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Alternative evolutionary strategies and tactics used by polyphagous insect to inhabit agricultural environment: *Ostrinia nubialis* as a case

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Substantial differentiation was found between *Ostrinia* populations, adapted
to feed on dicotyledonous and monocotyledonous host plants, which results
not only in oviposition and larval survival differences but also in formation of
ethological premating sex isolation mechanisms. Two strategies are surmised
in warmer and colder areas, correspondingly: wide range of host plant species
in combination with strict developmental stages of the plant, and alternatively,
few host plant are infested during almost all the stages of their development,
Inside these strategies, tactics are plastic. They are activated by the sensory
stimuli, such as temperature, humidity and odorants. The tactic of dispersal
flight before mating could be beneficial when the host plant is abundant,
but mating before the flight is a better choice under the situation of sparse
cornfields. There are still multiple questions to address for clear understanding
of *Ostrinia* behavior and evolution.

KEYWORDS

Ostrinia nubilalis, evolution, reproduction, behavior, plasticity

Introduction

Agroecosystems occupying vast and steadily growing areas (Green et al., 2005) create
evolutionary grounds where new trophic relationships, races, and biotypes are being rapidly
formed. The European corn borer (ECB) *Ostrinia nublilalis* Hübner (Lepidoptera:
Crambidae) is the key pest of corn and several other crops in Europe and North America
(Mason et al., 2018). And besides the great economic importance, ECB is an eminent model
species to study the process of evolution and speciation (Lassance, 2010). However, despite
the appearance of a number of excellent reviews (Lassance, 2016; Coates et al., 2018; Zhang,
2021, etc.), there is still a deficit of reviews and analytical publications that allow us to
streamline ideas about the evolution of this group of insects. The purpose of this article is
to discuss the unresolved or little-studied aspects of variability in the ECB and allies as an
integral phenomenon using the concepts of evolutionarily stable life strategies and

alternative reproductive tactics. The strategy will be defined as a set of rules that determine which behavioral model from the existing ones will be used by individuals of a particular population, and an evolutionarily stable strategy is understood as a life strategy that is used by the vast majority of individuals in the population, since any other life strategy does not have breeding advantages. By alternative reproductive tactics, we will understand one of several ways of acting existing in populations that individuals use, following one or another evolutionarily stable strategy. It is obvious that tactics characterize the specifics of a behavioral act, whereas its long-term goal is determined by strategy (Maynard Smith, 1982).

First, let us look at evolutionarily stable life strategies. The most important environmental factors causing the formation of complicated adaptation systems involving physiological, behavioral, and even morphological features seem to be eventually the ambient temperature, moisture, and food resources (Frolov, 1998). So, the specialized evolutionarily stable strategies are found in populations living in significantly different ecological conditions. It is the most interesting to discuss between and within species variation in sex pheromone composition and host plant specificity in *Ostrinia* species group with trilobed male uncus, which contain the economically important pests of crops.

The very similar to ECB adzuki bean borer (ABB), *O. scapulalis* (Mutuura and Munroe, 1970), was found to have the same sex pheromone polymorphism as ECB within its range (Takanashi et al., 2005). However, in zone of cohabitation with ECB in Europe both species are clearly separated by the sex pheromone composition, namely populations of ABB inhabiting Ukraine, Belarus and the European part of Russia use sex pheromone of E-race (99/1 E/Z 11-14:OAc) (Frolov, 1984; Frolov et al., 2007), while sympatrically occurring ECB utilizes the sex pheromone of Z-race (3/97 E/Z 11-14:OAc). The species exploit different host plants within the range of co-occurence: ABB infests dicotyledonous plants (mugwort, hemp, hop, etc.), while ECB develops mainly on cereals (corn, millet, sorghum). The species demonstrate a versatile difference on many physiological, ethological and ecological characters, including obligate prezygotic ethological reproductive isolation (Frolov et al., 2007).

In other words, when heterogametic pairs, both of natural and laboratory origin, were placed together in 0.5l cages, mating did not occur in the vast majority of cases. Otherwise in homogametic pairing the copulation was completed successfully in most cases. (Frolov, 1984, 1998). Absolutely the same data on differentiation of mugwort (E-race) and corn (Z-race) populations, except for morphological differences, were obtained in northern France (Calcagno et al., 2010). The recent studies on the host plant specialization and molecular aspects of pheromone biosynthesis of the E- and Z-races of the ECB (Leppik and Frérot, 2012; Bozsik et al., 2019) provide new directions hopefully producing important results. The materials obtained in Germany (Lorenz, 1993) also give us the reason to believe that the situation here is very similar to that observed in the north of France. So, it becomes clear that both species are characterized by weak gradual morphological

differences inherited olygogenically, and the unique distinctive feature that differentiates them in Europe seems to be their host plant specificity (Frolov et al., 2007, 2012). ABB was never detected on corn both in Europe and Asia (Ishikawa et al., 1999).

