Some Aspects of Interrelations between Ants (Hymenoptera, Formicidae) and Polistine Wasps (Hymenoptera, Vespidae)

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Abstract—Embodied, situated and enactive aspects of relationships of polistine wasps with ants are considered within the framework of the theory of autopoiesis. The idea of the embodied interaction implies specific nest-building and protective behavior in polistine wasps. The paper examines the adaptive role of applying ant repellent on the petiole and nest and the latitude gradient of such behavior in re-social wasp species. The situated interaction is considered in the environmental context: the mortality of *Polistes gallicus* (L.) colonies as a result of predatory attacks of ants *Myrmica bergi* Ruzsky is analyzed in the Lower Dnieper basin (Ukraine). The enactive interaction includes both spontaneous autonomous activity of its participants as a result of self-organization and specific features of the spatial structure of the prey's population forming under the impact of the predator. The applicability of some "predator-prey" models is discussed.

The synergetic approach, treating biological systems as self-organizing ones, has proved its efficiency in the recent decades (Camazine et al., 2001). According to H. Haken (cited after Knyazeva, 2000), such systems are characterized by the following properties: (1) they consist of several or many identical or different parts involved in interaction; (2) they are nonlinear and open (far from thermal equilibrium); (3) they undergo internal and external fluctuations; (4) they may become unstable and undergo qualitative changes; (5) they reveal new emergent properties in the process of development of spatial, temporal, spatio-temporal, or functional structures; (6) their structure may be ordered or chaotic; (7) in many cases they can be described mathematically.

Many aspects of behavior of social insects have been considered from the viewpoint of self-organization, in particular their building activity (Nikolis and Prigogine, 1990; Karsai and Penzes, 1993, 2000; Karsai and Wenzel, 2000), establishment of hierarchical relations (Theraulaz et al., 1995), decision making mechanisms (Deneubourg and Goss, 1989), etc.

Considering the specificity of the recent approaches to studying complex adaptive systems, it should be noted that the actual processes of interaction of self-organizing and self-sustained systems may be conveniently described using the dynamic approach (the theory of autopoiesis—Varela et al., 1991; Knyazeva, 2005) being developed within the framework of cognitive science. The theory of autopoiesis makes emphasis on mechanisms of organization stability.

This review is an attempt to apply the theory of autopoiesis to systems of interacting populations, namely those of ants (Hymenoptera, Formicidae) as predators and polistine wasps (Hymenoptera, Vespidae, Polistinae) as prey.

Many specific features of nest-building and protective instincts, colony foundation, and life cycle of polistine wasps have been acquired under the influence of predation by ants (Richards and Richards, 1951; Jeanne, 1970, 1975; Naumann, 1975; Chadab, 1979; West-Eberhard, 1982; London and Jeanne, 2000; Smith et al., 2001, etc.).

Let us consider the three principal aspects of interaction of complex systems, distinguished in the theory of autopoiesis, as applied to the populations of ants and wasps.

Embodied Interaction

The interaction of populations may be regarded as "embodied" since it is associated with the wasp nest as a specific substrate. It depends on the parameters of this nest and the specific forms of protective behavior of polistine wasps, and also the specific forms of hunt-

ing behavior of ants. The system of protective behavior of wasps includes the following elements: visual detection of ants, alarm demonstration (wing buzzing and gaster-flagging), and strikes aimed at repelling the predators (Chadab, 1979; Post and Jeanne, 1981; O'Donnell et al., 1998; Tongi and Giannotti, 2007, 2008). The colony defense is also facilitated by the structure of the nest itself (Jeanne, 1975; Wenzel, 1991). The species building nests on petiole without the protective envelope use a special method of chemical defense: they apply ant-repelling secretion on the petiole. This protective allomone is produced by Van der Vecht's gland located on sternite VI (Jeanne, 1970; Post and Jeanne 1981; Kojima, 1983b; Keeping, 1990). When applying the secretion, the wasp rubs its sternites against the nest petiole, expanding its abdomen and exposing the tufts of hairs associated with the gland. The secretion is also smeared upon the comb surface around the petiole, the substrate to which the nest is attached, and the back and side surfaces of the nest. A continuous series of rubbing movements represents an elementary act of defensive behavior (Keeping, 1990). In *Mischocyttarus drewseni* Saussure such an act lasts for 2–3 s, during which secretion is applied on nearly half of the petiole surface (Jeanne, 1970). The wasps can perform several such series in succession. This behavior was observed in representatives of the genera *Mischocyttarus* (Jeanne, 1970; Litte, 1981), *Belonogaster* (Marino Piccioli and Pardi, 1970; Keeping, 1990), *Polistes* (Corn, 1972; Turillazzi and Ugolini, 1979; Post and Jeanne, 1981; Kojima, 1993), *Ropalidia* (Darchen, 1976; Kojima, 1982, 1983b; Gadagkar, 1991), and *Parapolybia* (Kojima, 1983b).

