

SCIENTIFIC NOTE

# Interspecific differences in the questing behaviour of *Dermacentor andersoni* and *Dermacentor variabilis* (Acari: Ixodidae) larvae

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## Abstract

*Dermacentor variabilis* and *Dermacentor andersoni* (Acari: Ixodidae) parasitise the same range of hosts in western Canada and have largely allopatric ranges except for a zone of sympatry in southern Saskatchewan, where these species experience the same environmental conditions. We report herein the discovery of differences in the behaviour of *D. variabilis* and *D. andersoni* larvae after they emerge from eggs. A behavioural diapause observed in *D. variabilis* larvae was not detected in *D. andersoni* larvae that were exposed to the same environmental conditions. As unfed *D. variabilis* larvae can successfully overwinter, their behavioural diapause represents an adaptive strategy to synchronise their questing activity and life cycle stage to maximise the chance of larvae encountering a suitable rodent host at the onset of spring. Such strategy will be of a significant benefit for colonising individuals at the northern edge of the distributional range of *D. variabilis*.

## Introduction

The Rocky Mountain wood tick, *Dermacentor andersoni* Stiles, and the American dog tick, *Dermacentor variabilis* (Say) (Acari: Ixodidae), require three hosts to complete their life cycles, and they feed on many of the same species of mammalian hosts. Larvae and nymphs feed on small mammals (e.g., meadow voles, deer mice, western jumping mice, and red squirrels), whereas adults feed on medium- to large-sized mammals (e.g., raccoons, dogs, white-tailed deer, and cattle; Wilkinson 1984; Dergousoff *et al.* 2013; Lindquist *et al.* 2016). Although *D. andersoni* and *D. variabilis* have largely allopatric ranges in western Canada, they coexist in a zone of sympatry in southwestern Saskatchewan (Dergousoff *et al.* 2013), where they experience the same off-host environmental conditions. Nonetheless, the two species differ significantly in their phenology (Lindquist *et al.* 2016). In western Canada, the larvae and, to a lesser extent, the adults of *D. variabilis* overwinter (Yunik *et al.* 2015; Diyes *et al.* 2021), whereas nymphs and adults are the overwintering stages for *D. andersoni* (Wilkinson 1984). In this study, we describe the differences in the behaviour of *D. variabilis* and *D. andersoni* larvae after emergence from eggs and how this relates to the differences observed in the phenology of their life cycles.