However, in other parts of Europe, e.g., in Italy, maize is damaged by populations belonging to the E-race of ECB (Klun, 1975; Anglade et al., 1984), and in Switzerland, inhabiting maize ECB populations turn out to be polymorphic according to their sex pheromone composition (Peña et al., 1988). Experiments conducted with a number ECB and ABB populations showed, that moths feeding on maize in Europe diverged in their ethology in groups employing the two strategies in host plant exploitation: wide range of host plant species in combination with strict developmental stages of the plant development (reproductive phase) for egg laying and vice versa, utilizing few host plant species but during almost all the stages of their development (both juvenile and reproductive phases) (Frolov, 1994a, 1998). The first strategy is a characteristic of the ECB populations inhabiting southern Europe with its warmer climate: Italy, Serbia and Georgia, while the second one is followed by populations distributed in cooler regions like northern France, Germany, Ukraine, and Russia. Insects following one of the strategies become further separated from another by prezygotic reproductive barriers (Frolov, 1994a). Insects prefer to infest maize plants during later (reproductive) stages of plant development (i.e., after tasseling), since the feeding within leaf whorl is unfavorable for larvae due to toxic and antifeedant substances (Campos et al., 1989; Niemeyer, 2009), and plant defense further rises in response to the pest damage (Guo et al., 2019). To have time to complete the development in colder climates ECB populations are forced to start feeding largely on the whorl leaves, which requires development of certain physiological and behavioral adaptations and is associated with limitation of polyphagousness as well as segregation from populations retaining initial trophic connections with dicotyledonous host plants. So, substantial differentiation was found between insect populations, adapted to feed on dicotyledonous and monocotyledonous host plants, which results not only in oviposition and larval survival but also in emergence of ethological premating sex isolation mechanisms (Frolov, 1984, 1994a). Similar data on adaptation to mugwort and maize feeding were obtained in northern France (Malausa et al., 2007a,b; Pélozuelo et al., 2007, etc.), despite that in more southern areas, such as Italy, Serbia and Georgia such linking was never found (Anglade et al., 1984; Frolov, 1984; Gaspers, 2010).

It has now become quite obvious that ECB and ABB are genetically very close to each other, which is confirmed by a variety of tests (Zhou et al., 2020) and it is quite appropriate to consider them as species "in statu nascendi". Proposed by Frolov et al. (2007), taxonomic interpretation of the status of *O. nubilalis* and *O. scapulalis* is characteristic for the situation observed not only in the north of France and Russia, but also in other regions of the world, so the ECB and ABB are making sense to consider as semi-species, since their divergence is not complete (Mayr, 1996).

The greatest amount of data on ECB pheromone races was obtained in North America, i.e., in the secondary habitat of the insect. Already at the early stages of ECB intrusion into USA, deep differences in their preferences for host plants were noticed between geographically separated populations, e.g., in New England, the eastern part of New York State and in the Great Lakes region (Caffrey and Worthley, 1927; Huber et al., 1928; Dicke, 1932). Arbuthnot (1944) was the first who revealed the sexual isolation between races upon heterogametic crosses. Later, it became clear that Z- and E- pheromone races fail to form a panmictic system in places of their sympatry (Cardé et al., 1975, 1978; Klun, 1975; Liebherr and Roelofs, 1975).

The analysis of the published data suggests that ECB populations in North America, differ not only in the composition of the sex pheromone, but also in the strategies of host plant exploitation. The first, originally developing single generation per season Z-race (presumably from Hungary) obviously adheres to the strategy of feeding on cereals during both generative and juvenile phases of development, and the second originally developing multiple generations per season E-race (probably from Italy) uses the host-generalized, but stages-specialized strategy of host plant exploitation (i.e., different host species at and after flowering, but not vegetative stages of their development). Thus, it becomes clear why the reproductive isolation between races in North America is not as strong as in the north of France: interracial hybrids are found in nature, although their frequencies are sometimes lower than theoretically expected, suggesting only partial reproductive isolation between races (Harrison and Vawter, 1977; Klun and Maini, 1979; Roelofs et al., 1985; Klun and Huettel, 1988). Also, our assumption is supported by the results obtained in the United States, which did not find a close relationship between the race of the pest and preferences for feeding on corn or other host plants, i.e., similar to that observed in northern France (Coates et al., 2019).

