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Laboratory life cycle of *Ornithodoros puertoricensis* (Ixodida: Argasidae) collected in the Colombian Caribbean

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Abstract
Three studies on the biology of *Ornithodoros puertoricensis* are available in the literature, using different hosts and incubation temperatures. In a previous study, we identified *O. puertoricensis* in the Colombian Caribbean. The aim of the present work was to analyze life cycle data along one generation from these specimens under laboratory conditions. Eggs of *O. puertoricensis* were collected in between fragments of bahareque material in a rural dwelling in the municipality of Planeta Rica (Córdoba Department, Colombia), and transported to the laboratory. All post-egg stages (i.e., larvae, nymphs, and adults) were incubated at 27 °C and 85% RH and fed on laboratory mice (*Mus musculus*). Sixteen engorged larvae were obtained to start a laboratory colony. Average feeding period for larvae was 4.6 days (4–5). The first nymphal instar (N1) did not require feeding and the subsequent nymphal stages (N2, N3, and N4) and adults had feeding periods ranging from 55 to 75 min. Average pre-molting period in nymphs was 15 days (10–21). Most of the N3 molted to males and all N4 molted to females. Two gonotrophic cycles were recorded: the first had a preoviposition period of 12 days (7–18) and produced 190 eggs (171–223), the second lasted 6.6 days (6–7) and produced 146 eggs (104–201). The mean life cycle duration (from parental eggs to F1 eggs) was 70.7 days (58.7–82.7) without fasting periods. The collected data agree with previous studies even with differences in hosts and maintenance conditions.

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Introduction

The Argasidae family comprises about 220 species globally (Dantas-Torres et al. 2019; Muñoz-Leal et al. 2021). Among these, the genus *Ornithodoros* includes 122 species, 62 of them occurring in the Neotropical Region (Venzal et al. 2015; Muñoz-Leal et al. 2016, 2021). *Ornithodoros* ticks are nidicolous parasites of animals that live in burrows and caves, and are well adapted to starve in arid environments for prolonged periods (Hoogstraal 1985; Oliver 1989; Nava et al. 2017). They feed in a wide range of vertebrate hosts including humans, a fact that renders these parasites of public health concern (Gray et al. 2014; Bermúdez et al. 2017). Species of the genus *Ornithodoros* can cause inflammatory skin reactions in the host and systemic disorders (Mans et al. 2004). Moreover, they are vectors of relapsing fever group borreliae (RFGB) (Dworkin et al. 2008). An RFGB (*Borrelia puertoricensis* sp. nov.) was recently isolated from *Ornithodoros puertoricensis* in Panama (Bermúdez et al. 2021).

Ornithodoros puertoricensis was described in 1947 from specimens collected on *Rattus* spp. in Puerto Rico (Fox 1947). This species was further recorded in other Caribbean islands, such as Jamaica and Trinidad, and also in Colombia, Mexico, Nicaragua, Panama, and Venezuela (Fairchild et al. 1966; Bermúdez et al. 2015, 2017; Webb 1980; Thompson 1950; Jones et al. 1972; Kohls et al. 1965; Paternina et al. 2009). In Colombia, it has been recorded in the Departments of Cesar (Fairchild et al. 1966), Sucre (Paternina et al. 2009), Córdoba (López et al. 2021) (Colombian Caribbean Region), in the Pacific Region (Butler and Gibbs 1984) and Antioquia Department (Quintero et al. 2013, 2021; Londoño et al. 2017). Initial studies on the biological cycle of *O. puertoricensis* were published by Fox (1947) using laboratory rats (*Rattus norvegicus*) as hosts and under environmental conditions in Puerto Rico. Subsequently, Davis (1955) conducted additional biological studies using guinea pigs (*Cavia porcellus*) as vertebrate model. In a more comprehensive study, Endris et al. (1991) registered biological data at various temperatures using guinea pigs and mice (*Mus musculus*) to feed larvae and subsequent stages (i.e., nymphs and adults), respectively.

Although *O. puertoricensis* does bite humans in Colombia (López et al. 2021), few data on the distribution, biology, and transmitted pathogens are available in the country. The aim of the present work was to analyze life cycle data along one generation of *O. puertoricensis* from the Colombian Caribbean region under laboratory conditions, using mice as hosts.

Materials and methods

Origin of ticks and laboratory conditions

The ticks used in this study originated from eggs collected in December 2020 and were found together with several larvae, nymphs and adults within bahareque walls of a rural dwelling in the municipality of Planeta Rica (8°31°46"N, 75°39'51"W), Córdoba Department, northwestern Colombia (López et al. 2021). The obtained eggs and all subsequent

stages (from a single generation) were kept inside an incubator under controlled temperature (25 ± 2 °C) and humidity conditions (85 ± 1% RH).

