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Effect of extrinsic incubation temperature on transstadial and transovarial transmission of *Borrelia sp.* in *Ornithodoros (O.) savignyi* and infectivity to vertebrate host.

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ABSTRACT

Effects of three extrinsic incubation (EI) temperatures on vector competence of *Ornithodoros savignyi* to *Borrelia sp.* isolated from a natural population of the tick in Egypt were investigated. The EI temperature influenced the efficiency of *Borrelia sp.* transmission by the female *O. savignyi* to hamsters. An EI temperature for 27°C was optimum for successful transmission of *Borrelia sp.* where the highest infection rates (IRs) in hamsters occurred. Generally, the IRs in hamsters decreased by lowering the EI temperature to 17°C or rising it to 37°C in each of the corresponding experimental cases (number and postinfection period of the tick feeding per hamster) tested.

Ornithodoros savignyi kept at 27°C and 37°C maintained borrelial infection transstadially from nymph 1 to 7 and adults. The transstadially infected stages transmitted the spirochetes to hamsters with higher IRs at 27°C than 37°C. Transovarial transmission of *Borrelia sp.* occurred during the first and second (at higher rates) gonadotrophic cycle in the infected female ticks kept at 27°C and 37°C. However, no molting or oviposition occurred at 17°C.

Keywords: temperature, *Borrelia, Ornithodoros,* vertebrate

INTRODUCTION

Extrinsic temperature affects tick-pathogen relationships and transmission to the vertebrate host in various ways. Numerous studies have reported effects of temperature on biological and physiological processes in the vector tick (Cunliffe, 1922; Tatchell, 1964; Hafez *et al.*, 1972; Khalil, 1974 and Ouhelli *et al.*, 1987) and pathogen (Injeyan *et al.*, 1971; Young and Leitch, 1981; Lowengrub *et al.*, 1989 and Naumov *et al.*, 1998) and on the susceptibility of the tick (Dalgleish and Stewart, 1982; Shih *et al.*, 1995 and Helmy *et al.*, 2000 a, b and 2006) and vertebrate (Ochanda *et al.*, 1988; Shih, 1995; Schwan *et al.*, 1995; Young *et al.*, 2000 and Cugini *et al.*, 2003) to infection.

High temperature affects the competence of the vector ticks by affecting the persistence of the pathogen in the vector sp. of Lyme disease and relapsing fever. Shih *et al.* (1995) demonstrated that the persistence of spirochetal infection of Lyme disease *B. burgdorferi* in nymphal deer tick *Ixodes dammini* is reduced by incubation at temperature higher than 27°C for longer than two weeks and spirochetes became undetectable at four weeks thereafter. Increase of temperature more than 27°C has been found to stimulate or inhibit synthesis of certain proteins in the spirochete *B. burgdorferi* (Cluss and Boothby, 1990; Schwan *et al.*, 1995; Obonyo *et al.*, 1999 and Ramamoorthy and Scholl, 2001). In addition, Lyme disease spirochete, *B.*

burgdorferi, did not grow when cultured at temperature in excess of 37°C (Barbour, 1984). In contrast to findings of Shih *et al,*. 1995, the increase of the extrinsic incubation (EI) temperature of rearing the female *O. Savignyi* infected with *Borrelia sp.* (mostly of relapsing fever) from 17°C to 27°C and 37°C increased the mean number (no.), infection rate (IR) and prolonged persistence of the spirochetes in different organs of the vector tick throughout 90 days after the infective blood meal (Helmy *et al.*, 2009).

The sand tampan, *O. (O.) savignyi*, collected from different localities in Egypt has been found to be naturally infected with *Borrelia sp.* (Shanbaky and Helmy, 2000 and Helmy, 2000b) and is capable of experimentally acquiring and maintaining the spirochetal infection by transstadial and transovarial transmission in the tick population and transmitting it to the vertebrate host (Shanbaky and Helmy, 2000). These three biological processes are important criteria which must be considered in evaluating the efficiency of the tick as a reservoir for *Borrelia* and its competence as a vector of a disease (Hoogstraal, 1985).

