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PHEROMONES OF IXODID TICKS IN TICK CONTROL: FIFTY YEARS OF STUDIES, HOPES, AND FRUSTRATIONS

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In the present review, the data on studies of pheromones of hard ticks (family Ixodidae) accumulated since the discovery of tick pheromones is briefly analyzed from the point of view of usage of these semiochemicals in tick control. Some disadvantages of the use of pheromones in tick control can be explained by peculiarities of their role in tick sexual behavior in the wild and also by complicated character of their life cycle. Perspective new methods of tick control are also mentioned.

Keywords: ixodid ticks, tick control, pheromones

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STUDIES OF PHEROMONES IN METASTRIATE HARD TICKS (SUBFAMILY AMBLYOMMINAE)

The term pheromone is used for biologically active substances (or a group of substances) that are secreted by an animal specimen into the environment and affect other specimens of this species, providing the latter with the information necessary for inevitable changes in their behavior (definition by Leonovich, 2005). Copulation needs preliminary finding and identification of sexual partner; information on the safety of a shelter helps other representatives of the species to survive, etc. All these activities are regulated by pheromones (Sonenshine, 2005, 2006). Chemical substances that influence behavior between individuals of different species, e. g., chemical signals that repel predators are designated as allomones, and that attract them are called kairomones (Sonenshine, 2006).

In the present review, the author does not analyze pheromones revealed in other tick groups (e.g. Argasidae), pointing attention only to hard ticks (fam. Ixodidae), and mainly to ticks, important from the medical and veterinary points of view.

The first evidence on the presence of pheromones in ixodid ticks *Dermacentor variabilis* (Say), *Amblyomma americanum* (Linneaus), and *A. maculatum* Koch was obtained by Berger (Berger et al., 1971; Berger, 1972). During feeding of ticks on rabbits, after reaching some degree of engorgement, males had detached, searched for females, and copulated. When females were covered with cages penetrable for odors, males gathered near the border line, trying to penetrate into the cage. Applying of methylenchloryde extract of virgin females fed for 7–8 days, on males, resulted in the reaction of detachment of males and attempts of male-to-male copulation. The necessary condition of appearance of this reaction included feeding for no less than 7 days. At the same time, extract of males that had fed for no less than 7 days, did not result in any reactions of males and females, in spite of the degree of their engorgement. Hungry specimens of both sexes did not react to female extracts. Species specificity of extract was absent (Berger et al., 1971).

Similar data were obtained in ticks *Dermacentor andersoni* Stiles and *D. variabilis* (Sonenshine et al., 1974, 1977). The reaction of males included reattachment from the place of the primary attachment, orientation to the source of the pheromone (feeding female), active search for this site, and subsequent copulation. Active males, i. e., males that had fed for 7 days, copulated with females killed and covered with lacquer and not attractive before, after covering with extract of homogenates of engorged females in hexane. Species specificity of extract was absent.

Later, by methods of chromatography in combination with biological tests, this pheromone was identified as 2,6-dichlorophenol ($C_6H_3OHCl_2$) (Berger, 1972; Sonenshine et al., 1976; Leahy, Booth, 1978). At present, the presence of sex pheromones of this type was demonstrated in about 20 species of hard metastriate ticks, comprising representatives of the genera *Amblyomma, Dermacentor, Hyalomma, Rhipicephalus* (for more detail, see Leonovich, 2005). The author of the present review also paid a lot of attention to tick pheromones, even discovering the presence of the sex pheromone, 2,6-dichlorophenol, in the Desert tick *Hyalomma asiaticum* Schulze, dweller of sand deserts of Central Asia (Leonovich, 1981).

Independent of discovery and identification of sex pheromones in metastriate ticks, quite different pheromone reactions were revealed (Gladney, 1971; Gladney et al., 1974; Rechav et al., 1976, 1977; Rechav, Whitehead, 1977; Norval, Rechav, 1979).

It was found that males of some tick species during feeding start producing some volatile substance attracting hungry specimens of both species and even nymphs (Rechav et al., 1976). The reaction included orientation toward the source of the pheromone and the subsequent attachment of percipients near this source. Hungry males were not attractive at all (Rechav, Whitehead, 1977). Engorged specimens of both sexes were not attractive to fed males (source of the pheromone) (Berger et al., 1971). By the analogy with earlier described type of reaction in insects, this class of pheromones was designated as "aggregation-attachment pheromones" (Sonenshine et al., 2003; Sonenshine, 2006).

