Conspecific hyperparasitism in the *Hyalomma excavatum* tick and considerations on the biological and epidemiological implications of this phenomenon

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**Abstract**

**Objective.** This study presents for the first time a case of *Hyalomma excavatum* hyperparasitism and an analysis of this phenomenon in terms of its potential role in the biology of ticks and epidemiology of tick-borne diseases.

**Materials and method.** Two partially engorged *H. excavatum* females, one fully engorged female, and 5 males were collected from a naïve rabbit and placed together in a rearing chamber at a temperature of 25 °C and 75% humidity.

**Results.** 3–4 days after tick detachment from the host’s skin, one partially engorged *H. excavatum* female was observed attached to the idiosoma of the fully engorged conspecific female.

**Conclusions.** This study and observations of other authors confirm that partially engorged ixodid ticks can re-infest the host, and even co-feeding fully engorged ticks in order to collect the blood meal that is indispensable for important physiological processes. However, inefficient feeding of a partially engorged female on another conspecific female may reduce its reproductive performance and disturb the development of eggs and larvae. It seems that parasitism of a tick on another conspecific specimen, when at least one of them is infected by a microorganism, may be a yet poorly explored route of transmission of pathogens or symbionts between the ticks. Initiation of feeding by a hungry or partially engorged tick on a fully engorged specimen is an attempt to obtain food in the drastic conditions of the absence of a target host. Tick hyperparasitism with concurrent pathogen transmission can contribute to the genospecific diversity of pathogens in vectors and hosts.

**Key words**

ticks, *Hyalomma excavatum*, hyperparasitism, transmission of pathogens, tick feeding

**INTRODUCTION**

Ticks have a remarkable ability to adapt to various environments in the globally changing geoclimatic conditions, which contributes to the expansion of their distribution range. The increasing occurrence of ticks is accompanied by a growing risk to human and animal health posed by tick-borne diseases [1] and, hence, greater economic losses and costs [2, 3, 4]. Therefore, investigation of the biology of ticks and transmission routes of tick-borne pathogens is gaining importance.

Ticks are blood-ingesting parasites of terrestrial vertebrates, including humans. Ingestion of a blood meal by consecutive developmental stages is a prerequisite for tick survival and further development. The major mode of blood collection by ticks involves questing for a host, followed by successful feeding. Ticks are distinguished from other blood-ingesting arthropods by a variety of bioactive compounds secreted with saliva during feeding, which facilitate ingestion of a qualitatively and quantitatively sufficient meal during short- (Argasidae nymphs and adults) and long-term (Ixodidae) feeding [5], and ensure effective pathogen transmission [6].

Besides infesting their vertebrate hosts in order to collect blood, hungry ticks can also attack engorged conspecific or interspecific specimens. This phenomenon, called hyperparasitism, was described in ticks already at the end of the 19th century by Barber [7], who found an *Amblyomma variegatum* male (identified by the author as *Hyalomma venustum*) parasitizing a female from the same species. In the family Argasidae, hyperparasitism was noted mainly in representatives of the genus *Ornithodoros*. In turn, in the family Ixodidae, the phenomenon was reported from several species of the genus *Ixodes* (prostriata ticks), as well as genera *Amblyomma*, *Aponomma*, *Rhipicephalus* (*Boophilus*), *Dermacentor*, *Hyalomma*, and *Rhipicephalus* (metastriata ticks) (Tab. 1).

Since many viruses, bacteria, protozoa, and even some microfilaria, are transmitted with tick saliva secreted during the feeding process [1, 3, 8], it seems possible that parasitism of one tick on another may play a role in the spread of pathogens in the environment. The fact that conspecific...
### Table 1. Reports about cases of conspecific and interspecific hyperparasitism in ticks (Ixodidae)