Tick feeding

All stages (from parental larvae to F1 larvae) were fed on laboratory mice (*M. musculus*, Balb/C strain) using a standardized protocol (Veterinary Parasitology Laboratory, Faculty of Veterinary Medicine and Animal Science, National University of Colombia) previously approved by the Institutional Bioethics Committee. Animals were intraperitoneally anesthetized with a mixture of ketamine (80–90 mg/kg) and acepromazine (10–20 mg/kg) (Flecknell 2009). Larvae hatched from field-collected eggs were fed in a chamber glued onto the dorsum of the animals. The chamber was daily checked to observe and recover fully engorged specimens (Mateos-Hernández et al. 2020). Nymphs and adults were fed directly on mouse skin (Nuss et al. 2017). After feeding, larvae and nymphs were individually placed in wells of 200 µL inside an incubator, and daily inspected to record molting.

Obtained males and females were coupled 1 day before feeding on mice and subsequently housed together for an additional 7 days. Females were placed in 1 mL plastic microtubes with cotton caps until oviposition. Obtained eggs were transferred to a different plastic tube for hatching. Females were weighed before and after feeding, as well as their egg batches, with an electronic precision balance (Adam Equipment/PW 254). For an additional gonotrophic cycle, a 30-day-interval period was established for the next female feeding.

Egg production indexes (EPI) were obtained with the following formula: EPI = (weight of eggs/initial weight of engorged female) × 100 (Bennett 1974).

Results

The whole study comprised 1 year duration, from initial egg collection to the second gonotrophic cycle. In total, 36 viable eggs hatched and were used to start the laboratory colony. While larvae were feeding, six specimens got compressed in the feeding chamber edges or remained accidentally glued; in addition, 14 specimens did not attach to mice and died. Finally, a total of 16 larvae successfully engorged in around 4.6 days (4–5). Molting from larva to N1 instar lasted 4 days (4–5). The N1 instar did not require to feed and molted to N2 instar in an average of 11.6 days (10–12). In this and subsequent stages (i.e., N3 and N4) a feeding phase was required before molting, with an average feeding time of 56.2 min (28–111) (varying among nymphal instars) and an average pre-molting period of 20.8 days (16–24), as shown for each instar in Table 1.

Two out of the 16 specimens of N3 instar did not feed. From the 14 individuals that got fully engorged in this phase, 12 molted directly to adults (five females and seven males) and the remaining two required an additional nymphal instar (i.e., N4) to reach adulthood (two females). Adult feeding period lasted on average 74.8 min (20–131) (Table 1).

To observe and record reproductive data, in total five males and five females (five couples) were used; however, two of them died after feeding. The remaining couples were separated in tubes and placed inside the incubator; males remained with females for 7 days and then they were separated. Reproductive data registered along two gonotrophic cycles are summarized in Table 2. Average pre-oviposition period was 9.3 days (12 ± 5.5 and 6.6 ± 0.5 days for the first and second gonotrophic cycle, respectively). The oviposition was

Table 1 Biological parameters (mean ± SD, range in parentheses) of immature and adult stages of *Ornithodoros puertoricensis* under laboratory conditions, in this study and compared to literature data

Stage/instar	Biological parameter	F1 (This study)[a]	Fox (1947)[b]	Davis (1955)[c]	Endris et al. (1991)[d]
Larva	Feeding period (days)	4.6 ± 0.4 (4–5)	No data (ND)	5.3 ± 0.9	5.8 ± 1.5
	Pre-ecdysis period (days)	4 ± 0.2 (4–5)	3.1 ± 0.5	6.4 ± 0.9	3 ± 1.3 (2–14)
	Ecdysis	16 (100%)	ND	ND	135
N1	Pre-ecdysis period (days)	11.6 ± 0.6 (10–12)	6.8 ± 1.3	(16–31)	5.8 ± 0.9 (4–12)
	Ecdysis	16 (100%)	ND	ND	133
N2	Feeding period (min.)	51.3 ± 21.7 (19–84)	22 (14–54)	ND	ND
	Pre-ecdysis period (days)	13 ± 1 (12–15)	10.4 ± 2.5	(17–20)	7.2 ± 3 (4–37)
	Ecdysis	16 (100%)	ND	ND	131
	Molting to adult	None	ND	ND	1 female, 41 males
N3	Feeding period (min.)	78.5 ± 19.2 (41–111)	30 (16–57)	ND	ND
	Pre-ecdysis period (days)	17.7 ± 1.5 (16–21)	12.5 ± 15	(20–48)	10.3 ± 1.8 (5–17)
	Ecdysis	14 (87.5%)	ND	ND	88
	Molting to adult	5 females, 7 males	4 females, 9 males	1 female, 12 males	62 females, 25 males
N4	Feeding period (min.)	34 ± 8.4 (28–40)	38.4 (25–56)	ND	ND
	Pre-ecdysis period (days)	24 ± 0 (24)	14.3 ± 1	(23–55)	12
	Ecdysis	2 (100%)	ND	ND	1
	Molting to adult	2 females	4 females, 1 male	9 females	1 female
Adult	Feeding period (min.)	74.8 ± 31.6 (20–131)	(20–40)	ND	ND