The present work investigates the effect of three extrinsic incubation temperatures (17°C, 27°C and 37°C) on the ability of female *O. savignyi* to maintain the infection with *Borrelia sp.* within developing life stages and generations by transstadial transfer and transovarial transmission, respectively. Also, the ability of the tick to transmit infection to vertebrate host at each tested temperature at different intervals following the infective blood meal.

MATERIALS AND METHODS

Tick colonies:

Ornithodoros (O.) savignyi (Audouin), Argasidae, was collected from sand where cattle rest at Dahshore, Giza governorate, Egypt. Field collected uninfected adults were used to start uninfected colonies and were maintained at 27±1°C, 75% RH and 16 hrs light day. Ticks were fed on hamster, *Mesocricetus auratus*, as described by Helmy (2000). Infected colonies started by feeding clean ticks on laboratory infected hamsters which had been fed upon by naturally infected *O. savignyi*. Infected colonies were kept at three different temperatures of 17°C, 27°C and 37°C.

Detection of spirochetes:

Blood smears from tick and hamster (Helmy, 2000) were stained with Fontana stain (Conn *et al.*, 1960) or with direct (DI) (Piesman *et al.*, 1986) and indirect immunofluorescence (IDF) technique (Lane and Manweiler, 1988), respectively. For IDF, antigen slides were prepared from spirochetes obtained from the tick and cultured in modified kelly's medium (Barbour *et al.*, 1983).

Transstadial transfer of *Borrelia sp.* and transmission to uninfected hamsters:

About 300 uninfected nymph (N_1) *O. savignyi* were fed on hamsters infected with *Borrelia sp.* The engorged N_1 were collected and a sample of ten ticks were examined individually 1 hr after infective blood meal. Each N_1 was separately crushed in saline, stained with Fontana stain and/or DF technique and examined microscopically to ensure that spirochetes had been obtained with the infective blood meal. After the remaining N_1 had molted to N_2, 10-20 infected N_2 were fed on each of five uninfected hamsters. The hamster blood was examined for spirochetes 4-7 days later. This step was repeated for each subsequent nymphal instar and adult stages. Samples of ten ticks of each subsequent instar and adult stage were tested for spirochetes. A

drop of hemolymph (HL) was collected from broken tarsus of each tick after feeding and smeared and stained with Fontana stain and /or DF technique and examined microscopically for spirochetes transstadial transfer (TST). The aforementioned steps were repeated for ticks kept at each of the three tested temperatures.

Transovarial transmission of *Borrelia sp.* in the tick:

Laboratory reared virgin uninfected females of *O. savignyi* were fed on hamsters infected with *Borrelia sp.* Each of ten infected parent females (P_1) was placed individually in polyethylene tube with an uninfected recently fed male and observed for oviposition (first gonadotrophic cycle). When eggs hatched, 10 F1 larvae from each female were examined individually for spirochetes. After 30 days following first blood meal, females were offered a second but a clean blood meal, and observed for oviposition (second gonadotrophic cycle). Transovarial transmission (Tov) and filial infection rates (IRs) were calculated for females and their larval progeny (Hoogstraal, 1985) during first and second gonadotrophic cycle. These steps were repeated for tick kept at each of the three tested temperatures.

Transmission of *Borrelia sp.* infection from tick to hamster:

After 30, 60 and 90 days post feeding infective blood meal, different numbers (1, 3, 6 and 10 ticks) of adult female *O. savignyi* infected with *Borrelia sp.* isolated from the tick natural populations were fed on each of five clean uninfected hamsters. Four to seven days post feeding the tick, blood samples from each hamster was examined for spirochetes as described before. Those steps were repeated for each of the tested three temperatures.

Statistical analysis:

The percentages of the different life stages of the tick and that of *Borrelia sp.* infected blood samples collected from the vertebrate host were determined and compared using Chi-square test with the aid of statistical Package of Social Science (SPSS) version 8.0 for Windows.

RESULTS AND DISCUSSION

Effect of EI temperature on transstadial transfer of *Borrelia sp.* in *O. savignyi* and subsequent transmission to hamster:

At 17°C N_1 failed to molt, however at 27°C and 37°C the infected N_1 molted and transmitted spirochetes to 60% and 70% of the subsequent nymphal life stage (N_2) respectively (Table 1).