The hypothesis of the repellent function of the secretion applied on the petiole was first proposed by Jeanne (1970, 1972, 1975) based on the observations of *Mischocyttarus drewseni*. However, Darchen (1976), while studying *Ropalidia cincta* (Lepeletier), disagreed with this interpretation of the rubbing movements. Instead, these specific movements, initially described by Deleurance (1957) in the Palaearctic wasps *Polistes dominulus* (Christ) and by Yoshikawa (1962) in the Japanese species *P. fadwigae* Dalla Torre, were interpreted as elements of nest-building behavior.

The repellent effect of Van der Vecht's gland secretion was later confirmed by special tests using living ants (Jeanne, 1970; Turillazzi and Ugolini, 1979; Keeping, 1990; Post and Jeanne, 1981; London and Jeanne, 2000). In *Polistes fuscatus* (F.) the secretion of

Van der Vecht's gland includes two ant-repelling components; one of them was identified as methyl palmitate ($C_{17}H_{34}O_2$) (Post et al., 1984). In addition, the frequency of treatment of the nest petiole increased when some objects with strong odor of formic acid, acetic acid, or ammonia, as well as living ants, were placed near the wasp nest (Turillazzi and Ugolini, 1979; Keeping, 1990). Based on these facts, we regard this kind of activity as *application of ant repellent* (rubbing behavior).

It should be noted that the repertoire of this protective behavior is similar in different species of resocial wasps (Turillazzi and Ugolini, 1979; Kojima, 1982, 1983a, 1983b, 1993). At the same time, the frequency of rubbing behavior varies greatly depending on many factors, such as the number of females in the colony, the species of ants, the types of their foraging activity, and their density in the area surrounding the wasp nest.

Before the worker emergence, the rubbing activity of the lone foundress in a single foundress colony was found to be higher than that per one foundress on multiple foundress nest (Turillazzi and Ugolini, 1979; Kojima, 1982; Keeping, 1990; Tongi and Giannotti, 2007, etc.).

The pleometrotic foundresses apply the ant repellent on the nest with different intensity (Turillazzi and Ugolini, 1979; Post and Jeanne, 1981; Keeping, 1990). No correlation was observed between the social rank of the wasp and the rubbing behavior frequency in *P. dominulus* (Turillazzi and Ugolini, 1979); however, the rubbing behavior frequency was higher in α-females of *P. fuscatus* than in subordinate individuals of this species (Post and Jeanne, 1981). On the contrary, the subordinate foundresses of *Belonogaster petiolata* (Degeer) rubbed the nest petiole more frequently than the dominant ones (Keeping, 1990); the workers of this species showed no rubbing activity. According to our data, mature colonies of *Mischocyttarus injucundus* (Saussure) were characterized by high frequencies of rubbing behavior, performed not only by the foundresses but also by the workers. In a mature laboratory colony of *P. dominulus* with 8 workers rubbing behavior was observed quite rarely (8 times a day) but with regular intervals (Turillazzi and Ugolini, 1979).

At the same time, our analysis of videotape data revealed considerable variability of the duration of rubbing behavior on petiole and nest in sympatric species

of *Mischocyttarus* living in and around Caura Village (Trinidad Island). Before the worker emergence, the foundresses of monogynic nests of *M. collarellus* Richards spent more than 6% of their in-nest time budget to applying repellent on the nest surface (determined by 8 h of observations), whereas the females of *M. injucundus* and *M. alfkeni* (Ducke) spent only 0.79% and 2.37% (12 and 9 h) of their time, respectively. Such differences in the rubbing activity may be related to the specific shape of nest of *M. collarellus*, which has a much larger lateral surface of the comb that must be licked and treated with repellent.

It is known that after disappearance (death) of a solitary foundress, its brood is quickly destroyed by ants (Rusina, 2006). We studied the survival of brood in 5 orphaned nests of *M. injucundus*, 5 nests of *M. collarellus*, and 4 nests of *M. alfkeni*. Most colonies of *M. alfkeni* and *M. injucundus* perished, since their brood was consumed by ants in 1–4 days. One nest of *M. injucundus* (no. 6) survived because workers emerged 2 days after disappearance of the foundress. However, in 3 out of 5 nests of *M. collarellus* the brood remained undamaged by ants for over 10 days, even though it finally died of drying. Such a result may be related to a higher intensity of rubbing behavior in this species.

Survival of pupae and emergence of adults in orphaned colonies may constitute an important part of adaptation to the influence of predators, since the brood stages duration of wasps is longer in the tropics than in the temperate zone (Giannotti and Machado, 1994). For example, the average duration of the pupal stage in the tropical *Polistes lanio* (L.) is 23 days (Giannotti and Machado, 1994), and in *P. erythrocephalus* Latr., 23.8 days (West-Eberhard, 1969), whereas the pupal stage of *P. dominulus* and *P. gallicus* (L.) in the temperate zone lasts 13–15 days (our data). The average duration of development from egg to adult in these species is 87, 68, 32, and 35 days, respectively.

There are also data on the latitudinal gradient of rubbing activity, determined by geographic variability of the species composition and activity of predatory ants (Jeanne, 1979; Kojima, 1993). Analysis of the literature and original data (Fig. 1) shows that the frequency of rubbing behavior in pre-emergence haplometrotic colonies decreases as the latitude grows ($r_s = -0.83$, $n = 14$, $p < 0.001$).

