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**THE PHENOMENON OF ATTACHMENT AND FEEDING
OF UNFED TICKS (IXODOIDEA) ON FED AND FEEDING SPECIMENS
OF THE SAME OR DIFFERENT SPECIES:
BIOLOGICAL AND EPIDEMIOLOGICAL ISSUES**

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Hyperparasitism, characterized by attachment and feeding of unfed ticks on engorged or feeding specimens of the same species (tick-to-tick attachment and feeding) has been extensively documented in laboratory colonies of ticks of the Ixodoidea superfamily. Existing literature generally assumes that hyperparasitism operates similarly across tick species in both main families, Argasidae and Ixodidae. However, a closer examination of the available data reveals distinct biological mechanisms underlying this phenomenon in different groups. In argasid ticks, hyperparasitism in laboratory colonies primarily involves unfed specimens stealing blood from their fed relatives, especially under stress of starvation or overcrowding. It remains uncertain whether this behavior of argasid ticks occurs under field conditions. If it does happen naturally, it may have originated as a consequence of the nidicolous lifestyle exhibited by soft ticks. In *Ixodes* ticks (Ixodinae or Prostriata), hyperparasitism of males on unfed or feeding females appears to be a side-effect in the male attempts to copulate while hyperparasitism in Amblyomminae (Metastrata) ticks is likely an aberration in feeding. This difference between Argasidae and Ixodidae may stem from independent adaptation to blood-feeding within the two Ixodoidea families. Experimental evidence of pathogen transmission between aggressor and victim during hyperparasitic feeding has only been demonstrated under laboratory conditions specifically in *Ornithodoros* species (Argasidae). The practical importance of this route of pathogen transmission is still unclear. Although there is an assumption in the literature that hyperparasitic pathogen transmission occurs in the taiga tick *Ixodes persulcatus*, it is important to know that no current data is available to support this presumption.

Keywords: argasid ticks, *Ixodes*, Ixodinae (Prostriata), Amblyomminae (Metastrata), feeding, copulation, hyperparasitism

The first documented case of unfed tick attachment to a feeding specimen (tick-to-tick attachment and feeding or hyperparasitism) dates back to the late 19th century (Barber, 1895). In that instance, a male *Amblyomma variegatum* (*Hyalomma venustum* according to old terminology) “by accident attached himself to a distending female (of the same species – I.U.) – a mistake which resulted in the premature death of both” (p. 199). Throughout the 20th century, multiple cases of tick-to-tick attachment, mostly involving ticks of the same species (conspecific), but occasionally heterospecific (and even heterogeneric) were described (see Wheler, 1906; Hooker et al., 1912, as examples of earlier work). These observations spanned ticks of both major families of Ixodoidea, namely Argasidae and Ixodidae, with a greater predominance in the former.

Our preceding communication addressing discrepancies in terminology regarding the phenomenon of hyperparasitism, which were particularly prevalent in publications from the former Soviet Union, has been submitted in Russian (Uspensky, 2023). In the present communication, we focus on the biological and epidemiological aspects of this phenomenon, which, to the best of our knowledge, have not been previously explored in a comprehensive manner.

Biological significance of the phenomenon

Argasid (soft) ticks

The feeding of argasid ticks on other specimens of the same species has been observed many times but in laboratory conditions, typically during tick rearing or among field-collected ticks taken to the laboratory. In earlier observations these occurrences were considered incidental or intriguing. The feeding of unfed males and younger (small) nymphs on fed or feeding males, females and more mature (larger) nymphs was the most commonly observed pattern. The death of tick victims was infrequently documented (Pospelova-Shtrom, 1953; Filippova, 1966). A unique case of unfed female attaching to a fed male was described by Francis (1938). The proportion of unfed ticks attacking blood-engorged specimens increased under conditions of overpopulation or in response to starvation stress (Helmy et al., 1983; Oliver et al., 1986). These factors could lead to single unfed females attacking other females, resulting in the death of the tick victim (Helmy et al., 1983). The number of reported hyperparasitism cases varied from isolated instances (Beck et al., 1986; Llanos-Soto et al., 2019) to more frequent observations (Bhat, 1969; Helmy et al., 1983). However, not all authors working with argasid tick colonies reported this phenomenon, suggesting that its occurrence depends on tick species and specific conditions of tick rearing. *Ornithodoros coniceps* demonstrated a higher propensity for hyperparasitism (Filippova, 1966), even attaching to specimens of multiple *Argas* species (Theodor, 1932;