<table>
<thead>
<tr>
<th>Hyperparasitic species and degree of engorgement</th>
<th>Host species and degree of engorgement</th>
<th>Distribution of tick species/habitat</th>
<th>Main animal hosts</th>
<th>References</th>
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<tbody>
<tr>
<td><strong>Conspecific hyperparasitism</strong></td>
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<tr>
<td>Argasidae ticks</td>
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<tr>
<td>Ornithodoros turicata(^1) unengorged female</td>
<td>Ornithodoros turicata(^1) fully engaged female</td>
<td>Southern part of North America, from Kansas south to central Mexico, with a disjunct population in Florida/ caves and ground squirrel or prairie dog burrows</td>
<td>Mammals, e.g. rodents that live in burrows, domestic pigs, cattle and other livestock; birds, e.g. owls; reptiles, e.g. snakes; tortoises (A, I); Wood according to [28]</td>
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<tr>
<td>Ornithodoros turicata(^2) (former Ornithodoros turicata americanus)</td>
<td>Ornithodoros turicata(^2) fully engaged male</td>
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<tr>
<td>Ornithodoros turicata(^3) starved female</td>
<td>Ornithodoros turicata(^3) fully engaged male</td>
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<td>Francis 1938 according to [28]</td>
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<tr>
<td>Ornithodoros turicata(^4) unfed fourth stage nymph</td>
<td>Ornithodoros turicata engorged nymph</td>
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<td>Francis 1938 according to [28]</td>
</tr>
<tr>
<td>Ornithodoros parkeri(^1) unengorged last nymphal stage</td>
<td>Ornithodoros parkeri(^1) fully engorged last nymphal stage</td>
<td>Southern USA and Latin America/ various ecological habitats in caves and burrows of hosts</td>
<td>Mammals, e.g. ground squirrels and prairie dogs (A, I)</td>
<td>[66]</td>
</tr>
<tr>
<td>Ornithodoros parkeri(^2) unengorged males</td>
<td>Ornithodoros parkeri(^2) fully engaged female</td>
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<td>[69]</td>
</tr>
<tr>
<td>Ornithodoros erraticus(^1) males and nymphs that produced males</td>
<td>Ornithodoros erraticus(^1) females and nymphs that produced females</td>
<td>North and East Africa, Near East, South-Eastern Europe/ burrows of pig pens or other habitats of hosts</td>
<td>Mammals, e.g. pigs, bovine, sheep, rodent, and rarely also birds (A, I)</td>
<td>[50]</td>
</tr>
<tr>
<td>Ornithodoros tartakowskyi(^5)</td>
<td>Ornithodoros tartakowskyi(^5)</td>
<td>Central Asia/ burrows of various rodents</td>
<td>Mammals: rodent species, but primarily the great gerbil, Rhombomys opimus (A, I)</td>
<td>[49]</td>
</tr>
<tr>
<td>Ornithodoros (Alectorobius) puertoricensis(^6)</td>
<td>Ornithodoros (Alectorobius) puertoricensis(^6)</td>
<td>Central Asia/ burrows of various rodents</td>
<td>Reptiles (A, I)</td>
<td>[8]</td>
</tr>
<tr>
<td><strong>Ixodidae ticks (Prostriata ticks)</strong></td>
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<tr>
<td>Ixodes holocyclus(^7) males</td>
<td>Ixodes holocyclus engorged females</td>
<td>Australia, mainly along coastal eastern area/ areas of high rainfall, e.g. wet sclerophyll forest and temperate rainforest</td>
<td>Small mammals, birds; sometimes reptiles (I); mammals, mainly carnivores and ungulates (A, I)</td>
<td>[9]</td>
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<tr>
<td>Ixodes holocyclus(^8) male</td>
<td>Ixodes holocyclus(^8) female</td>
<td></td>
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<td>[29]</td>
</tr>
<tr>
<td>Ixodes pilosus(^9) males</td>
<td>Ixodes pilosus(^9) females</td>
<td>Africa – tropical part/bush, humid habitats</td>
<td>Mammals, mainly carnivores and ungulates (A, I)</td>
<td>[30]</td>
</tr>
<tr>
<td>Ixodes trianguliceps(^10) males</td>
<td>Ixodes trianguliceps(^10) female</td>
<td>Euroasia/forests, hedgerows and heaths, open areas</td>
<td>Mammals, mainly insectivores and rodents</td>
<td>[31]</td>
</tr>
<tr>
<td>Ixodes (Afriodes) moriel(^11) males</td>
<td>Ixodes (Afriodes) moriel(^11) females</td>
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<td>[32]</td>
</tr>
<tr>
<td>Ixodes persulcatus(^12) males</td>
<td>Ixodes persulcatus(^12) females</td>
<td>Euroasia, from Nord-Eastern Europe through Central and Northern Asia to the Peoples Republic of China, Taiwan and North Korea, and northern Japan/ usually mixed deciduous-coniferous forests, taiga Holarctic region, mainly northern latitudes or mountain regions of southern latitudes in North America, also Japan, and Eastern Russia/ cool, moist habitats, including forests (particularly coniferous tracts), and along the shores of rivers. Rarely found outside the nest of its host.</td>
<td>Small and medium-sized mammals, birds, and reptiles (I); Medium-sized and large mammals, mainly wild and domestic ungulates, hares and dogs (A)</td>
<td>[70]</td>
</tr>
<tr>
<td>Ixodes angustus(^13) male</td>
<td>Ixodes angustus(^13) female</td>
<td></td>
<td></td>
<td>[73]</td>
</tr>
<tr>
<td><strong>Ixodidae ticks (Metastriata ticks)</strong></td>
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</tr>
<tr>
<td>Amblyomma variegatum(^14) male [formerly Hyalomma venustum]</td>
<td>Amblyomma variegatum(^14) engaged female</td>
<td>West-Central and Central Africa, Asia (Southern Arabia and several islands in the Indian Ocean); several islands in the ntic Ocean and Caribbean/ Savannah</td>
<td>Small mammals, ground-feeding birds, and reptiles (I); livestock, camels, antelope, and other wildlife ungulates (A)</td>
<td>[7]</td>
</tr>
<tr>
<td>Rhizophagus (Boophilus) annulatus(^15) unengorged female [formerly Boophilus annulatus]</td>
<td>Rhizophagus (Boophilus) annulatus(^15) (sex is unknown) [former Boophilus annulatus]</td>
<td>Africa, America, Asia and Australia, tropical and subtropical regions/ areas with canopyed mesquite and mixed brush vegetation</td>
<td>Mammals, mainly undulates (cattle, buffalo, bison and cervids, e.g. deer, antelopes, etc.)</td>
<td>[71]</td>
</tr>
</tbody>
</table>
and interspecific tick contacts have been observed not only in the laboratory but also in nature, prompts consideration of this route of transmission of pathogenic and symbiotic microorganisms among ticks [9].