Thus, despite the similar structure of the nest and elements of defensive behavior in resocial wasps, they have considerable specificity, indicating the existence of species-specific mechanisms of defense from ants.

The brood of nomosocial species (except for species of *Apoica*, most *Agelaia*, and some *Ropalidia*) is protected from ants by the nest envelope with a narrow defended opening (Jeanne, 1975; Wenzel, 1991). The workers can deter scouting and mass foraging ants by wing buzzing, gaster-flagging or stinging attacks, and even knock them off the nest.

Situated Interaction

The interaction of populations of ants and wasps may be regarded as "situated" since it is associated with a particular period of development of the wasp brood and/or with a particular biotope.

There are extensive data indicating that a considerable part of the population of resocial wasps perishes before the worker emergence, so that this phase of colony development is considered to be one of the most vulnerable in the life cycle (Miyano, 1980; Jeanne, 1982; Strassmann et al., 1988; Rusina, 2006). The haplometrotic colonies suffer greater damage from invertebrate predators.

Let us consider the role of ants as a factor of mortality of *Polistes gallicus* colonies in the Black Sea Biosphere Reserve (BSR, Kherson Prov., Ukraine). These wasps usually inhabit forb-reed meadow and wormwood-grass steppe communities, whereas during the periods of maximum abundance (2003) they can also be found on halophytic and alkaline vegetation. In 2003–2005 the nests were built on shoots of *Artemisia marschalliana* Spreng, *Elytrigia elongata* (Host) Nevski, *Phragmites australis* Trin., *Verbascum lychnitis* L., and *Tanacetum vulgare* L.

The known ant fauna of BSR includes over 40 species; of these, 13 inhabit the zonal steppe biotopes, 16 occur in the meadows, and 7 in the halophytic meadow communities (Radchenko, 1984; Bondar and Rusina, 2003).

In 2003–2005, the author in collaboration with L.A. Firman observed the development of 580 wasp colonies until their death or emergence of the reproductives. The colonies that produced the sexual generation were regarded as successful. The group of destroyed colonies included the damaged nests abandoned by the foundresses (weakly or strongly damaged, or completely destroyed) as well as those in which the brood disappeared before the normal seasonal disintegration of the colony. Our observations
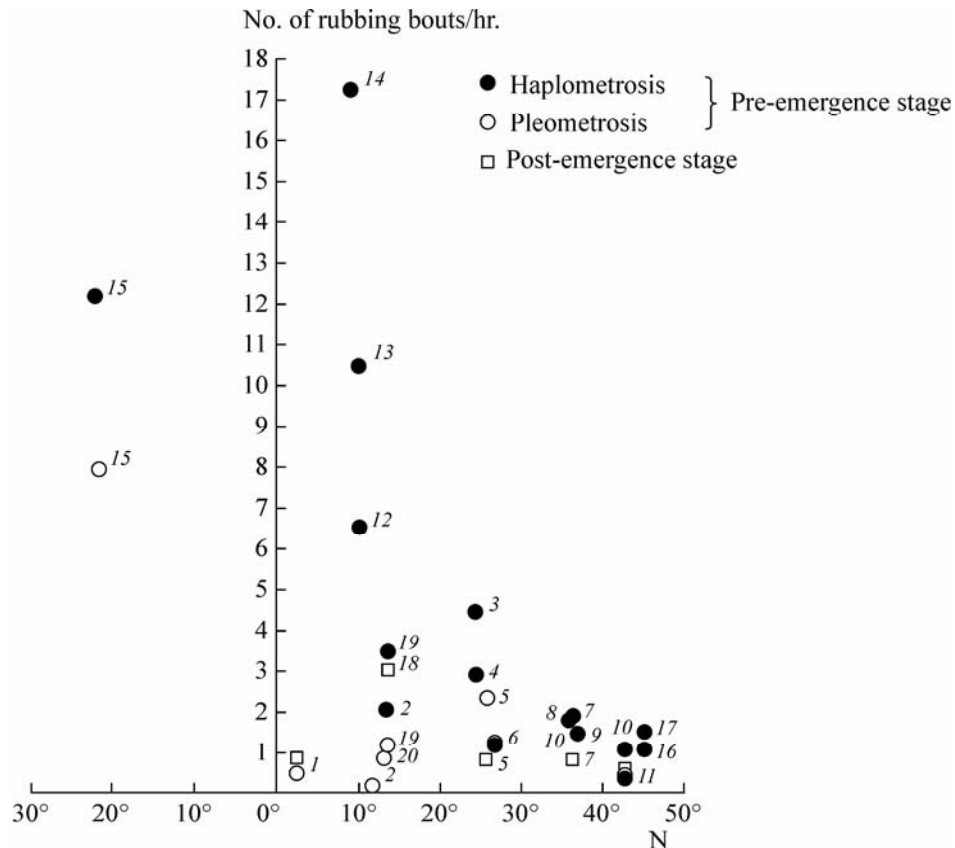
No. of rubbing bouts/hr.