Table (1): The percentage of transstadial transfer of *Borrelia sp.** infection in nymphal and adult *O. savignyi* kept at 27°C and 37°C and spirochete transmission form these stages to uninfected hamsters.

Tick life stage	% infection in tick HL		% infection in hamster	
	27°C	37°C	27°C	37°C
N_{1**}	100	100	-	-
N_2	60	70	50	30
N_3	50	60	70	40
N_4	60	70	80	50
N_5	40	50	60	40
N_6	50	60	80	50
N_7	50	60	100	60
Male	40	50	90	50
Female	60	80	100	70

**Borrelia sp.* was isolated from natural population of the tick.

***N_1* was fed on infected hamster while other stages were fed on uninfected hamster.

The IRs in HL of the following nymphal instars and adults fluctuated between 40% to 60% at 27°C and 50% to 80% at 37°C with no significant differences among them at each temperature ($P > 0.05$) or between each life stage at 27°C and 37°C. Spirochetes were transmitted to hamsters which were fed upon by the transstadially infected life stages (N_2 – N_7 and adults). The IRs in the hamsters (Table 1) ranged from 50% to 100% and 50% to 70% at 27°C and 37°C, respectively with no significant

difference among the hamsters (P > 0.05) at each temperature. However, there was a significant decrease (P < 0.05) of IRs with *Borrelia sp.* in hamsters fed upon by each of the different transstadially infected life stages kept at 37°C less than at 27°C.

These results showed that with the exception of 17°C (which prevented molting), the two other tested temperatures (27°C and 37°C) seemed to have no significant effect on TST of *Borrelia sp.* in *O. savignyi*. However, results of *Borrelia sp.* transmission to hamster were in accordance of those by Shih *et al.* (1995) on *b. burgdorferi* where they found that incubation of *I. dammini* nymphs at temperature higher than 27°C for two weeks or longer were not permissive for the transmission of the spirochetes to mice.

Effect of EI temperature on transovarial transmission of *Borrelia sp.* in *O. savignyi*:

Female *O. savignyi* failed to oviposit at 17°C, however 60% and 70% of infected females kept at 27°C and 37°C transmitted *Borrelia sp.* transovarially to their eggs and about 15% and 23% of the emerged larvae were infected with *Borrelia* during the first gonadotrophic cycle (Fig. 1).

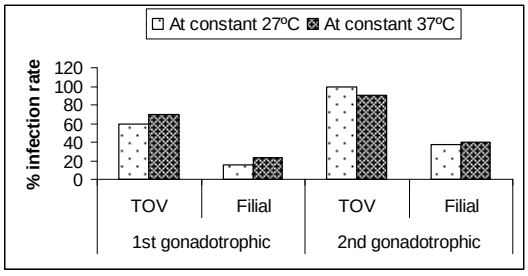

Fig. 1: Transovarial and filial infection rates of *Borrelia* sp. in *O. savignyi* during the 1st & gonadotrophic cycle of the parent female kept at 27 and 37ºC

A second but a clean blood meal induced higher (P < 0.05) transovarial (100% and 90%) and filial (37.5% and 40%) IRs in the same females during the second gonadotrophic cycle than that in the first gonadotrophic cycle at the two tested temperatures. There was no significant difference (P > 0.05) between each of the percent of transovarial transmission or filial IRs of F_1 larvae of *O. savignyi* when parent females were kept at 27°C and 37°C during each of the first and second gonadotrophic cycle.

Similar data were obtained by Gaber *et al.* (1984) and who found that infected female *O. erraticus* transmitted spirochetes, *B. crocidurae* transovarially to their eggs and F_1 larvae in higher percentages during the second gonadotrophic cycle than the first cycle. These findings suggested that spirochetes number progressively increases during the successive egg developmental cycles of the tick.

The dispersal of borrelial infection in various organs of *O. savignyi* (Helmy *et al.,* 2009) and ability of the tick to transmit the spirochete transovarially and transstadially (at 27°C and 37°C and to transmit the spirochete while feeding on uninfected hamsters at the temperatures tested in the present work prove the capacity of this tick species to serve as vector and reservoir (Hoogstraal, 1985) of *Borrelia sp.* in Egypt. Furthermore, this suggestion is supported by the fact that the three tested temperatures are most prevailing temperatures during the year (Helmy 2000b) in Giza governorate, Egypt where the tick was collected. In accordance with the present findings the field data of Helmy (2000b) in the same locality where high prevalence of *Borrelia sp.* infection was found in field collected nymphs and adults of *O. savignyi* during summer months while low infection rates were found in winter months during which the highest and lowest temperatures were recorded, respectively.

