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Proc. Zool. Inst. Russ. Acad. Sci., 289, 2001: 155-160

Bird nest's consortia: insects as components of nest ecosystems

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Bird nests are specific habitats, where many insects and other arthropods are concentrated. More than 1000 species were included into lists of insects found in bird nests in the World (Hicks, 1959, 1962, 1971). Insect community, nest, and its host (bird) could be considered as a specific ecosystem named consortium. Like consortia of mammal burrows (Krivokhatsky, 1994), the bird nest's consortium has no its own producer and can be classified as heterotrophic (biotrophic) in contrast to autotrophic consortium of plants. The bird nest's consortia are included into the surrounding ecosystems. They are characterized as local and temporary ones.

Nidicoles (nest-dwelling arthropods) have a part on all levels of destruction of organic material concentrated in the nest due to the bird activity (Nordberg, 1936; Mulyarskaya, 1953; Woodroffe, 1953; Popendiker, 1956). Different species of insects from the different taxa have precedence in abundance, density, and biodiversity among other nidicoles.

The study is based on material collected in the "Forest on the Vorskla River" Natural Reserve, recently renamed "Belogorye", in the Belgorod Region of Russia during 1984-1986. Insect populations from the nests of 16 species of birds were studied. Some results of exploratory work, including the methods of examining material and the lists of species, have already been published (Krivokhatsky, 1990; Krivokhatsky & Nartshuk, 2001). More than 100 species of insects of various ecological specialization were discovered. The nutritional categories of nest-dwelling insects were discussed in the above papers, a new ecological classification of nidicoles was proposed, and a row of levels of consortive organization was described. It has been established that species diversity and complexity of consortia increase from smaller to larger, from homogeneous to more composite, from annual to perennial nests.

Obligatory nidicoles have the permanent connections with nests and cannot exist outside of bird nests at least during one developmental stage. Facultative nidicoles usually develop in the nests, but can be found in other natural and anthropogenous organic substrates. Accidental nidicoles can use the nests for some stages of the life cycle as well as other closely re-

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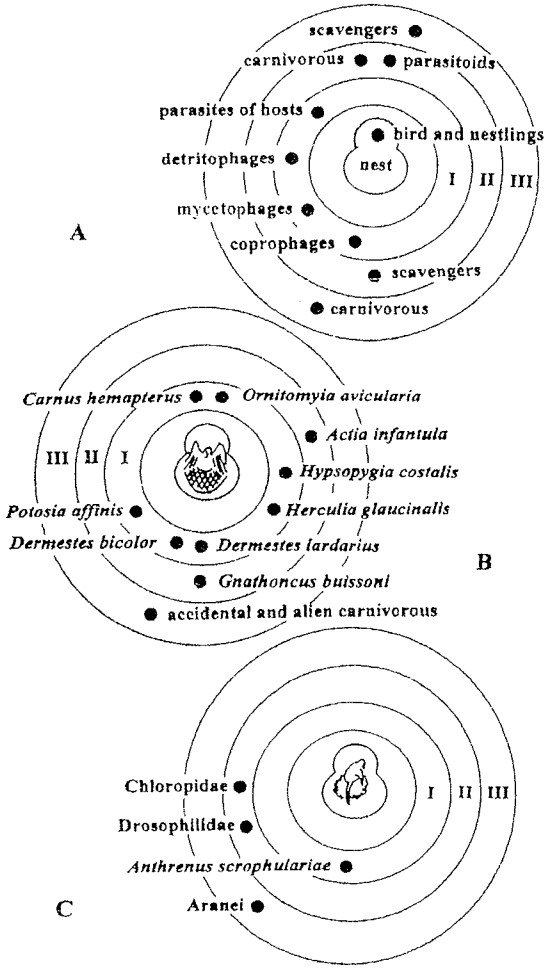
lated habitats. The species alien to the nests are the species characteristic of the surrounding biotopes; they can be found in nests during their migratory activities or they can be brought accidentally by a bird with building material or as food.