Fig. 1. The latitudinal variation in rubbing frequencies per colony in resocial polistine wasps (after Kojima, 1993, with additions): *Mischocyttarus drewseni* (Jeanne, 1972) (*1*), *Ropalidia gregaria* (Kojima, 1982) (*2*), *Polistes formosanus* (Kojima, 1993) (*3*), *P. rothneyi* (Kojima, 1993) (*4*), *Belonogaster petiolata* (Keeping, 1990) (*5*), *Ropalidia fasciata* (Kojima, 1983a) (*6*), *Parapolybia indica* (Kojima, 1992b) (*7*), *Polistes chinensis* (Kojima, 1993) (*8*), *P. mandarinus* (Kojima, 1993) (*9*), *P. snelleni* (Kojima, 1993) (*10*), *P. fuscatus* (Post and Jeanne, 1981) (*11*), *Mischocyttarus injucundus* (our data: Trinidad Island, October 2004–January 2005. $N_{colonies}$ = 8, $N_{hours\ of\ observation}$ = 21) (*12*), *M. collarellus* (N_c = 4, N_h = 8) (*13*), *M. alfkeni* (N_c = 4, N_h = 12) (*14*), *M. cerberus* (Togni and Giannotti, 2007) (*15*), *Polistes gallicus* (our data: the Lower Dnieper basin, Ukraine, May–June 2003–2005. N_c = 18, N_h = 60) (*16*), *P. dominulus* (N_c = 30, N_h = 52) (*17*), *P. stigma* (Bangalore, India, September–October 2002. N_c = 1, N_h = 6) (*18*), *Ropalidia cyathiformis* (N_c = 7, N_h = 23) (*19*), *R. marginata* (N_c = 15, N_h = 40) (*20*).

showed that the death of brood and entire colony of *P. gallicus* was related to the disappearance of the foundress, mostly during foraging (Fig. 2). After the death of the foundress, the eggs, larvae, and pupae were taken away by the ants *Lasius paralienus* Seifert, *L. psammophilus* Seifert, *Temnothorax* spp., *Tetramorium caespitum* (L.), and *Myrmica bergi* Ruzsky within one day. The nests with brood were damaged or completely destroyed by predators (birds) and natural factors (storms, fires). In some cases the cause of death of the colony could be determined from indirect evidence. For example, the presence of damaged cells in the center of the comb abandoned by the foundress before the worker emergence suggested that the nest could have been damaged by the grasshopper *Decticus verrucivorus* L. (Orthoptera, Tettigoniidae).

During the seasons of observation, 15.2% of all the colonies reached the maturation phase, 24.1% perished

as a result of disappearance of the foundress, 35.5% perished after being damaged by predators, 14.3% were destroyed by anthropogenic factors (including relocation into artificial nests), and 10.9% of the colonies perished for unknown reasons.

A small number of colonies perished as a result of attacks by ants. We recorded only 4 cases of *P. gallicus* nests being ravaged by the ants *M. bergi*. All these events happened in 2003 (Fig. 2), during the population peak of *P. gallicus* when its nests were observed even in areas of high density of the ants. The attack of the ants could be directly observed only in one of the cases. In the night of May 25/26, 2003 a colony of *M. bergi* resettled under a tussock of the couchgrass *Elytrigia elongata*. The nest of *P. gallicus* with a foundress, eggs, and larvae was located nearby on *Artemisia marschalliana*. The hunting was observed on May 26, from 14:32 until dusk (Rusina,
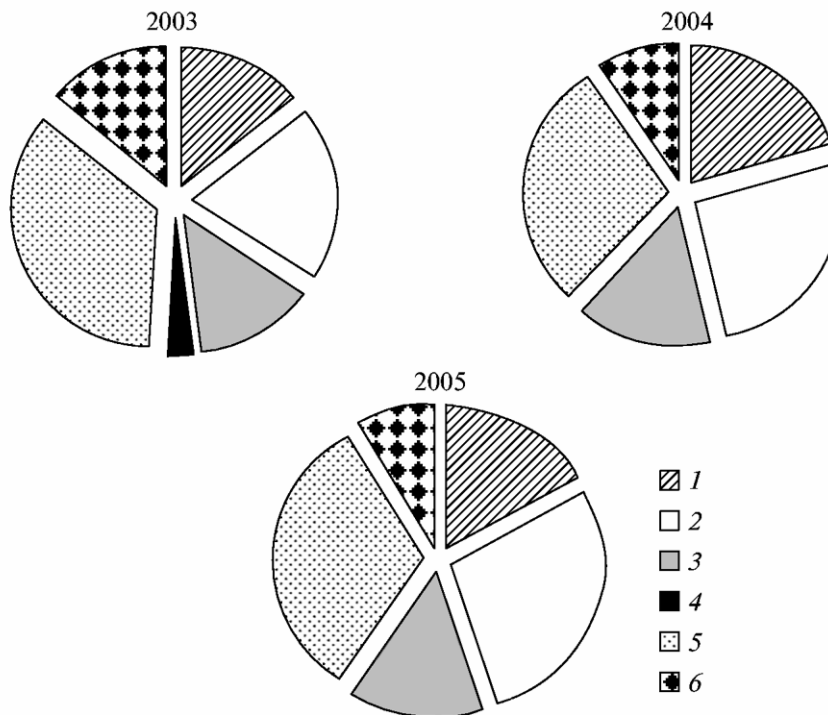
Fig. 2. The causes of mortality of *Polistes gallicus* (L.) colonies in 2003–2005: completion of life cycle (the successful colonies) (*1*), loss of the foundress (*2*), anthropogenic factors (*3*), predation by ants (*4*), predation by birds and *Decticus verrucivorus* (*5*), and unknown causes (*6*).