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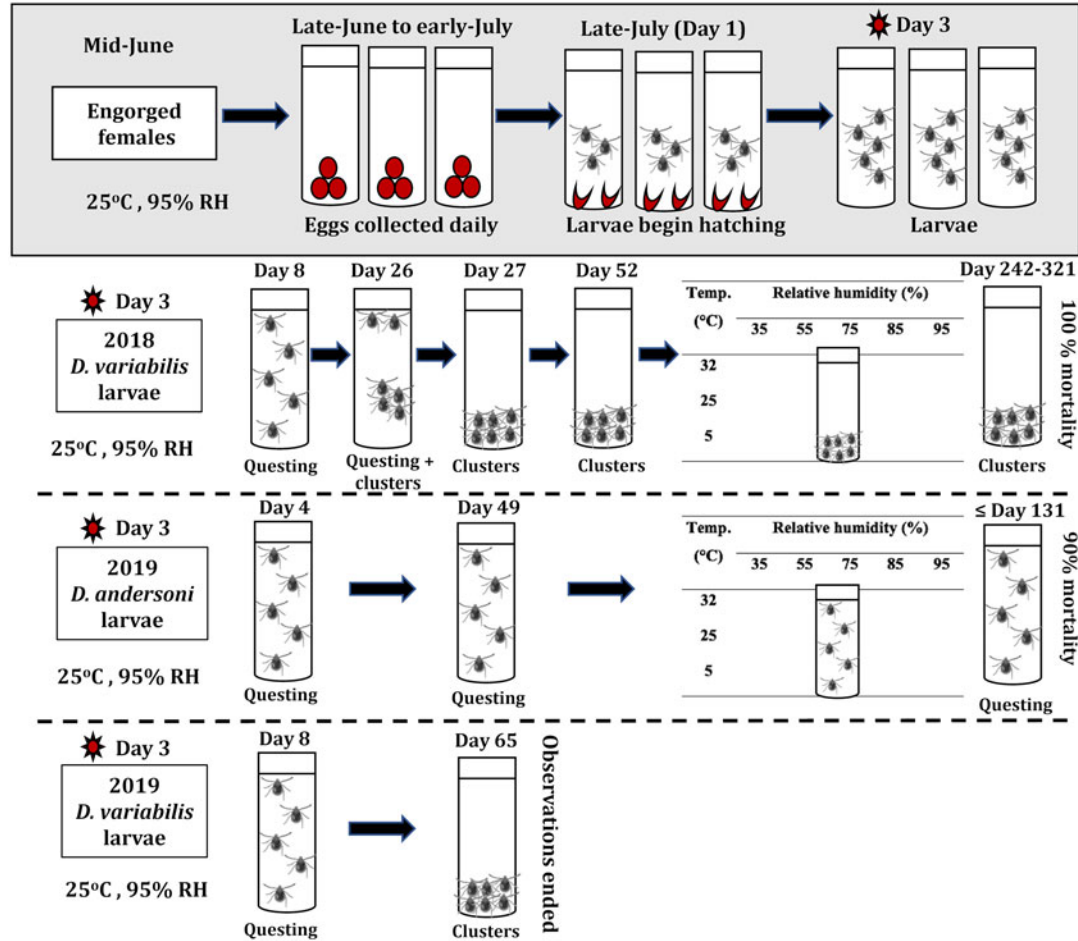
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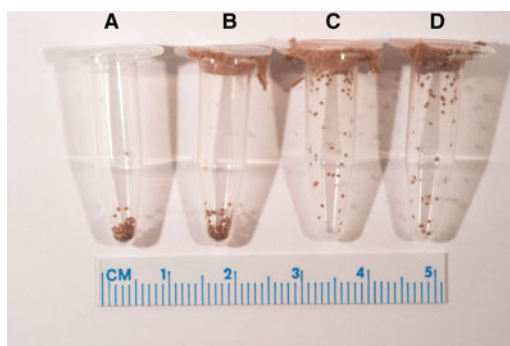
The larvae used in this study were the progeny of questing adult ticks collected in the field during June 2018 and June 2019. The collection site for *D. variabilis* in both years was Lizard Lake Community Pasture (52.405, -107.912), located approximately 50 km north of Biggar, Saskatchewan, whereas *D. andersoni* were collected in 2019 in an area adjacent to Chin Lakes Reservoir (49.643, -112.208) in Alberta, Canada. Conspecific male and female ticks were attached to Canadian Arcott sheep as described in Diyes *et al.* (2021). Different sheep were used as hosts for the two tick species. Egg clutches were obtained from 28 engorged *D. variabilis* females (16 in 2018 and 12 in 2019) and 12 engorged *D. andersoni* females (all in 2019) that had been placed individually into sterile glass tubes (21 × 65 mm) capped with perforated rubber stoppers. These vials were maintained at a constant 25 °C, 95% relative humidity, and in darkness (Fig. 1). A saturated potassium nitrate (KNO<sub>3</sub>) solution was used to maintain the 95% relative humidity (Winston and Bates 1960). Females started laying eggs 2–7 days after completing the blood meal, in late June to early July. On each day of the oviposition cycle, all eggs laid by a female tick (= an egg pool) were carefully transferred into a sterile plastic 0.5-mL tube with a perforated lid and maintained under the same constant environmental conditions as the ovipositing females (Fig. 1). Observations were made daily to determine when eggs in each pool began to hatch (= day 1 on Fig. 1). Two days after hatching, the newly emerged larvae from each egg pool were transferred into a new sterile plastic 0.5-mL tube with a perforated lid. A fine nylon mesh was placed inside the lid of each tube to prevent larval escape. Tubes containing larvae were kept in darkness at 25 °C and 95% relative humidity. Larvae in each tube were observed for movement over 2–3 minutes using a STEMI SV 8 Zeiss microscope (Oberkochen, Germany) without a light source. In 2018, the behaviour of the *D. variabilis* larvae derived from 278 egg pools (*i.e.*, comprising 11–887 larvae per pool) was observed daily for a maximum of 321 days. In 2019, daily observations were made on the behaviour of 230 pools (7–979 larvae per pool) of *D. andersoni* larvae and 201 pools (9–744 larvae per pool) of *D. variabilis* larvae (Fig. 1). Observations in 2019 ended when the mortality rate reached 90% for *D. andersoni* or by 65 days for *D. variabilis* (Fig. 1). In experiments conducted in 2018 to determine the survival times of *D. variabilis* larvae (Diyes *et al.* 2021) and *D. andersoni* larvae in 2019, some larval pools were transferred on day 49 or 52 (*D. andersoni* and *D. variabilis*, respectively; Fig. 1) to one of 15 combinations of three constant temperatures (5 °C, 25 °C, and 32 °C) and five relative humidities (35, 55, 75, 85, and 95%). All larvae were kept in darkness, and observations were made daily of larval behaviour during these experiments.