The attraction-aggregation-attachment pheromone is actually a mixture of three or more specific compounds that mediate different behaviors leading to the formation of species-specific feeding clusters on a host. As mentioned, the attraction-aggregation-attachment pheromone is produced exclusively by males, but is attractive to both unfed males and females of the same species. It is secreted by unusually large glands, the Type 2 dermal glands located on the ventral surfaces of the feeding males. Two components, namely, o-nitrophenol and methyl salicylate were identified by high-pressure liquid chromatography (HPLC) in extracts of these glands dissected from fed male ticks (Diehl et al., 1991). In the tick *Amblyomma variegatum* Fabricius, aggregation-attachment pheromone was represented by a mixture of two substituted phenols, methyl salicylate and o-nitrophenol and nonanoic acid (Shoni et al., 1984; Pheromone biochemistry, 2014).

In the present case, the pheromone provides feeding of parasite females only on the host where ready for insemination males are already present.

Thus, within metastriate ticks (Abmlyomminae) two types of volatile distant pheromones were revealed: non species-specific sex pheromone and species-specific (at least in known cases) attraction-aggregation-attachment pheromone. These pheromones also differ in their chemical structure (Sonenshine, 2004).

The analysis of the available data demonstrates the existence of two types of the involvement of pheromones in metastriate tick sexual behavior, based on the existence of two types of pheromones (Leonovich, 1981, 1981a). In the first case, hungry males and females are able to feed independently on a host, and selection of attachment place depends only on reactions on different stimuli of the host itself. Females, after attachment to the host, stay in the attachment site till the end of engorgement. Copulation strongly depends on the degree of engorgement, because spermatogenesis and ovogenesis in metastriate hard ticks finishes only after engorgement i.e., copulation is possible only in really "mature" males and females (for more details, see Leonovich, 2005). It is evident that some factors signaling on the readiness (or potential readiness) of a female for copulation in conditions where successful fertilization and egg development must exist. This signal is mostly successfully performed by a chemical volatile substance produced in special glands after completion of ovogenesis (in other words, the sex pheromone). Being percept by males, this factor results in detachment of males that move towards the source of the pheromone and reattach near this source (in reality, near the half-engorged female). The probability of successful copulation is provided by delayed development of non-fertilized females and their long stay in this state (Balashov, 1967). Production of the pheromone in this case is not blocked, providing finding of such half-engorged females by males ready for copulation

The second type of pheromone-dependent behavior is typical of ixodid species where attraction-aggregation-attachment (AAA) pheromones were revealed (Rechav et al., 1976, 1977; Rechav, 1978; Rechav, Whitehead, 1977; Gladney et al., 1974, etc.). These pheromones, as mentioned above, are produced only by males during feeding on host blood.

In the latter case, females are unable to feed on hosts in the absence of feeding males (Rechav, 1978b). Thus, the AAA pheromone, produced by males and species-specific serves as such a signal. Later, pheromone reactions are realized in the way described above for the first type of pheromone involvement in tick behavior. Some advantage of the latter case is explained by the fact that fertilization is guaranteed for virtually all the females. In this case, the sex pheromone serves only as a signal informing male on the readiness of a female for copulation.

Genital pheromones provide mounting of males, and thus are designated as mounting pheromones (Hamilton et al., 1989; Sonenshine, 2005). These pheromones are cholesteryl ethers, in particular, cholesteryl oleate (Sonenshine et al., 1992; Sonenshine, 2005; Pheromone biochemistry. 2014). These pheromones are contact ones, but they were also used in tick control (see below).

Quite another type of pheromones was also found in ixodid ticks. These pheromones are named arrestment (or assembly) pheromones. Arrestment pheromones decrease locomotor activity. When ticks come in contact with other conspecific individuals, or waste material deposited by such individuals, they cease activity and remain quiescent. Often, clusters of arrested individuals occur in vegetation or, in the case of nidicolous species, in the duff on the floor of caves or burrows (Sonenshine, 2006).

STUDIES OF PHEROMONES IN PROSTRIATE HARD TICKS (SUBFAMILY IXODINAE)

An assumption on the existence of pheromones in ticks of the subfamily Ixodinae, represented in the world fauna by a single genus *Ixodes*, was based on the existence of hungry fertilized females (for more details, see Leonovich, 2005). Many publications where pheromones of tick of the genus *Ixodes* are mentioned are based on works by Graf (1975, 1978), who proposed the existence of sex pheromones in the tick *Ixodes ricinus*. The detailed acquaintance with these works, however, results in many doubts on the reliability of these data, because no any quantitative data of his experiments are given. Later, his data were disproved by several authors (e.g., behavior experiments on *Ixodes holocyclus* Neumann (Treverrow et al., 1977), and also on *I. ricinus* L. and *I. persulcatus* P. Sch. (Uspensky, Emeljanova, 1980). According to the cited authors, ticks of the genus *Ixodes* produce a pheromone, but not the sex pheromone, but the aggregation pheromone. The author of the present review did not find any evidence on the existence of volatile (distant) sex pheromones or other pheromones (aggregation pheromones), providing formation of aggregations in ticks *I. ricinus* and *I. persulcatus* from natural populations. A propos, Uspensky and Emeljanova (1980) rightfully mention that the assembly pheromone found in the examined species is most likely a relic, that had survived in the evolution of Ixodinae, and play no significant role at present. In my opinion, their data (mean number of ticks forming aggregations in a small Petri dish (10 cm in diameter) constituting 2-3 tick out of 10 (!), being statistically significant, are doubtful in relation to existence of the pheromone.