Filippova, 1966). It has been proposed that hyperparasitism is a byproduct of ticks fasting for extended periods (Gray et al., 2014), although evidence suggests that long-term fasting does not always stimulate tick feeding (Phillips et al., 1995).

The origin and significance of tick-to-tick attachment and feeding have not been thoroughly explored. It has been hypothesized that this behavior might be a remnant of entomophagy inherited from tick ancestors (Beklemishev, 1948; Balashov, 2006). In fact, entomophagy as a legacy of ancestors is observed in various arachnid and insect groups, including those well-adapted to hematophagy. For instance, occasional observations of ixodid ticks attached to horse flies have been described (Pavlovsky, 1941; Dobrynina, 1956; Boshko, Sklyar, 1981).

An important question is whether this phenomenon occurs under natural field conditions. Some authors who witnessed this phenomenon in the laboratory discussed its potential epidemiological significance based on the assumption that it also takes place in nature (Petrishcheva, 1947; Chebotarevich, 1950; Pospelova-Shtrom, 1953; etc.). However, the tick-to-tick feeding among soft ticks has never been observed under field conditions. The only indication of its occurrence was the observation by Beck et al. (1986) of “feeding scars on the cuticle of field-collected” *O. turicata* specimens. An assumption made by Hoogstraal et al. (1979) that “this phenomenon probably has no biological significance in nature” (p. 405), concerned only intergeneric hyperparasitism described by Theodor (1932).

Given the secretive lifestyle of argasid ticks and their short blood-feeding period (Pospelova-Shtrom, 1953; Filippova, 1966; Uspensky, 2008; Gray et al., 2014), obtaining conclusive evidence to support or refute this statement is challenging, and apparently no attempts have been made to address this question. Additionally, the number of field studies focused on argasid ticks is disproportionally small compared to those on ixodid ticks.

The potential absence or infrequent occurrence of this phenomenon under field conditions might be explained by the existence of regulatory mechanisms that prevent overcrowding in natural tick populations. Evidence of such mechanisms, including decreased female fertility, increased egg mortality, prolonged oviposition and egg development, and changes in the age structure of the nymphal population has been observed in overcrowded laboratory colonies of *Ornithodoros* species (Vasilieva, Ershova, 1980a,b; Ershova, Vasilieva, 1988). A fecundity-reducing pheromone has been found in crowded conditions and its effect intensified with the additional increase in adult tick crowding (Khalil, 1984). Phillips et al. (1995) speculated on the mechanisms that contribute to the starvation-hardiness of *Ornithodoros* ticks. However, it remains unclear how the results of laboratory observations correlate to field conditions, considering the specific habitats in which nidicolous ticks reside.

Nevertheless, it is tempting to speculate that this phenomenon might be advantageous for argasid ticks, since nidicolous ticks depend heavily on the presence and abundance of host specimens in their refuge as well as the density of tick population within that refuge. Feeding of unfed ticks on fed or feeding specimens of the same species could be an additional strategy to secure blood meal for as many ticks as possible, thereby ensuring the survival of the tick population under unfavorable conditions. The adaptive value of the phenomenon is supported by minimal losses of tick victims (decrease in the egg production, shorter life span etc.) when ticks feed on specimens of the same species.

A certain similarity of the same phenomenon has been observed in a group of nidicolous insects, specifically in kissing bugs from the subfamily Triatominae (Hemiptera, Reduviidae) (Ryckman, 1951; Sandoval et al., 2000). However, the different level of adaptation to hematophagy between argasid ticks and kissing bugs prevents a direct comparison of this phenomenon in both groups of arthropods. Kissing bugs demonstrate not only bloodmeal-stealing through hyperparasitism but also entomophagy (hemolymphagy) utilizing a wide range of invertebrates as food source (Alves et al., 2011; Otálora-Luna et al., 2015; Justi, Galvão, 2017; Schmidt et al., 2019). The phenomenon is primarily observed in laboratory-reared bug colonies or under laboratory conditions using field-collected specimens (Garrido et al., 2021), which parallels the situation with argasids.