Facultative nidicoles are predominate among the sampled species of insects. Two species of obligate nidicoles and ten of facultative ones were estimated as highly abundance (100-1000 specimens per nest). These data are supporting evidence for the concept of specific construction of bird nest's ecosystems. The concept was corroborated by the results of studies of nest's insect communities for different regions, and different types of bird's nests (e.g. Erik & Glukhova, 1974; Borisova, 1978; Hood & Welch, 1980; Romaneev *et al.*, 1985).

The general consortium (see Figure, *A*) can be shown as a number of circles (trophical concentres of different levels) concentrated around the nucleus of consortium. The nucleus has a double structure comprising the host of consortium (bird) and the nest. Parasites of birds, saprophages on the products of bird metabolism (e.g. scavengers and coprophages), and saprophages on nest materials (e.g. detritophages and mycetophages) gathered at the first concentre. The second concentre is crowd by predators (carnivorous), parasitoids, and scavengers (necrophages) on the first concentre's members. The third concentre – is the crown of consortium, it includes nonspecific predators and saprophages of the last level of destruction. A large number of obligatory and facultative nidicoles are concentrated at the first and second concentres.

The general consortium of bird's nests of the "Forest on the Vorskla River" Natural Reserve is the result of unification of specific consortia of different species of birds, which formed from the individual consortia of each nest. Every individual consortium differs from others in composition of concentres and abundance of consorts. More complete consortia, close to the general one, were described in perennial nests of *Butheo butheo* having a complex structure (see Figure, *B*), other individual consortia usually have lacks in one or two concentres (see Figure, *C*), and some annual homogeneous nests were nearly empty.

Exact definition of consortium (Rafes, 1980) is the "totality of organisms connected with the nucleus in the common fate." Those connections after initiation can be involved in a long coevolutional process. The descent of consortia was initiated by origin of double-form nucleus, which primarily consisted of bird with its own parasitic consortium and evolutionary new nest. Next supposition was the presence in the surrounding ecosystems (including parasitic consortia of birds) of any potential consorts – species, which can use new environments due to convenient trophic and topic specialization.



The structure of the consortia of birds nests. A – general consortium; B – consortium of nest of *Buteo buteo*; C – consortium of nest of *Lanius collurio*

The analysis of ecological and systematical positions of modern consorts in terms of both suppositions make it possible to propose an evolutionary scenario of shaping and development ofbird nest's consortia.

1. The hatching of eggs is the fundamental characteristic feature of homoiothermal birds. Nevertheless, the hatching and the nesting are different events. The hatching without nesting is primitive condition in the evolution of birds. More 'plesiomorphic' birds (*Palaeognathae*) have no distinct nests.

2. First primitive nests or separate nesting places known as bird's rookery, are characteristic of the more primitive *Neognathae – Colymbomorphae* known since the Upper Cretaceous. Modern species of nidicoles, which originated in that period, belong to the high-level taxa with obligatory connections with bird's rookery. Beetles of the family Cavognathidae are known from the guano and bird's rookeries in New Zealand (*Zeonidicola, Neocercus*), Australia (*Cavognatha*) and Chile (*Taphropiestes*) (Watt, 1980). This type of distribution is unique to the taxa, which originated in the Cretaceous of Gondwana (Krivokhatsky, 1985). Some fleas (Aphaniptera) became nidicoles at the same time (Marshall, 1981).

3. True large nests are characteristic of *Pelargomorphae (Neognatha)*. Some of them build new nest every time (Steganopodes, Anseres), others (Ardeae, Accipitres) have perennial nests. It seems plausible that nesting function has origin in different Pelagomorphae independently. Most of obligatory and facultative nidicoles came to the nests at that period (Paleocene). Many recent species of nidicoles have closely related species, which are nidicoles too. Some taxa of generic level (*Carnus, Ornithomyia, Protocalliphora, Tripocalliphora* from Diptera, *Ceratophylus* s. str. from Aphaniptera) and some subgeneric species groups (in *Attagenus* from Coleoptera, *Monopis, Tinea* from Lepidoptera) are almost all nidicoles; few exceptions represent the primary nidicoles losing connections with the nests secondarily. Flies of the family Carnidae are known as facultative (*Meoneura*) or obligatory nidicoles (*Carnus*). The larvae of those genera live in the organic substrate of nests. The origin of the *Carnus*, which includes the ectoparasites on birds, can be dated to the Eocene – Miocene; hypothetical ancestor has divided into 6 species due to the geographical isolation (Grimaldi, 1997).