This current study presents an interesting case of Hyalomma excavatum female parasitism on another conspecific female, and analyses the biological and epidemiological implications of tick hyperparasitism.

The H. excavatum tick is widespread in the Mediterranean region as well as steppe areas of North Africa and South Asia [10]. However, the predicted changes in temperature and precipitation rates will alter the distribution of various species, including H. excavatum, which differ in their degree of engorgement [11].

Adult stages infest wild and domestic animals, mainly buffalo, cattle, sheep, goats, camels, horses, and donkeys [12, 13], but can also attack humans [14, 15]. Larvae and nymphs parasitize hares, hedgehogs, and rodents [10].

Since this tick was previously identified as Hyalomma anatolicum and can still be mistaken for this species due to the high morphological similarity, the competence of H. excavatum to transmit tick-borne pathogens is not known. Theileria buffeli/orientalis, Babesia spp., Anaplasma/Ehrlichia [16], Coxiella burnetii [17, 18], Spotted Fever Group Rickettsiae [19, 20], and Crimean-Congo Haemorrhagic Fever Virus (CCHFV) [21] were detected in H. excavatum removed from animals. CCHFV is spread in 30 countries and infections with this virus have a fatal outcome in as many as 50% of cases in humans [22]. Furthermore, Borrelia burgdorferi sensu lato and Rickettsia aeschlimannii were isolated from H. excavatum ticks collected from patients’ skin [23].

To the best of the authors’ knowledge, to date hyperparasitism has not been described in H. excavatum. In the available literature, only two publications were found on hyperparasitic ticks from the genus Hyalomma. Both papers focused on the same species, i.e. a H. detritum tick foraging on another conspecific specimen. An unengorged Hyalomma mauritanicum nymph (at present H. detritum) attached to an engorged nymph was found by Sergent [24] during investigations of the foraging of these ticks on a calf, and a H. detritum male attached to an engorged female of this species was observed by Usakov [25].