Estimates of the time that has elapsed since the divergence of ECB pheromone races are in the range of 75–150 thousand years, which means that they diverged long before the introduction of corn and other cereals into Europe (Malausa et al., 2007b). Thus, the hostplant shift cannot be the reason for splitting the moth species into pheromone races. It is worth mentioning, that pheromone polymorphism is characteristic not only of ECB, but also of ABB, whose combined range covers vast territories of Eurasia. Since ECB separated from ABB on the maize introduction, it is clear that the origin of pheromone races lies in the ABB or even earlier in the evolution.

Although the research on ECB and ABB adaptation to their forage plants using the molecular markers has a very short history, it has been able to prove that feeding on dicotyledonous forage plant species in the genus *Ostrinia* is an ancestral trait (Yang et al., 2021). Genetic mechanisms of the hostplant shifts in ECB and ACB was found to be fundamentally different (Midamegbe et al., 2011; Alexandre et al., 2013), despite multiple ecological parallelisms (Bourguet et al., 2014; Calcagno et al., 2017). Transcriptomic analisys also found genes responsible for the

adaptation of ECB and ABB to the microorganisms associated with them (Orsucci et al., 2018a,b).

It is well known that moisture is required for the development of ECB throughout its entire life cycle from eggs and larvae, especially young instars, to pupation and oviposition. Furthermore, the habitat moisture is an important factor in the ECB population dynamics (Chiang and Hodson, 1972; Hudon and LeRoux, 1986; Frolov and Grushevaya, 2020). According to phylogenetic analysis, evolution in the genus *Ostrinia* (Mutuura and Munroe, 1970; Zhou et al., 2020) was directed to habitats with more arid climates from primitive *O. penitalis* (Grote) developing on *Nelumbo* in water through *O. obumbratalis* (Lederer) and *O. palustralis* (Hübner) feeding on *Polygonum* in wetlands to prairie *O. kasmirica* (Moore) on *Cirsium* spp. Regular changes in genes encoding the structure of male midtibiae (*invagination* and *Massive tibia*) of ABB populations on the East European Plain reveal a close relationship with changes in average precipitation rates (Frolov, 1994b). A reliable correlation was also found between seasonal fluctuations in the frequency of *invagination* allele in ABB populations in the Krasnodar Territory and the amount of precipitation during the adult flight period (Frolov, 1984). And finally, the data from a number of observations show clear tendency for E-race to inhabit more humid places than Z-race (Klun, 1975; Anglade et al., 1984; Frolov, 1984, 1994c). Moreover, laboratory studies revealed the highest female calling at 75% relative humidity for Z-race and 100% for E-race (Webster and Cardé, 1982) and a corresponding decrease in Z-race male responses in flight tunnel under humidities above 80% (Royer and McNeil, 1993).

Thus, there are good reasons in favor of the hypothesis of the formation of pheromone polymorphism as a response adaptation to specific ranges of humidity. Probably, the emergence of a more moisture-loving E-race may have been confined to areas with heavy precipitation (foothill areas of the Alps, Carpathians, Caucasus), a more dry-loving Z-race — to the drier marine climate of Europe. It is obvious that such evolution, at least at the initial stages, proceeded more allopatrically than sympatrically, which is in full agreement with the speciation model as understood by Mayr (1963). The mechanisms of reproductive isolation are beleived to arise as a result of interspecific relationships, but the processes at the population level probably play a very important role, as it was recently proposed (De Pasqual et al., 2021). The proposed hypothesis suggests that pheromone polymorphism originated as an adaptation to environmental features and only later become a factor of sexual isolation.

Effective implementation of an evolutionarily stable life strategy requires taking into account the local living conditions of the population. Alternative reproductive tactics (Oliveira et al., 2008), evolving in a certain strategy, affect sexual behavior and the behavior of host plant choice integrated into a single complex of reactions (Landolt and Phillips, 1997). In contrast to the strategy of exploitation of the host plant, where the individual is deprived of choice, reproductive tactics are flexible (Hopper et al., 2003), following one

or another tactic depending on the environmental conditions preserved considerable freedom of choice (Hopper, 1999).