2006). Despite the activity of the foundress, manifesting itself in intensive rubbing behavior and direct aggressive behavior towards the ants, the attackers were able to capture the nest. During 1.5 h of continuous observation the female applied ant repellent more than 150 times and lunged towards the approaching ants 161 times; 63 ants were knocked off to the ground.

Judging from indirect evidence, in the other three cases the attacks took place at night.

An attack of the nest of *P. dominulus* by *M. bergi* ants was observed on May 27, 2009.

The foundresses of *P. gallicus* and *P. dominulus* apply the repellent secretion on their nests. However, as can be seen from the above examples, this defense is not efficient enough in case of group hunting by the ants. This may be one of the reasons for scarcity of nests of polistine wasps in the biotopes with high densities of *M. bergi*.

A similar enhancement of rubbing behavior (from 4 to 15 acts/h) and protective behavior was observed in a haplometrotic nest of *Ropalidia marginata* Lepeletier located in the attic of a building (02.10.2002, Bangalore, India), when a foraging trail of the ants

Tapinoma sp. appeared within 5 cm of the nest. Later on, the foundress disappeared and the colony perished.

It is generally assumed that the frequency of rubbing behavior decreases after the emergence of workers, in relation to the increasing number of defenders (Kojima, 1992b). However, our observations of a mature colony of *Mischocyttarus injucundus* with a foundress and 12–15 workers, carried out for a month, revealed a different situation. The nest of this colony, including over 60 cells, was located on a leaf of *Dracaena fragrans* (L.). The elongated margin of the leaf bent down, apparently under the weight of the nest, and approached the stem on which the ants were running. The movement of ants along the stem was quite intensive, with up to 28 ants crossing the reference line during a 10-min period. From time to time, some ants approached the nest and ran under it. It was not surprising that the total rubbing activity of this colony was 9 times as high (60 as compared to 6.6) as in the haplometrotic females of this species which nested in more favorable places during the same period. The colony' survival testifies to its efficient defense.

Thus, the participation of ants in regulating the abundance of resocial polistine wasps may be determined not only by the stage on which the colony is attacked, but also by the specific surrounding of a particular nest.

The role of mass foraging ants as factors of brood mortality for nomosocial wasps remains insufficiently studied. For example, 21 out of 103 nests of *Polybia occidentalis* (Olivier) examined early in the morning were found to contain the ants *Crematogaster rochai* Forel (in 10 nests), *Camponotus rectangularis* Emery and *C. atriceps* F. Smith (in 5 nests each), and *Solenopsis* sp. (in 1 nest), whereas no ants had been observed in these nests in the preceding evening (Bouwma et al., 2007). These findings were interpreted as evidence of night attacks by the ants.

The ants *C. rectangularis* may attack a colony of *P. occidentalis* during several hours and even several days (up to 4 days) before retreating (Bouwma et al., 2007). Even in case of a successful attack, only the brood is lost but the colony usually survives. The wasp workers quickly build a new nest and effectively defend the brood from ants (Jeanne, 1975; Jeanne and Bouwma, 2004). At the same time, in several cases *C. rectangularis* ravaged the same wasp colonies repeatedly after 3–39 days (Bouwma et al., 2007).

Wasps of this group probably recognize ants by their scent (Chadab and Rettenmeyer, 1975, 1982; Forsyth, 1981; Chadab, 1979; London and Jeanne, 2005). Sensing the approach of mass foraging *Eciton* army ants, the queens and workers quickly abandon the nest and migrate in a swarm to another place where they built a new nest. However, in *Agelaia yepocapa* Richards, which nests in tree hollows and builds combs without envelopes, the swarm waits till the army ants *Eciton burchelli* Westwood are gone and then returns home (O'Donnell and Jeanne, 1990). This behavior may be related to the scarcity of available nesting places.

Social insects (ants and wasps) make a considerable part of the diet of some *Eciton* species (LaMon and Topoff, 1981; Rettenmeyer et al., 1983; Zakharov, 1986). According to the data of Chadab (1979), 10–27% of wasp colonies lose their brood every year to predation by army ants. The repeated founding of colonies affects their size. For example, the colonies of *Polybia occidentalis* and *Metapolybia azteca* Araujo reach a larger size in the seasonal dry forest where the army ants are scarce, than in the rainforest where predation of these ants is intense (Forsyth, 1981).

As regards their influence on the succession processes in ecosystems, the army ants were compared with grazing animals (Rettenmeyer et al., 1983).

Enactive Interaction

According to the authors of the autopoiesis concept (Varela et al., 1991), the enactive interaction implies, on the one hand, autonomous activity of the subjects of interaction based on endogenous processes of self-organization, and on the other hand, close interaction between the predator and prey mediated by their activity.