To conclude, it remains unclear whether hyperparasitism represents a genuine strategy employed by argasid ticks in their habitats or if it only occurs under artificial conditions of tick maintenance or laboratory experiments.

Ixodid (hard) ticks of the subfamily Ixodinae (Prostriata)

The phenomenon of hyperparasitism has been regularly mentioned in ixodid ticks of the genus *Ixodes* (subfamily Ixodinae or Prostriata group), which is considered similar to that in argasid ticks (Oliver et al., 1986; Buczek et al., 2019; Rodrigues et al., 2023). Unlike soft ticks, hyperparasitism of *Ixodes* males has been observed not only under laboratory conditions but also among specimens collected in the field. For proper interpretation, it is necessary to consider certain features of *Ixodes* biology. Males are unknown for some *Ixodes* species, especially among nidicolous ticks, while for other species males have not been observed attached to their hosts (Arthur, 1962; Balashov, 1972; Leonovich, 2022). Actual blood-feeding (with a minimal amount of blood) has been detected on rare occasions only in the most advanced subgenus *Ixodes* (Balashov, 1972; Leonovich, 2022). Males of the *Ixodes* genus can copulate and inseminate females off host before feeding (Arthur, 1962; Balashov, 1972; Uspensky, Repkina, 1978; Ioffe-Uspensky, Uspensky, 2017).

Some authors have speculated that male attachment to feeding or engorged females is connected with copulation (Nilsson, 1975; Ioffe-Uspensky, Uspensky, 2017), while other specialists view copulation and male attachment to females to be independent (Norval,

1974; Moorhouse, Heath, 1975). However, considering the totality of known information, the two events are most likely related. Unfed males often attach to unfed females, as documented by scars on the female cuticle (Norval, 1974; Moorhouse, Heath, 1975; Alekseev, 1991). Since it is impossible to procure blood from unfed females, there must be a different reason for male attachment. Furthermore, the following facts should be taken into account: 1) attached males were found on feeding females, usually together with copulating males (Moorhouse, 1966; Norval, 1974; Ntiamoa-Baidu, 1986); 2) the majority of parasitizing males attach to females near the genital aperture (Moorhouse, 1966; Nilsson, 1975; Ntiamoa-Baidu, 1986; Durden et al., 2018); 3) the position of mouthparts and palps of attached males is the same as that of copulating males (Durden et al., 2018). Thus, the most likely scenario is that males attached to unfed, feeding or engorged females imitate copulation when they reach the female after another tick has already initiated copulation. It is clear that in *Ixodes*, the biology of hyperparasitism is different from that in soft ticks, where the goal is blood-stealing by unfed ticks from ticks with blood.

An interesting case described by Buczek et al. (2018) who observed oral-anal contact between field-collected unfed male *I. ricinus* and unfed female *Dermacentor reticulatus* is apparently of the same nature. Other cases of attacks of *Ixodes* males on females from the subfamily Amblyomminae (Moorhouse, Heath, 1975; Oliver et al., 1986) might also be interpreted as male attempts at copulation.