<table>
<thead>
<tr>
<th>Hyperparasitic specimen and degree of engorgement</th>
<th>Host specimen and degree of engorgement</th>
<th>Distribution of tick species/habitat</th>
<th>Main animal hosts</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Rhipicephalus (Boophilus) annulatus</em> unengorged male</td>
<td><em>Rhipicephalus (Boophilus) annulatus</em> (Margaropus annulatus)</td>
<td>Central and Southern Asia, Near East; Southern Europe; North-Western Africa; humid areas in steppes, deserts, and semi-deserts</td>
<td>Mammals, mainly cattle and other ungulates (A, I)</td>
<td>Hooker et al. 1912 according to [28]</td>
</tr>
<tr>
<td><em>Rhipicephalus haemaphysaloides pilans</em> partially engorged female</td>
<td><em>Rhipicephalus (Boophilus) microplus</em> fully engorged female</td>
<td>R. haemaphysaloides: South-East Asia (Nepal, Burma (Myanmar), India, Taiwan, Sri Lanka, China, Indonesia, Thailand, Vietnam)</td>
<td>R. microplus: as mentioned above</td>
<td>[28]</td>
</tr>
<tr>
<td><em>Amblyomma fuscolineatum</em> two males</td>
<td><em>Amblyomma fuscolineatum</em> engorged female (formerly <em>Aponomma crusipes</em>, <em>Aponomma fuscolineatum</em>)</td>
<td>South and Central America (Argentina to Mexico, including the Caribbean Islands) and southern part of Florida / savannah, forest savannah and rainforest habitats</td>
<td>Small mammals, mainly rodents that live in burrows, and birds (I); large mammals (A)</td>
<td>[27]</td>
</tr>
<tr>
<td><em>Hyalomma excavatum</em> partially engorged female</td>
<td><em>Hyalomma excavatum</em> fully engorged female</td>
<td>Central and South-West Asia; Middle and Near East; South-Eastern Europe and southern Africa/warm arid and semi-arid habitats</td>
<td>Mammals, mainly ungulates and carnivores (A, I)</td>
<td>Buczek et al. present study</td>
</tr>
<tr>
<td><em>Ixodes</em> sp. male</td>
<td><em>Ixodes vespertilionis</em> female (formerly <em>Aponomma vespertilionis</em> Schulze)</td>
<td><em>Ixodes</em> sp. as mentioned above</td>
<td>B. a. Mammals: e.g. wombats</td>
<td>[9]</td>
</tr>
<tr>
<td><em>Ixodes</em> sp. male</td>
<td><em>Rhipicephalus (Boophilus) microplus</em> female</td>
<td><em>R. microplus</em> as mentioned above</td>
<td><em>R. microplus</em>: mammals, mainly ungulates and carnivores (A, I)</td>
<td>[9]</td>
</tr>
</tbody>
</table>
Tick hyperparasitism may not be as rare in nature as suggested by data provided by some authors [24, 28]. This is indicated by multiple traces of tick bites (scars) that were found on the idiosoma of engorged specimens representing prostriata ticks [9, 29–33], and metastriata ticks [27] that were close to other hungry or partially engorged conspecific specimens. In the opinion of the authors of the current study, the dark-coloured permanent scars on the tick idiosoma and some exoskeletal anomalies in specimens collected in nature [34–37] may have been caused by other ticks that parasitized these specimens, or their earlier stages, i.e. nymphs (own observations, unpublished data).

As many as 27.8% of 162 Ixodes trianguliceps females examined were found to have been attacked by conspecific males. The number of scars on the female bodies increased with the higher degree of engorgement. Scars were noted in 41% of partially fed females. The female genital opening was the most common site of attachment of males [31].

One specimen can be parasitized by several other individuals. In Ixodes (Afxirodes) moreli females, 1–9 scars were noted. One female of this species was simultaneously parasitized by up to 5 males. Approximately 32.4% of I. (A.) moreli males attached to females [32], which may indicate a high frequency of this phenomenon.

Scars left by male tick bites on the bodies of Ixodes persulcatus females collected in nature were observed more frequently during hotter seasons than during seasons with moderate temperatures [33].

In certain circumstances, hyperparasitism can be the only way to obtain food by hungry tick specimens. In natural conditions, questing for a host by some species may be difficult, as they react to stimuli emitted by the host when present at a short distance from the source, e.g. Argas reflexus responds at a distance of a few cm from the host [38]. Moreover, non-nidicolous ticks with an ambush host-seeking life strategy, e.g. Dermacentor reticulatus, Ixodes scapularis, or Ixodes ricinus, cover short distances.