The hypothesis of the adaptive nature of rubbing behavior in resocial wasp species is largely based on the fact that the frequency of petiole treatment by the foundresses increased considerably after a mere presentation of an ant (Turillazzi and Ugolini, 1979; Keeping, 1990).

Moreover, the adaptive nature of rubbing behavior can be inferred from its temporal organization, since before the emergence of workers, this behavior in haplometrotic foundresses is connected with two other forms of activity: foraging and nest building (Post and Jeanne, 1981). For example, in haplometrotic foundresses of *Ropalidia gregaria* (Saussure), *Parapolybia indica* Saussure, and *Belonogaster petiolata* nearly half of the foraging departures are preceded by petiole treatment (Kojima, 1992b, 1993; Keeping, 1990). In most species except *P. indica*, this action usually follows such forms of building behavior as licking of the petiole and comb (Post and Jeanne, 1981; Kojima, 1982, 1992b; 1993). The association of rubbing behavior with foraging may be explained by a greater risk of an ant attack in the absence of the female; the association with building activity may result from the need to renew the repellent coating of the nest.

This temporal association is preserved under laboratory conditions, in the absence of ants and with sufficient food, which may suggest that the relation is endogenous. On the other hand, even under natural conditions rubbing behavior appears to be spontaneous (not associated with any external stimuli) and unevenly distributed. Such facts usually avoid consideration, even though they may be regarded as manifestations of a self-organizing process (Nikolis and Prigogine, 1990).

We have analyzed the nature of rubbing behavior and the temporal organization of this behavior in
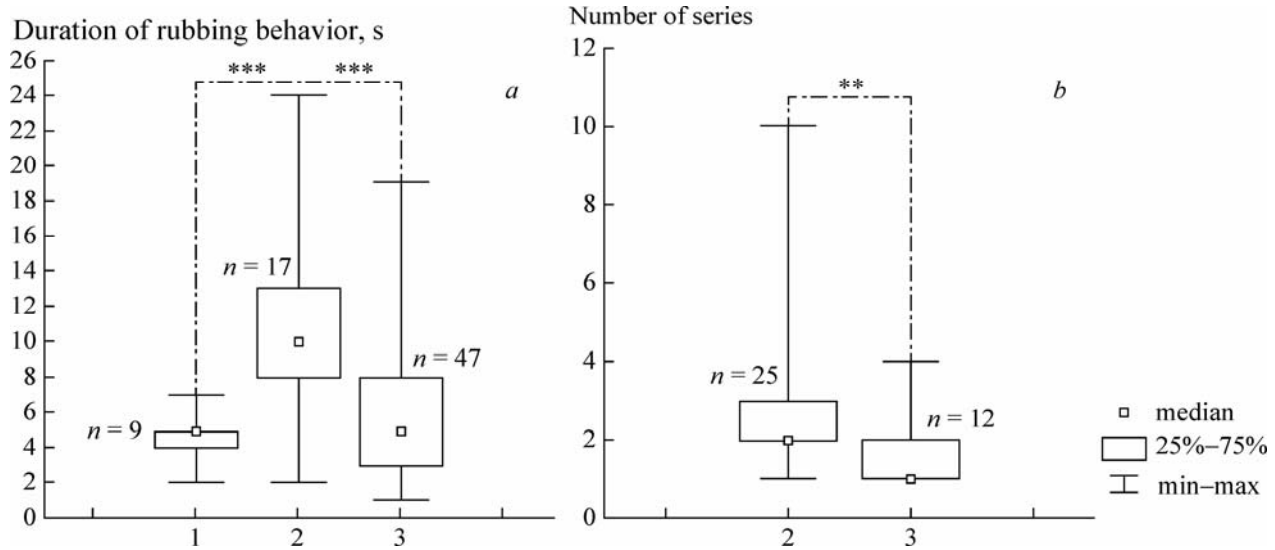
Fig. 3. Duration (*A*) and the number of series of rubbing behavior (*B*) on the petiole (*1*), petiole and nest (*2*), and nest (*3*) by the foundress of *Mischocyttarus alfkeni* (Ducke) (20–23.11.2004, Trinidad Island). Kruskal-Wallis test: $H = 19.85$ ($N = 73$) (*A*); Mann-Whitney test: $U = 55$ ($N = 37$). ** $p < 0.01$, *** $p < 0.001$.

a foundress of *Mischocyttarus alfkeni* based on video records with a total duration of 6 h. During the observation period the comb consisted of six cells, containing 2 eggs and 1 pupa. No building activity and no return with prey was observed; water for cooling was brought three times. The foundress left the nest for brief periods only, no longer than 1–2 min. Three types of rubbing activity could be distinguished: rubbing behavior of the petiole was less frequent (9 out of 73 cases, or 12.3%), whereas rubbing behavior of the nest was more frequent (47 out of 73 cases, or 64.4%); the combined treatment of the petiole and nest was observed in 23.3% of the cases. rubbing behavior of the petiole and that of the nest were shorter than the combined rubbing behavior of the two structures (Fig. 3*a*).

In 5 out of 30 cases (16.7%), the repellent was applied by the female 1 min before leaving the nest. In 46.7% of the cases, the female probed the petiole with its antennae before leaving the nest.

Licking of the nest and petiole was observed twice, followed by rubbing behavior in both cases.