Living in agroecosystems under crop rotation conditions requires ECB moths to move around constantly (Mazzi and Dorn, 2012), because the overwintering grounds and egg laying areas for emerging adults are spatially separated from each other. The most common tactic of reproductive behavior is the flight of the moths from wintering sites to the current year corn plots. Moths than choose spots for mating that are adjacent to cornfields and covered by short (0.5–1.0 m high) and dense, mostly cereal vegetation (Sappington, 2005; Reardon et al., 2006). Spatial distribution of ECB adults in the North Caucasus reveals a fundamentally similar pattern: places of aggregations, where adults of both sexes of overwintered generation concentrate, are covered with dense short vegetation and located in immediate proximity to cornfields, usually in areas protected from adverse meteorological influences from 3–4 sides by forest lanes, typical for the Russian agricultural environment (Frolov and Trishkin, 1992).

This behavior tactic entitled as "mating after settlement" appears to provide: (1) an energy saving by females for flight activity, since the spermatophore mass significantly increases the body weight of females and, consequently, the energy expenditure, (2) repeated mating taking place at aggregation sites, contributing to increased fecundity (Fadamiro and Baker, 1999), and (3) the probability of inbreeding obviously decreases due to the adults arriving from different overwintering grounds. This model suggests higher flight activity in males compared to females, since males would check multiple places looking for females.

However, not all ECB populations use such tactics of reproductive behavior. It turned out that in the north of Switzerland ECB adults have a completely different reproductive behavior — here up to 90% of the overwintered females mated in places where they overwintered, i.e., before settling after the dispersal flight directed to the finding a host plant. Unlike females, males preferred to stay in hatching areas after wintering. Thus, the fundamental difference between the reproductive tactics of "mating before settlement" is that there are fewer males than females in the current year's corn fields, and they arrive already mated, and not virgin (Cordillot and Duelli, 1989).

The new foci of damage by ECB were formed in the north of the corn-growing area (Belarus, Central Russia). Local populations of the pest demonstrate "mating before settlement" tactics of reproductive behavior, namely, a significant proportion of moth mates in the places of emergence and already mated females fly out to search for the current year crop. Accordingly, when the current year's corn field (where pheromone traps are placed) is located rather far (1.5 km and more) from the last year's fields (the source of overwintered pest adults), the traps catch very few males, if any, not because the pheromone is unreliable, but because the males do not reach these traps (Frolov and Ryabchinskaya, 2018). It is obvious that the main disadvantage of ECB sex pheromone from the point of view of pest monitorng is that it attracts only males (Witzgall et al., 2010), whereas the harmful generation appears from eggs laid by females. The problem of ineffective sex pheromone monitoring

is solved easily by using baits that are attractive for females, i.e., semiochemicals of plant origin or UV LEDs (Tóth et al., 2016; Frolov et al., 2020). The evolutionary preadaptation for such a strange reproductive tactic, as we may speculate, arose before corn cultivation moved northward, the main food resource here was millet (Shpanev et al., 2019), which was the ancient host plant for the evolving moth species, later known as ECB (Caffrey and Worthley, 1927). Nowadays the area under millet has steadily declined (Patil, 2016). Accordingly, in order to survive under conditions of low host plant occurrence, moths are forced to develop a different reproductive pattern behavior, in which an already mated female searches for a host plant to lay eggs. As a result, the flight activity of females of local populations significantly exceeds that of males. Comparison of the field trapping results carried out in Poland with light traps in the mid-1950s (Pieprzyk and Romankow, 1960), when corn had just started to be actively cultivated, and after more than 50 years (Bereś, 2012), indicates that the local populations of the pest retain the characteristic feature of "mating before settlement" reproductive tactis — significantly higher flight activity of females in comparison with that of males.

Unfortunately, the peculiarity of evolutionary strategies and tactics by which populations of herbivorous insects adapt to agroecosystems is still poorly studied, even in relation to the model species, despite its fundamental importance and practical use for the improvement of plant protection techniques. Better understanding of strategy and tactics in pest evolution and spread requires the combined efforts of researches to predict insect responses to global changes in agrotechnics and climate. It is also necessary to study in more detail the mechanisms of prezygotic isolation, which even in such a well-refined group as the genus *Ostrinia* have not yet been sufficiently understood. We hope that the materials presented in the paper will serve as an impetus for further study of the population variability of the ECB and its allies.

Author contributions

AF: conception, original draft writing and discussion. MZ: discussion and editing. All authors contributed to the article and approved the submitted version.

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Conflict of interest

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