Effect of EI temperature on tick transmission of *Borrelia sp.* to hamsters:

Adult female *O. savignyi* infected with *Borrelia sp.* transmitted the infection to hamsters fed upon at the three EI temperatures tested in the present study (Table 2).

Table (2): Effect of number and post infection time of female *O. savignyi* kept at three different temperatures on transmission of *Borrelia sp.* to uninfected hamsters.

Infected ticks No./hamster	Temp.	% of infected hamsters by feeding of ticks			
Days after infective meal at different temp.		1	3	6	10
30	17°C	0	0	20	60
	27°C	60	80	100	100
	37°C	20	40	60	100
60	17°C	0	0	0	20
	27°C	40	60	80	100
	37°C	0	20	40	60
90	17°C	0	0	0	0
	27°C	0	20	40	60
	37°C	0	20	20	40

At each temperature, *Borrelia* IRs in hamsters gradually increased ($P < 0.05$) by increasing the number of infected ticks feeding on each hamster from six to ten and from one to ten at 17°C and 27°C or 37°C, respectively. Generally, IRs in hamsters gradually decreased ($P < 0.05$) by increasing the time passed after the ticks had the infective blood meal from 30 to 90 days (Table 2).

The present results agree with those of Piesman and Sinsky (1988) who found that efficiency of transmitting *B. burgdorferi* in *I. scapularis* had increased by increasing the number of feeding infected ticks per host animal. Also Lane *et al.* (1994) found that the plasma antibody titer to *B. burgdorferi* increased from 1 : 128 to 1 : 256 in mice exposed to feeding by one or two infected nymphs, respectively, of *I. pacificus*. Varma (1956) found that nymphs and young adults of *O. turicata* transmitted the infection with *B. turicata* better than old adults. He attributed this to a decrease in intensity or death of spirochetes in the salivary glands of old adults. Nikitina (1965) stated that F_1 larvae of infected female *A. persicus* rarely transmitted *B. anserina* because there were few spirochetes in the larvae. She believed that after larvae had fed and digested the meal, spirochetes multiplied and their numbers in nymphs increased to a point of causing infection in fowl hosts. Crippa *et al.* (2002) demonstrated that transmission of *B. burgdorferi* from *I. ricinus* nymphs to mouse increased with duration of tick attachment. Balashov (1972) suggested that spirochetes within the tick body need to reach a threshold level to be able to infect vertebrate.

At each temperature tested in the present work, the gradual decrease of IRs in hamsters exposed to feeding of infected ticks after different time intervals following tick infective blood meal (30 to 90 days) suggested a decrease of efficiency in transmitting *Borrelia sp.* from *O. savignyi* to hamster as the post infection period of the tick was prolonged. This decrease might be attributed to the general decrease of IRs and no. of spirochetes or their disappearance (Helmy *et al.*, 2009) from the tick organs (Helmy *et al.*, 2009) during the delayed intervals of tick post infection (60 – 90 days); specially in organs responsible for transmitting infection to vertebrate host (salivary glands and coxal organ).

In the present study, EI temperature greatly influenced the efficiency of female *O. savignyi* in transmitting *Borrelia sp.* to hamster. Rearing the tick at 27°C was optimum for successful transmission of *Borrelia sp.* from the tick to hamster. At this temperature the highest IRs in hamsters occurred (Table 2). However, IRs in hamsters generally decreased ($P < 0.05$) by lowering EI temperature to 17°C or rising it to 37°C in each of the corresponding experimental cases (number and post