In 74.1% of the cases, rubbing behavior alternated with inspection of the cells, petiole, and nest walls, or with the resting state.

It should be noted that rubbing activity was non-uniform. Series of repeated rubbing behavior could be distinguished (from 2 to 10 acts in succession, on average 2.8), the tendency to repetition being more distinct during treatment of the petiole and nest walls

(Fig. 3*b*). This behavior may be characterized as ordered because acts of rubbing behavior were arranged in series and showed a temporal correlation: the fewer rubbing behavior acts were in the series, the longer was the interval between them ($r_s = -0.54$, $n = 73$, $p < 0.001$).

In addition, analysis of the temporal rubbing behavior structure showed that the logarithm of the number of rubbing behavior decreased at a constant rate as their duration increased (Fig. 4).

The activity of ants near the wasp nest was very low: 0.3 ind./10 min. Individual ants were present near the nest from 2 s to 1 min.
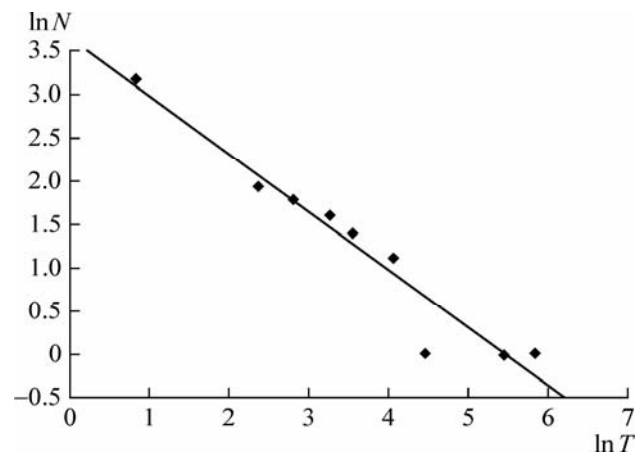

Fig. 4. Temporal organization of rubbing activity in the foundress of *Mischocyttarus alfkeni* (Ducke). Abscissa: logarithm of rubbing duration; ordinate: logarithm of the number of rubbing acts.
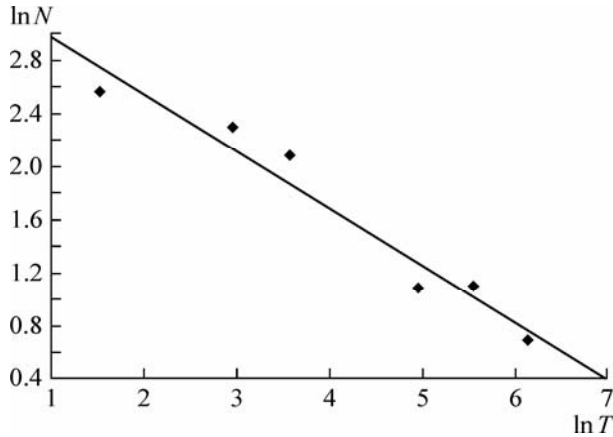
Fig. 5. Temporal activity of ants near the nest of *Mischocyttarus alfkeni* (Ducke). Abscissa: logarithm of duration of intervals during which ants were absent near the nest; ordinate: logarithm of the number of such intervals.

Analysis of the temporal activity of ants at such dynamic densities also showed power dependence: the logarithm of the number of intervals during which the ants were absent near the nest decreased at a constant rate as the duration of such intervals increased (Fig. 5). Thus, behavior of both the predator and the prey revealed a considerable degree of invariance, indicating that both systems were self-organizing and existed "on the verge of chaos" (Podlazov, 2005).

Some data indicate that the ordered nature of animal behavior is compatible with its adaptive functions (Nepomnyashchikh and Podgornyi, 1994). For example, analysis of the seeking behavior of larvae of the caddis fly *Chaetopteryx villosa* Fabr. (Trichoptera, Limnophilidae) showed that random sequences of stimuli not only did not disrupt the ordered behavior but represent one of the conditions of its development, interacting with the behavior shaping mechanism.

Simulation of this behavior showed that perception and response to a stimulus also depended on interaction between stimulation and unpredictable fluctuations in the CNS and receptors (Nepomnyashchikh and Podgornyi, 1994). In this model, the noise (CNS fluctuations) affected the nonlinear behavior shaping mechanism and resulted in a phase transition. The cited authors concluded that the model in question represented a self-organizing process combining stochastic properties with certain correlations between consecutive responses to external stimuli.

A question arises, how the ordered rubbing activity of the wasp can facilitate adaptation if the temporal parameters of absence of ants near the nest are charac-

terized by irregularity and power dependence. A prolonged presence of one ant (marking the substrate) near the nest may "designate" the appearance of other ants in the future. The tendency of the wasp to repeat similar actions may in some cases correspond to the distribution of the predators; in addition, it may increase the rubbing activity when numerous predators suddenly appear.

The second aspect of the enactive interaction is indirectly reflected by the spatial distribution of wasp colonies, since their habitat preferences depend on the activity of entomophages, including ants.

In particular, in the tropical regions a high density of wasp colonies was observed in anthropogenic landscapes where the raids of army ants were less frequent (Richards and Richards, 1951).