Ixodid (hard) ticks of the subfamily Amblyomminae (Metastricata)¹

A number of reports describes the attachment of unfed or underfed tick specimens to feeding or engorged ticks, primarily females, in several genera in the subfamily Amblyomminae (Metastricata group): *Amblyomma* (Barber, 1895; Labruna et al., 2007; Rodrigues et al., 2023), *Aponomma* (Roubaud, Colas-Belcour, 1935), *Dermacentor* (Hooker et al., 1912), *Hyalomma* (Sergeant, 1930; Uzakov, 1961; Buczek et al., 2019), *Rhipicephalus* (Sharif, 1930), *Rhipicephalus* (*Boophilus*) (Hooker et al., 1912; Klyushkina, 1956). Tick-to-tick attachment and feeding have been observed in both field-collected specimens and those brought from the field to the laboratory. There have also been observations of intergeneric tick-to-tick attachment (Hooker et al., 1912). Such cases are relatively rare in this younger subfamily compared to Ixodinae (Prostricata). We tend to agree with Moorhouse and Heath (1975: p. 572) who view these cases as “aberrations in feeding”. This conclusion is supported by the high rate of mortality among parasitizing ticks in this group. And yet, we cannot completely exclude the possibility that these observations represent aberrations in copulation as suggested by Sharif (1930). The scarcity of details in these reports makes it difficult to draw a definitive conclusion.

¹ The status of Amblyomminae as a subfamily is after Filippova (1997).

Epidemiological importance of the phenomenon

Argasid (soft) ticks

Many authors who have described cases of hyperparasitism believe that the phenomenon enables the transmission of tick-borne pathogens from infected ticks to uninfected specimens, regardless of their position as aggressor or victim (Petrishcheva, 1947; Chebotarevich, 1950; Pospelova-Shtrom, 1953; etc.). However, there is limited experimental evidence to support this logically plausible suggestion.

Two reports demonstrated the transmission of filariid nematode *Dipetalonema viteae* to naïve ticks *Ornithodoros tartakovskyi* feeding on infected ticks, and further to their warm-blooded hosts (Votava et al., 1974; Londoño, 1976). Helmy et al. (1983) showed direct and reciprocal transmission of *Borrelia crocidurae* from infected *O. erraticus* ticks to naïve specimens, which fed on infected ticks, and subsequently to their warm-blooded hosts. Similar results have recently been obtained for *B. hermsii* and *O. hermsi* (Williamson, Schwan, 2018). Importantly, all of these data were obtained only in laboratory experiments.

Therefore, despite the confidence of many authors that this phenomenon facilitates horizontal transmission of tick-borne pathogens in argasid ticks, there is only limited supporting evidence obtained through laboratory experiments. It remains unclear whether such transmission occurs under field conditions and, if it does, how significant this mode of transmission is. The question posed by the initial authors who described pathogen transmission through hyperparasitism, whether “this phenomenon occurs in nature” (Votava et al., 1974: p. 479), still holds relevance today.

Ixodid (hard) ticks

We examine the data in this Subsection in greater detail, to address certain misinterpretations of this subject in the literature. Specifically, it is still unknown whether in *Ixodes persulcatus*, the virus of tick-borne encephalitis is transmitted from infected female to males feeding on them, despite claims that such transmission does occur (Alekseev, Chunikhin, 1990; Alekseev, Dubinina, 1996b).

In the 1990 paper by Alekseev and Chunikhin, the authors rely on two earlier publications (Moorhouse, Heath, 1975; Ntiamoa-Baidu, 1986) to support their claim. However, the first cited paper merely discusses the theoretical possibility of pathogen transmission by this route (“it seems possible”, p. 572). The paper by Ntiamoa-Baidu (1986) does not even mention the problem of pathogen transmission, while focusing on the biology of *I. moreli*, which is not known to be a vector of any pathogen. In the 1996 paper (Alekseev, Dubinina, 1996b), the authors support the claim of pathogen transmission by citing Alekseev (1991) who, in fact, only considered it as a possibility (“it seems quite probable”, p. 59). The same applies to the speculation about *B. burgdorferi* transmission by *I. persulcatus* (Alekseev, Dubinina, 1996a, b). The authors admit that they “have no conclusive evidence” (Alekseev, Dubinina,

1996a, p. 353). of this mode of transmission, and to our knowledge, no such evidence has been forthcoming to this day. In spite of this, the paper by Alekseev and Dubinina (1996a) has been repeatedly cited as a confirmation of hyperparasitic transmission of *B. burgdorferi* by ixodid ticks (Buczek et al., 2019; Rodrigues et al., 2023).

While the possibility of pathogen transmission through hyperparasitism in hard ticks is theoretically plausible, there is no direct evidence to support its occurrence. As a result, the epidemiological importance of the phenomenon in ixodid ticks remains unknown.