4. Relatively 'young' birds from *Alectoromorpha* and *Coraciimorpha* are adapted to the different environments and have almost all types of nests including their secondary absence. The nests are mostly annual. Obligatory nidicoles recorded there, penetrated from the ancient perennial nests and nests of complex structure. Facultative nidicoles (e.g. *Ptinus, Tenebrio, Potosia* from Coleoptera) came from other relatively similar habitats, like hollows of trees, caves and burrows. Accidental nidicoles lacking coevolutionary connections with nests, may occur there having penetrated from the surrounding biotopes, where the nest is situated (e.g. crown, soil).

It would be erroneous to support the presence of any coevolution of nidicoles and nest's hosts, from the ancestor to descendants. Only possible way is expansion of nidicoles to the nests of 'young' taxa of birds from the nests with more complicated structure of more 'ancient' birds. There are no mono- or oligotopic nidicoles as a result of this evolution. The nidicoles can select (if select) the type of nest, not the host. For instance, the poor

fauna of tineid moths in the annual bird's nests represented by the species, which constantly live in the perennial nests with more complicated structure of other birds in the same localities (Zaguljaev, 1983).

By this means imperfect consortia of annual and friable nests of birds, usually lacking parasites, are outcomes of consortia of perennial nests with much complex structure. The lack of parasites in those nests can be considered as an adaptive reaction during the nest building activity of birds.

Compound, complicated, and long used nest having originated as a result of necessity for the hatching of eggs and protection of nestlings, has turned into the area for vital activity of a new ecosystem, threatening for the hosts. Birds during the evolution had used different mechanisms for the protection against this menace, e.g. sanitary activity such as cleaning of old nests, replacement of nesting from year to year, shortage of the nestling period, and decrease of complexity of nest up to complete absence of nests.

The studies were carried out with financial support of State Scientific-Technical Program "Biological Diversity" and the Russian Foundation for Basic Research (grants nos. 99-04-49809 and 00-15-97826).

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Proc. Zool. Inst. Russ. Acad. Sci., 289, 2001: 161-166

The odor of aphids as a signal for termination of the trophic diapause in the lady beetle *Harmonia sedecimnotata* (Fabr.) (Coleoptera, Coccinellidae)

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In insects, including lady beetles, the role of the photoperiod, temperature, and food in induction and termination of both photoperiodic and trophic diapauses is well understood (Danilevskii, 1961; Hodek, 1973; Masaki, 1980; Zaslavskii, 1988).

Olfactory stimuli are known to play an important role in insect life, being very diverse in their functional properties. From the very beginning, our investigations of the trophic diapause in the lady beetle *H. sedecimnotata* (Fabr.) based on an assumption, that the olfactory stimulus in itself can be of no trophic value, being a kind of volatile substance produced by aphids and perceived by females (Zaslavskii *et al.*, 1998). Indeed, even our first preliminary results have demonstrated weak but rather distinct reaction of females to aphid odor. In these first experiments, females were dissected in order to estimate the state of ovaries; therefore, it was impossible to reveal any influence of aphid odor on the speed and dynamics of maturation of females. In this connection, we conducted a series of special experiments to solve the problem mentioned.

Materials and methods

All experiments were performed with the use of an original simplified olfactometer. This device allowed to analyze the influence of aphid odor on females of *H. sedecimnotata* with and without simultaneous visual stimulation (ability or inability for beetles to see aphids), or influence of the visual stimulation alone; influence of aphid host plant was also studied. *H. sedecimnotata* specimens were collected from environs of Guangzhou, southeastern China (Semyanov, 2000).

After the adult eclosion, males and females were maintained together. Beetles were fed until all females became mature. Then females were separated from males and fed on carbohydrates (10% sugar solution) for 30 days in order to induce the trophic diapause. After that, females were divided into 2 groups. Females from one group (experimental), were affected with the following odors for a day (24 h): odor of a certain number of