Special adaptations are present in the wasps living under the protection of *Azteca* ants (West-Eberhard, 1989). On 20.12.2004, we observed a settlement of *Polybia rejecta* (Fabr.) near Caura (Trinidad Island), which consisted of 11 colonies located on three closely spaced trees populated by *Azteca* sp. In other places we found only 5 solitary nests of these wasps. It was previously noted that *P. rejecta* preferred nesting on trees with *Azteca* ants or with *Pseudomyrmex ferruginea* F. Smith (Vesey-FitzGerald, 1938; Richards and Richards, 1951; Herre et al., 1986, etc.), but the interactions between these wasps and ants were not described. At the same time it is known that the wasps *Metapolybia azteca* under similar conditions thoroughly bit and mouth the area surrounding their nest removing in such a way trail substance left by *Azteca* ants (West-Eberhard, 1989).

The wasps *Mischocyttarus insolitis*, building peculiar nests with cells not united in a comb but raised on individual petioles, also live under the protection of the ants *Allomerus octoarticulatus* Mayr or *Pheidole* sp. (Herre et al., 1986).

These species of ants also have mutualistic relations with the trees *Tococa guianensis* Aublet and *Maieta poeppigii* Mart. ex Triana. The diet of these ants consists exclusively of the secretions of scale insects and special glands on the leaves. The ants attack any insect that appears on the leaves but behave indifferently towards the wasps. During their raids, the ants *Eciton burchelli* and *E. rapax* Smith do not examine the trees occupied by *A. octoarticulata* and *Pheidole* (Herre et al., 1986).

Ants were named among the principal factors determining the spatio-ethological and demographic structure of both nomosocial and resocial wasp species (Forsyth, 1981; Jeanne, 1981; Jeanne, 1979; Strassmann, 1981). At the same time, the mode of colony founding (independent founding or swarm founding) in wasps was found to be correlated with the specific parameters of anti-ant defense, involving the structure and activity of exocrine glands, behavior, and even nest structure (London and Jeanne, 2000). The resocial species with small colonies, independent-founding, open combs, and annual life cycles mostly rely upon chemical defense, i.e., application of the repellent secretion of Van der Vecht's gland on the nest petiole. The nomosocial species, having large perennial colonies founded by swarms and nests protected by envelopes can rely upon physical means of defense from ants. Van der Vecht's gland is either absent in most of such species, or its secretion is not repellent (Smith et al., 2001).

The relatively low significance of ants as a factor of mortality of resocial wasps in the temperate zone may be related to frequent application of anti-ant repellent on the nest petiole (Post and Jeanne, 1981; Kojima, 1994; our data). The frequency of rubbing behavior may increase by an order of magnitude depending on the ecological situation, including the species composition of ants.

On the other hand, the role of ants as a factor of polistine wasp mortality in the Palaeotropical region may be grossly underestimated. Hornets are often regarded as the principal invertebrate predators (Gadagkar, 1991; Yamane, 1996), because the results of their predation can be directly observed (they consume the brood and damage the nest) with no need for daily observations. For comparison, more than 5400 day-to-day surveys were carried out in order to analyze the interactions between *Polybia occidentalis* and ants of the genera *Camponotus* and *Crematogaster* (Bouwma et al., 2007).

At the same time, the interactions between wasps and ants represent a convenient model for studying self-organization in the behavior of animals. In particular, studies of spontaneous variability of behavior showed that such variability may allow the animals to adapt to rapid and unpredictable changes in the environment (Nepomnyashchikh and Podgornyi, 1994).

On the other hand, simulation of the seeking behavior of predators revealed their ability to respond to the non-uniform distribution of prey by changing the rate of movement in the prey density gradient (Hassell and May, 1973; Tyutyunov et al., 2002). This behavior of the predators may cause local elimination of the prey, whereas the areas of low density are characterized by stable coexistence of the predator and prey populations. Intensive seeking activity of the predators is correlated with non-uniform spatial distribution of the trophic communities, their spatial dynamics being characterized by continuous movement of density patches of the interacting populations (Tyutyunov et al., 2002). The above data on the spatial distribution of wasp colonies agree with this model.

At the same time, some individuals in the populations of resocial wasp species show preference of different modes of colony foundation: singly or in groups, close to the maternal nest or in a new habitat (Rusina, 2009). The selection of habitats by the wasps results in the appearance of patches of varying density of prey (trophic resource for the predator). In our studies in the Black Sea Reserve, the random distribution of *P. dominulus* nests was shown to be replaced by the aggregated one under the influence of predators (mostly birds) (Rusina, 2008). The distance between wasp nests and the settlement density varied from season to season, probably affecting the seeking behavior of predators. Simulation of the habitat selection process demonstrated how it could increase, decrease, or stabilize the number of individuals in a population (Holt, 1987).

The complex and nonlinear nature of direct and feedback actions may be interpreted as signs of co-determination and co-evolution in the predator-prey system. The interaction between wasps and ants can be understood as a dynamic (embodied, situated, and enactive) structure-process (Knyazeva and Kurdyumov, 1994), which has been only partly analyzed in a few species.

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