Over 7 weeks, D. reticulatus females and males at an average temperature of 18.3°C and 56.7% humidity in the habitat, moved horizontally over a distance of only 66.35±100 cm...
Felis catus s.l. [57] or Crimean-Congo
[33]. Furthermore, and [45], and
(Tab. 1). Attachment of a hungry or partially engorged
consequently, the number of offspring.
the amount of blood ingested by
hungry and partially engorged ticks can be caused by the
in animals [47]. In natural conditions, the detachment of
same host [44–46], and some chemicals used for tick control
in previous tick infestations, other species co-feeding on the
nutritional status of the host, host immunisation acquired
of time and effectiveness of the feeding [43]. The weight of
changes in the quality of ingested blood meal.
the components of tick saliva introduced during feeding and
from the host may be caused by a high concentration of
Detachment of partially engorged
ricinus
Higher than that of hungry ticks; it increases 190-fold in
instances by flagging methods (unpublished data). This means,
erythema migrans (unpublished data). In the current study,
spirochetes, which was manifested by the development of
erthyme migrants (unpublished data). In the current study,
partially engorged nymphs of I. ricinus were sampled several
times by flagging methods (unpublished data). This means,
that ticks need to take some critical portion of blood before
metamorphosis (unpublished data).
Earlier, Anastos [28] described a partially engorged
Rhipicephalus haemaphysaloides paulopunctatus female attached
to a fully engorged male from a different species, i.e. Rhipicephalus (Boophilus) microplus. The specimens were
found among several thousand ticks collected from domestic
animals in the Dutch East Indies (today Indonesia).
Hard ticks usually attach to their host and detach only
after ingestion of the maximum portion of a blood meal.
The body weight of fully engorged specimens is several-fold
higher than that of hungry ticks; it increases 190-fold in I.
ricinus females, and 88-fold in D. reticulatus females [43].
Detachment of partially engorged H. excavatum females
from the host may be caused by a high concentration of
ticks, which triggers a strong local reaction in rabbit skin to
the components of tick saliva introduced during feeding and
changes in the quality of ingested blood meal.
The greater the intensity of tick invasion, the greater the
changes in the parasitic phase parameters, such as the length
of time and effectiveness of the feeding [43]. The weight of
engorged females can be influenced by other factors, e.g.
nutritional status of the host, host immunisation acquired
in previous tick infestations, other species co-feeding on the
same host [44–46], and some chemicals used for tick control
in animals [47]. In natural conditions, the detachment of
hungry and partially engorged ticks can be caused by the
death of the host [48]. The amount of blood ingested by
a female determines the number of oviposited eggs and,
consequently, the number of offspring.
Different tick developmental stages, such as adult stages
(males and females) and nymphs, can be hyperparasites
(Tab. 1). Attachment of a hungry or partially engorged
tick to an engorged specimen may be a desperate way of
obtaining food in the absence of a target host, or a way of
replenishment of food reserves by specimens detached from
host skin before ingestion of a full portion of blood. Feeding,
which involves alternate insertion of saliva and sucking host
blood portions, promotes transmission of microorganisms
from an infected to non-infected specimen, or even an
exchange of pathogens between two infected ticks. During
host blood ingestion, microorganisms present in the infected
tick multiply intensively and spread with the haemolymph
around the organism [49]. In a systemic infection, pathogens
are present in many tick organs which can be penetrated by
the mouthparts of another specimen. The long mouthparts
of species from the genera Ixodes, Aponomma, Amblyomma,
and Hyalomma are able to reach deep into the tick’s body.
Similarly, for example, Reháček [50] wrote that during the
generalized form of tick infection, rickettsiae were registered
in haemolymph, intestine, salivary glands, Malpighi glands,
ovoaries, or testes of ticks, i.e. in the whole body of the tick.
Conspecific hyperparasitism may contribute to the spread
of pathogens within a tick population in natural conditions.
This is suggested by the results of previous laboratory
investigations confirming transmission of Dipetalonema vitaeae in Ornithodoros tartakovskyi [51], Borrelia crocidurae in
Ornithodoros erraticus [52], and Borrelia burgdorferi s.l. spirochetes in Ixodes persulcatus [33]. Furthermore,
symbiotic bacteria or fungi whose biological role is not fully
known can be transmitted during physical contact between
ticks [53–55]. Many symbiotic microorganisms that turned
out to be human and animal pathogens have been identified
in ticks [56]. It seems that tick hyperparasitism can contribute
to the high genospecific diversity of some pathogens, for
instance Borrelia burgdorferi s.l. [57] or Crimean–Congo
haemorrhagic fever virus [58], as well as multiple pathogen
coinfections in ticks [59–64] and in hosts [65–67].
The current study indicates that partially engorged ixodid
ticks can re-infect a host in order to accumulate an amount
of food indispensable for their survival and further development.
Hyperparasitism may be a yet poorly known route of
microbial transmission in ticks, which may contribute to the
spread and maintenance of pathogens in nature. It is probably
responsible for the occurrence of genospecific diversity of
pathogens in ticks and their hosts. Future investigations
of the epidemiology of tick-borne diseases in humans and
animals should consider this route of pathogen transmission
and explain its role in natural conditions.

REFERENCES