Laboratory conditions: [a]25 °C, 85% RH, host: mouse; [b]26.9–29 °C, unknown RH, host: rat; [c]22 °C, 79% RH, host: guinea pig; [d]27 °C, 95% RH, host: guinea pig (larvae) and mouse (nymphs, adults)

Table 2 Reproductive parameters (mean ± SD, range in parentheses) of *Ornithodoros puertoricensis* females in two gonotrophic cycles under laboratory conditions, in this study and compared to literature data

	F1 (This study)[a]		Davis (1955)[b]	Endris et al. (1991)[c]
Gonotrophic cycle (GC)	First	Second	No data (ND)	9.8 ± 4.4 (3–17)
No. females	3	3	ND	196
Weight before blood meal (mg)	7.9 ± 0.06 (7.9–8.0)	8.1 ± 0.2 (8.0–8.4)	ND	ND
Weight after blood meal (mg)	17.5 ± 1 (16.9–18.7)	18.7 ± 5.6 (13.5–24.8)	ND	ND
Preoviposition period (days)	12.0 ± 5.5 (7–18)	6.6 ± 0.5 (6–7)	12.6 ± 6.1	8.4 ± 12.4 (5–35)
Oviposition period (days)	9.6 ± 1.5 (8–11)	7.6 ± 2 (6–10)	ND	9.1 ± 10.3 (4–24)
No. eggs	190 ± 28.6 (171–223)	146.6 ± 49.5 (104–201)	182 ± 40 (1st GC); 389 ± 52 (2nd GC)	117 ± 79 (4–403)
Weight of eggs (mg)	4.7 ± 4.1 (6.3–7.9)	5 ± 1.5 (3.9–6.8)	ND	ND
Incubation period of eggs (days)	16.3 ± 0.5 (16–17)	13.3 ± 2.3 (12–16)	16.2 ± 3.1	ND
EPI (%)[d]	39.7 ± 3.5 (37.28–42.25)	26.9 ± 2.2 (24.4–28.8)	ND	ND

Laboratory conditions: [a]25 °C, 85% RH, host: mouse; [b]22 °C, 79% RH, host: guinea pig; [c]27 °C, 95% RH, host: mouse

[d]EPI = (weight of eggs/initial weight of engorged female) × 100

continuous with an average period of 8.6 days (9.6 ± 1.5 and 7.6 ± 2 days for the first and second gonotrophic cycle, respectively) (Table 2).

Two females required two feeding processes to trigger the first gonotrophic cycle and an additional meal for a second one. The average number of eggs laid in the first and second cycles was 190 (171–223) and 146.6 (104–201), respectively. Egg production indexes (EPI) were 39.7 ± 3.5 and 26.9 ± 2.2 for the first and second gonotrophic cycle, respectively. Noteworthy, males occasionally fed on engorged females while mating (hyperparasitism).

The total cycle duration (egg-to-egg period), not considering fasting periods, was on average 70.7 days (58.7–82.7). The maximum larval survival period was on average 73.5 days (48–106).

Discussion

Different species of rodents have been used to feed tick colonies and develop studies on their biology. Herein, we used laboratory mice to study the biological cycle of *O. puertoricensis*, mirroring what Endris et al. (1991) did to feed nymphs and adults of the same soft tick species. Rats (Fox 1947) and guinea pigs (Davis 1955) have also served as animal model to collect biological data of *O. puertoricensis*. In the present study, a shorter feeding period was recorded for larval stages compared to those reported by Endris et al. (1991) and Davis (1955). We also observed that N1 molted to N2 without feeding requirement, which agrees with previous studies for the species (Fox 1947; Davis 1955; Endris et al. 1991).