infection day of tick feeding per hamster) tested. Shih *et al.* (1995) suggested a maximal threshold temperature of EI to regulate susceptibility of the tick to infection and development of *B. burgdorferi* and to increase competence of the vector tick, *I. dammini*, as a host for Lyme disease spirochetes. They concluded that EI temperatures in excess of 27°C are not permissive for transmission of *B. burgdorferi* to mice and pointed at disappearance of spirochetes from all nymphs at 37°C as a possible reason of the tick failure in transmitting the spirochete to mice at this temperature. However, findings on effects of EI temperature on borrelial infection in organs of *O. savignyi* (Helmy *et al.*, 2009) suggest that a decrease of IRs, no. and disappearance of spirochetes in organs of female *O. savignyi* might be considered as a possible reason of the decreased success of *Borrelia* transmission to hamsters at 17°C but not at 37°C as observed in the present study. Localization study of *Borrelia sp.* in various organs of female *O. savignyi* showed no significant difference between IRs and no. of spirochetes in each organ (including salivary glands and coxal organ) on the corresponding post infection days at 27°C and 37°C throughout a period of 90 days after the tick infective meal (Helmy *et al.*, 2009). Therefore, the observed decrease of *Borrelia sp.* transmission to hamster at 37°C less than 27°C might be attributed to a probable change or interference with production of borrelial protein associated with transmission of spirochetes to the vertebrate host. Reciprocal expression of two main outer surface (lipo) proteins OspA and OspC occurs as *B. burgdorferi* is transmitted from its vector tick, *I. scapularis*, into mammalian host (Schwan *et al.*, 1995). It was suggested that synthesis of OspC by spirochete during tick feeding may play an essential role in the capacity of *B. burgdorferi* to successfully infect mammalian host including human. A shift to higher temperatures (34°C and 37°C) appears to be one important stimulus for triggering the induction of OspC (Schwan *et al.,* 1995 and Yang *et al,.* 2000).

Contraversy between effects of temperature on transmission of spirochetes to vertebrate host might be attributed to differences between tick and borreliae species used in the aforementioned studies. For better understanding of the effects of temperature on transmission of *Borrelia* from ticks to vertebrate hosts further investigations are required on the outer surface and other proteins of borreliae not only in argasid ticks but also in ixodids other than *I. scapularis*.

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ARABIC SUMMARY

تأثير درجة حرارة البيئة المحيطة على نقل العدوى *بالبورليا* من طور الى طور ومن جيل الى جيل فى قراد *الأورنيثودوروس سافيجنياى* وعلى كفائتة فى نقل العدوى لعوائلة من الفقاريات

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2- مركز الأبحاث والدراسات والتدريب لناقلات الأمراض – كلية العلوم – جامعة عين شمس

تم دراسة تأثير ثلاث درجات حرارة بالبيئة المحيطة على كفاءة القراد *الأورنيثودوروس سافيجنياى* فى نقل *البورليا* (المعزولة من مجموعات القراد المصابة فى الطبيعة بمصر) وقد وجد أن درجة حرارة البيئة المحيطة تؤثر على نقل العدوى *بالبورليا* من أنثى القراد الى الهامستر (حيوان التجارب) وقد اتضح أن درجة حرارة 27ºم بالبيئة المحيطة للقراد أكثر كفاءه فى نقل العدوى *بالبورليا* فى الهامستر حيث سجلت أعلى معدلات الأصابة. وعموماً وجد أن معدلات الأصابة قى الهامستر تنخفض بانخفاض درجة حرارة بالبيئة المحيطة الى 17ºم أو أرتفاعها الى 37ºم فى جميع التجارب التى أجريت (من حيث عدد القراد ومدة إصابتة *بالبورليا* لكل هامستر).

وقد أوضحت الدراسة أن العدوى تنتقل من طور الى طور فى الحوريات من الأول الى السابع وكذلك الطور البالغ لقراد *الأنيثودوروس سافيجنياى* المتواجد فى درجة حرارة 27ºم و 37ºم وقد نقلت الأطور المصابة العدوى للهامستر بدرجة أعلى عند حرارة 27ºم منها عند 37ºم . كما أن نقل *البورليا* من جيل إلى جيل حدث خلال فترة التغذية المبيضية الأولى وبدرجة أعلى فى الفترة المبيضة الثانية للإناث المعدية المتواجدة فى درجة حرارة 27ºم و 37ºم .أما فى درجة حرارة 17ºم فم يحدث إنسلاخ للقراد أو وضع الأناث للبيض.