a, 1875) may possibly refer to a sibling species of *umbratus* (cf. Wilson 1955).

and Williams' (1956; cf. Batschelet 1965, but only for a two-sample case) test: if the samples are considered random, $F_{q-1, N-q} = [(N-q)(\Sigma R-R)] / [(q-1)(N-\Sigma R_i)] = 3.58$ and $P < .05$ [$N = 33$ (species), $q = 4$ (genera), R_i refers to the combination vector for all the species in each genus, and R refers to the combination vector of all genera].

Figure 2 shows that for the three genera of this tribe with enough species records, the flight hours of the species within a genus are strikingly similar, exceptions being the one morning species of *Lasius* and the two afternoon species of *Formica.* Comparison of the flight hours by the Watson and Williams test again shows the likeness within genera to be greater than that between genera ($P < .001$).

It seems noteworthy that a single rhythm character would characterize a genus this well. A preliminary test for generality of the within-genus likeness of flight hour was made on eleven genera from five subfamilies of ants (all of those from which literature records of at least three species per genus were at hand). The Watson and Williams test gives a value of $P < .001$; this is true also if the three formicine genera are omitted and only the other eight considered.

By including all species records no matter what tribe, it is possible in a few cases to rank workers from early to late within each given locality (McCluskey, unpublished). Again species appear grouped generically, giving further suggestive evidence of a taxonomic or historical explanation of the phase differences (as opposed to a strictly ecological or geographical explanation).

An example of a physiological character earlier shown to correlate well with a previously-established classification is that by Priesner (1968). Male moths throughout the family Saturniidae were shown to react to pheromone from the females in a manner roughly corresponding to taxonomic grouping.

It should be added that some of the phase relationships considered here might in fact be explained by response to temperature, since these are records from the field rather than a constant temperature laboratory. But this consideration does not change the fundamental nature of the conclusion drawn. Further, certain ants which have been studied in constant temperature exhibit a phase relationship to the light cycle similar to that in the field (McCluskey 1963, 1965, 1969; McCluskey and Carter 1969).

Summary

Literature records of field mating flight and worker rhythms indicate the phase to be much more alike from species to species within

a genus than between genera. The analysis is based on about a third of the world species in each of several genera of the tribe Formicini. Comparison in more genera, from several subfamilies, again indicates this prominent within-genus likeness of behavior.

Acknowledgements

I thank P. Y. Yahiku for help with statistics, and L. R. Brand, D. G. Kissinger, and R. E. Ryckman for reading the manuscript.

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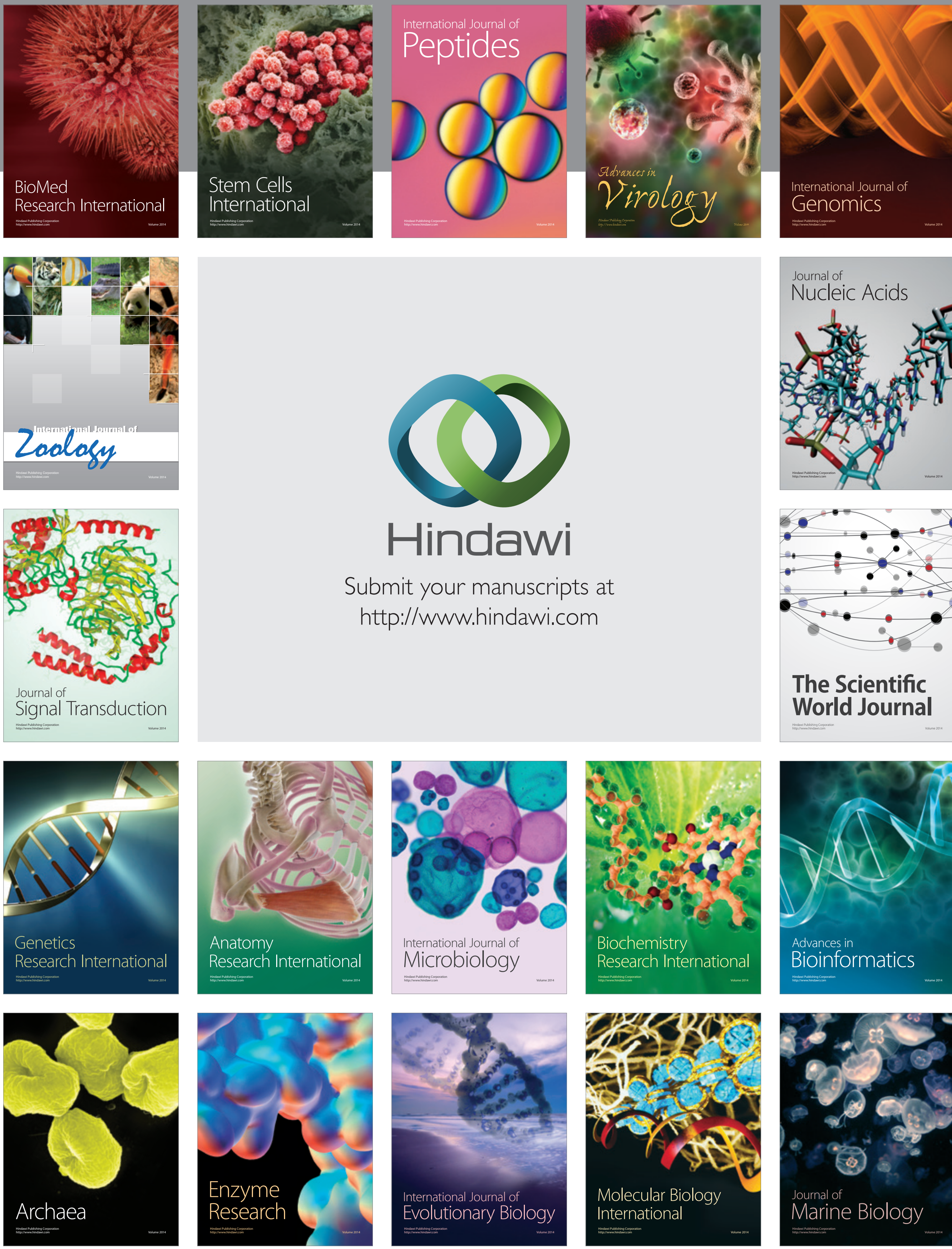
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