According to the private opinion of the author (together with his experience in field and laboratory experiments with the dog tick and the Taiga tick), no assembly pheromones are present in the mentioned species of the genus *Ixodes* (*I. ricinus* and *I. persulcatus*), and finding of hungry fertilized females in the wild can be quite correctly explained without applying the pheromone hypothesis (for more details, see Leonovich, 2005). Besides, contradictory opinions also exist in available literature (Romanenko, 1991).

It should be mentioned that the sex pheromone of metastriate ticks (namely, 2,6-dichlorophenol) affects some receptor cells in the Haller's organ of *Ixodes ricinus* (Leonovich, 2014). In electrophysiological experiments with intracellular recording of action potentials, a specific sensory cell in the distal knoll olfactory sensillum of the Haller's organ responded to very low concentrations of 2,6-dichlorophenol (Leonovich, 2004). This sensillum also responded to phenol compounds (ortho-chlorophenol, ortho-methylphenol (also named ortho-cresol). In spite of electrophysiological response, adults of both sexes, nymphs, and larvae of *Ixodes ricinus* were not attracted to 2,6-dichlorophnol. They also were not repelled by the odor of this chemical substance; in other words, their behavioral reaction to 2,6-dichlorophenol was neutral (Leonovich, 2005).

Attraction of ticks of the mentioned species to components of ticks excreta (such as guanine) were observed (e.g. Benoit et al., 2008), but are they really pheromones (substances specially produced in special glands for providing another specimen of the same species with information changing the behavior?) In my opinion, not every attractant is the pheromone.

We do not analyze other types of pheromones, best of all described in a review by Sonenshine (2006), because they were not used in attempts of tick control with the use of pheromones.

The first thing that is rather evident is the use of pheromone-acaricide mixtures in order to kill ticks attracted by a pheromone. Attempts to apply this method in practice are used in some countries even nowadays (Bhoopathy, Ravi, 2017). But what kind of pheromones (and, hence, what tick species can be affected by this method?)

Arrestment pheromones seem to be most useful for tick control. In some cases, combining the components of the arrestment pheromone with an acaricide (i.e., toxicants used to kill ticks) in a slow-release delivery system, a substantial increase in tick control was achieved (Sonenshine et al., 2003).

Some US patents on the use of arrestment pheromones in combination with acaricides exist, e.g., patent US5296227A (Allan et al., 2001): A patent for controlling of the bont tick *Amblyomma hebraeum* Koch with the use of pheromones, which includes a pheromone composition having 1% by weight each of said decoy of O-nitrophenol and methyl salicylate; 0.2% by weight in volume of said decoy of 2,6-dichlorophenol; and 0.1% by weight of phenylacetaldehyde; an acaricide selected from the group consisting of organophosphorous compounds and pyrethroid compounds; and a matrix material selected from the group consisting of polyvinylchloride, nylons and waxes, said matrix material being impregnated with said pheromone composition (Alan et al., 2001).

In vitro experiments also demonstrated effectiveness of the use of pheromone-acaricide mixtures, e. g. against larvae of *Rhipicephalus sanguineus* (Latreille), *R. (Boophilus) microplus* (Canestrini), *R. haemaphysaloides* Supino, *Hyalomma marginatum* Koch and *Haemaphysalis bispinosa* Neumann, and adults of *R. sanguineus* and *R. microplus* (Ranju et al., 2018). The problem with such experimental works is the transition of laboratory methods into natural conditions (see below) - the basic circumstance hampering the use of these method in practice.

Mounting sex pheromones mixed with acaricides were also used in tick control, at least, a patent on this method also exists (Sonenshine et al., 1992).

Methods of strengthening the effectiveness of commonly used tail or ear tags impregnated with acaricides by admixture of pheromones, turning them into decoys, were used for the control of the bont tick, *Amblyomma hebraeum* (Acari: Ixodidae), on cattle in Zimbabwe (Norval et al., 1991, 1996).

In spite of the mentioned attempts to use pheromones for tick control in nature, the method in general did not succeed. The most difficult problem of all remains: the translation of laboratory research into the extremely diverse parasite control requirements of farming systems in a way that is practically useful (Willadsen, 2006). The methods can be widely used only if it is not expensive.