The feeding duration for N2 and N3 was longer than that registered by Fox (1947). This could be explained by different feeding temperatures. In our study, mice were maintained in a room with environmental temperatures oscillating between 16 and 20 °C (average 17 °C). The average molting periods for these nymphal stages (N2–N4) were longer that those recorded by Fox (1947) and Endris et al. (1991), who also incubated the eggs at slightly higher temperatures (26.9–29 and 27 °C, respectively) than we did (25 ± 2 °C). Our results reinforce the conclusions of Endris et al. (1991) who compared biological data at different incubation temperatures, noting that pre-ecdysis periods were shorter at higher temperatures, therefore accelerating the biological cycle.

In our experiment, adults molted from N3 in comparable proportions for males and females, though with higher numbers for the former. This concurs with previous records made by Fox (1947) and Davis (1955) with incubation temperatures of 22 and 26 °C, respectively. Likewise, Endris et al. (1991) described adults emerging from N2 nymphs at 27–33 °C, with higher proportions of males. However, in the same study, adults emerging from N3 recorded a higher proportion of females which differs with results recorded in our study and those registered by Fox (1947) and Davis (1955).

Adult-feeding period recorded in this study (74.8 min) is higher than the period recorded by Fox (1947) for nymphs and adults (20–40 min) and constitutes the first specific register for this stage (adults). Regarding the reproductive data, one female required a unique meal and mating event to initiate oviposition, whereas the other two oviposited after a second feeding phase and an additional 7-day exposure with males to begin oviposition. That some females fed and mate once in order to initiate their first gonadotropic cycle and oviposit agrees with Endris et al. (1991), who showed that an additional feeding phase is not necessary for a female to lay an average of 600 eggs with

a unique exposure to a male. On the other hand, females that required a second feeding to trigger their first gonotrophic cycle, required an additional mating to oviposit.

Pre-oviposition and oviposition periods recorded in this study were longer in the first gonotrophic cycle than in the second. Despite slight differences in incubation conditions, this is in accordance with what Davis (1955) and Endris et al. (1991) recorded. Similarly, the average number of eggs was higher for the first than for the second gonotrophic cycle. Davis (1955) noticed on average 182 and 389 eggs for the first and second gonotrophic cycles, respectively. Endris et al. (1991) registered on average 117 eggs, yet no information was given regarding the gonadotrophic cycle's number. In relation to the egg production index (EPI) (Bennett 1974), our study reports for the first time values for *O. puertoricensis*, which were higher during the first gonotrophic cycle when compared to *O. brasiliensis* (Ramirez et al. 2016) and *O. rostratus* (Ribeiro et al. 2013).

This study was limited to 1 year, thus restricting the number of gonotrophic cycles observed (i.e., two) to one generation only. By contrast, Endris et al. (1991) stated that 10–20 gonotrophic cycles could be recorded in 1 year, under optimum incubation temperatures such as 33 °C. Therefore, considering that 30 °C is the average environmental temperature where we collected *O. puertoricensis* in this study, one can infer that the in situ life cycle might include at least more than one gonotrophic cycle yearly.

Interestingly, here we recorded a male feeding on engorged females which was also registered by Endris et al. (1991). Hyperparasitism has been commonly described in soft ticks (Argasidae) and less frequently in hard ticks (Ixodidae) (Moorhouse and Heath 1975). This phenomenon has been reported in at least eight species of *Ornithodoros* (Llanos-Soto et al. 2019), suggesting that this strategy could be a potential survival mechanism during long fasting periods in absence of available hosts (Gray et al. 2014). Also, it would constitute an alternate mechanism for pathogen transmission between ticks (Labruna et al. 2007; Williamson et al. 2018).

The average life cycle length registered for *O. puertoricensis* in this study was 70.7 days, clearly shorter than the estimate of 91.2 days made by Endris et al. (1989). Interestingly, in a subsequent study, Endris et al. (1991) recorded a length of 52.5 days at 27 °C, which is comparable to the temperature used in our study. These data reinforce the general observation that environmental conditions and other extrinsic factors (e.g., host type) directly influence the development of ticks and life cycle length (Sonenshine and Roe 2013; Klompen and Oliver 1993). Davis (1955) recorded 8 years as the maximum survival period of fasting *O. puertoricensis* nymphs and adults, under laboratory conditions, whereas Endris et al. (1991) recorded a period of 3–4 years. This survival period is related with optimal environmental conditions in a laboratory setting, that seldomly could be extrapolated to natural conditions.

Further studies should continue to investigate the biology of *O. puertoricensis* under laboratory and natural conditions, and expand the knowledge of this species, its vertebrate hosts, pathogen transmission, and potential management and control strategies.

Author contributions All authors contributed to the study conception and design. LNRS: Material preparation, data collection and analysis were performed. LNRS, ÁAFM, ARH, SML: The first draft of the manuscript was written, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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