CONCLUSION

The potential for horizontal passage of pathogens during tick-to-tick feeding is a highly relevant topic, especially since many tick species are vectors of human and animal pathogens. Of particular interest are the evolutionary aspects and biological mechanisms of tick-to-tick attachment and feeding. Regrettably, all these topics are far from the forefront of contemporary medical acarology.

Based on the currently available data, it is likely that hyperparasitism in soft and hard ticks has different underlying mechanisms. In argasid ticks, while this phenomenon is frequently observed in laboratory colonies of ticks, especially in overcrowded conditions, it remains unknown whether it occurs in natural populations and, if it does, how significant it is for population survival. In the case of *Ixodes* ticks, the hyperparasitism of males on unfed or feeding females appears to be primarily a byproduct of the males' attempts to copulate, while in *Metastrata* ticks it is probably nothing more than a rare aberration in feeding behavior.

It is plausible that the differences between the two families of Ixodoidea result from their independent adaptation to blood-feeding environment, leading to variations in feeding styles and multiple aspects of their biology at various levels (Mans et al., 2002; Mans, Neitz, 2004).

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The author of this work declares that he has no conflicts of interest.

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ФЕНОМЕН ПРИСАСЫВАНИЯ И ПИТАНИЯ ГОЛОДНЫХ КЛЕЩЕЙ (IXODOIDEA) НА СЫТЫХ И ПИТАЮЩИХСЯ ОСОБЯХ СВОЕГО ИЛИ ЧУЖОГО ВИДОВ: БИОЛОГИЧЕСКИЕ И ЭПИДЕМИОЛОГИЧЕСКИЕ АСПЕКТЫ

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Ключевые слова: аргасовые клещи, *Ixodes*, Ixodinae (Prostriata), Amblyomminae (Metastricata), питание, копуляция, гиперпаразитизм

РЕЗЮМЕ

Присасывание голодных клещей к напитавшимся или питающимся особям своего вида и питание поглощенной ими кровью (гиперпаразитизм) многократно отмечались в лабораторных колониях иксодоидных клещей, преимущественно семейства Argasidae. До настоящего времени гиперпаразитизм у аргасовых и иксодовых клещей рассматривается как явление одного и того же порядка. Анализ разрозненных описаний этого явления у различных видов клещей обоих

семейств позволяет представить его альтернативное объяснение. У аргасовых клещей питание голодных особей на клещах с кровью представляет собой реальное явление для лабораторных колоний, особенно в условиях перенаселенности и/или длительного голодания. Остается неясным, проявляется ли этот феномен в природных условиях. Вполне возможно, что подобный тип питания (ведущий свое начало от энтомофагии предковых форм) может проявляться у аргазид как следствие их нидикольного образа жизни. У клещей рода *Ixodes* (подсемейство Ixodinae или группа Prostriata) гиперпаразитизм самцов на голодных, питающихся или сытых самках – это вероятнее всего побочный эффект при попытках спаривания в ситуации, когда другой самец уже находится *in copula*. У клещей подсемейства Amblyomminae (группа Metastricata), где явление гиперпаразитизма отмечается достаточно редко, это всего лишь аберрация питания. Возможно, что указанное различие объясняется независимой адаптацией к питанию кровью у аргасовых и иксодовых клещей в процессе эволюции. Несмотря на уверенность большинства авторов в том, что возможна горизонтальная передача патогенных микроорганизмов от клещей-носителей интактным особям, этот вопрос остается открытым. Такая передача была достоверно продемонстрирована только для нескольких видов рода *Ornithodoros* (Argasidae) и только в лабораторных условиях. Практическое значение этого пути передачи возбудителя до сегодняшнего дня остается неясным. Что касается иксодовых клещей, то утверждения о гиперпаразитической передаче возбудителей (вирус клещевого энцефалита и *Borrelia burgdorferi* s. l.) у таежного клеща *Ixodes persulcatus* основаны не на результатах экспериментальной проверки, а лишь на убеждении авторов в том, что такая передача возможна.