But more important thing is that actually the use of pheromones very poorly affects the life cycle of the tick in nature. Adults ticks can be killed with acaricides mixed with pheromones in higher degree than killed by acaricides only. But, nevertheless, if only some females will survive (and it is inevitable), they will produce such number of eggs that will restore tick population. Larvae and nymphs, in the majority of cases (except for one-host ticks), feed on small mammals; the latter cannot be eliminated in natural biotopes. Hence, pathogens will exist in natural foci, surviving in host-parasite systems, involving larvae – small mammals – nymphs – medium–size mammals – adults – large mammals.

Attachment of ticks precedes production of pheromones – hence, the tick will be killed, but after infecting of a host with pathogens.

The same story is true when we concern the use of acaricides themselves (without admixture of pheromones). This method is still widely used in tick control practice (Jensenius et al., 2005). Satisfactory tick control is often difficult due to unrealistic expectations and because of constant re-infestation pressure. Some of the most important factors are changes in tick distributions, our inability to control wildlife tick hosts and differences in tick control approaches. These factors probably cause most real and perceived product failures (Dryden, 2009).

The use of acaricides, nevertheless, being mixed with pheromones or not, also have very important disadvantages. The main of the latter includes growing resistance of ticks against acaricides. For example, an increase of multi-acaricide resistant *Rhipicephalus* ticks in Uganda was observed (Vudrico et al., 2016).

The use of repellents seems more reliable: in this case we do not kill ticks but prevent tick bites, which is very important for protecting humans, preventing transmission of pathogens from ticks to humans. The use of tick repellents in cattle seems to be rather expensive and, thus, useless (Ginsberg, 2014). But it can be expedient for pets.

Finding natural repellents of the plant origin seems useful because they do not pollute the wild. Some data on plants that are (and can be) used as tick repellents can be found in a review by Benelli et al. (2016). Repellent effect against tick vectors of public health importance (*Ixodes ricinus, Ixodes persulcatus, Amblyomma cajennense* (Fabricius), *Haemaphysalis bispinosa, Haemaphysalis longicornis* Neumann, *Hyalomma anatolicum* Koch, *Hyalomma marginatum rufipes* Koch*, Rhipicephalus appendiculatus* Neumann, *Rhipicephalus (Boophilus) microplus, Rhipicephalus pulchellus* Gerstaker, *Rhipicephalus sanguineus* and *Rhipicephalus turanicus* Pomerantzev). The most frequent botanical families exploited as sources of acaricides and repellents against ticks were Asteraceae (15 % of the selected studies), Fabaceae (9 %), Lamiaceae (10 %), Meliaceae (5 %), Solanaceae (6 %) and Verbenaceae (5 %).

Genetic control methods become more and more popular, trying to decrease environmental pollution and selection of drug resistant ticks. E.g., preventing (silencing) the expression of a single RNA gene (subolesin) with the use of RNA interference resulted in appearance of ticks with diminished reproductive performance that prevented successful mating and production of viable offspring of *Rhipicephalus (Boophilus) microplus* (Fuente de la et al., 2006; Merino et al., 2011). But now, these methods develop only in laboratory and are pointed mainly to the detailed analysis of tick genetics associated with reproduction (Nijhof et al., 2006). In the future, however, genetic studies seem rather perspective.

In order to decrease losses in cattle population caused by ticks and cattle diseases transmitted by the latter, some authors point to the necessity of affecting the cattle rather than ticks (Shyma et al., 2013). The authors point to the fact that chemical control of diseases has been found to be ineffective and also involving large cost. To reduce our reliance on these chemical products, it is necessary to embark on programs that include habitat management, genetic selection of hosts, and development of a strain capable of inducing host resistance to ticks. Selection for disease resistance provides alternate method for sustainable control of tick-borne diseases. Domestic livestock manifests tick-resistance by skin thickness, coat type, coat color, hair density, skin secretions, etc (Shyma et al., 2013).

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ФЕРОМОНЫ ИКСОДОВЫХ КЛЕЩЕЙ И ИХ ИСПОЛЬЗОВАНИЕ В БОРЬБЕ С КЛЕЩАМИ: ПЯТЬДЕСЯТ ЛЕТ ИССЛЕДОВАНИЙ, НАДЕЖД И РАЗОЧАРОВАНИЙ

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Ключевые слова: иксодовые клещи, борьба с клещами, феромоны

РЕЗЮМЕ

В обзоре кратко проанализированы данные по феромонам иксодовых клещей (семейство Ixodidae) накопленные за пятьдесят лет их исследований, начиная с работы первооткрывателей, с точки зрения возможностей и результатов использования феромонов в практике борьбы с опасными видами клещей. Принципиальные ограничения использования феромонов для сокращения численности опасных видов клещей объясняются особенностями феромонных реакций клещей в реальной природе, а также сложным жизненным циклом клещей. Кратко анализируются новые перспективные методы ограничения вреда, наносимого клещами.