After hatching from the eggs, both *D. variabilis* and *D. andersoni* larvae climbed and aggregated on the side wall of each tube (Fig. 1). During this stage, the translucent larvae were motionless with their legs tucked beneath their bodies, and they did not engage in any questing activity for several days. This period of inactivity corresponds to the period during which there is sclerotisation of the tick cuticle (*i.e.*, a maturation phase in the life cycle), which ranges for 4–7 days in other tick species (Gladney *et al.* 1970; Davey 1986). However, differences between the two tick species were observed when host-seeking activity commenced and in the duration of this questing behaviour. For *D. andersoni*, larvae began questing on day 4 (Fig. 1). These larvae moved upwards and downwards within the tube (Fig. 2), and this movement was interspersed with the clustering of larvae at the top of the tube. In this position, larvae remained motionless except for the outstretching of their forelegs. This behaviour was observed in the larvae produced by all 12 *D. andersoni* females. *Dermacentor andersoni* larvae continued their questing activity, regardless of the environmental conditions to which they were exposed, until death – a maximum of 131 days at 25 °C and 95% relative humidity and 114 days at 5 °C and 95% relative humidity.

For *D. variabilis*, larvae began questing on day 8, and their behaviour was the same as that seen for *D. andersoni* larvae. However, on day 25, some *D. variabilis* larvae continued questing and others began to aggregate on the side walls of the tubes. By day 26, all larvae from the 16 *D. variabilis* females (in 2018) formed clusters and remained motionless at the bottom of the tubes. The same behaviour was observed for the larvae produced by the 12 *D. variabilis* females in 2019 (Fig. 1). Moreover, the larvae kept under different environmental conditions also maintained



**Figure 1.** The experimental procedure used for obtaining *Dermacentor variabilis* and *Dermacentor andersoni* larvae and assessing their behaviour and mortality under different laboratory conditions. *Dermacentor variabilis* larvae displayed questing activity and clustering while *D. andersoni* larvae displayed continuous questing activity until their death. RH, relative humidity.



**Figure 2.** Representative image of the activity of *Dermacentor variabilis* and *Dermacentor andersoni* larvae 106 days posthatch. **A** and **B**, *D. variabilis* larvae showing clustering activity/larval aggregations at the bottom of each tube; **C** and **D**, dispersed *D. andersoni* larvae showing questing behaviour.

their behavioural diapause. This behavioural diapause for *D. variabilis* larvae continued until their death or the termination of the experiment. *Dermacentor variabilis* larvae in 2018 ceased engaging in questing activity for a maximum of 294 days (from 18 August 2018 to 7 June 2019). Behavioural diapause in ticks is either obligatory, which is determined genetically, or facultative, which is controlled by environmental cues, such as changes in photoperiod (Belozero 2009; Leal *et al.* 2020). Smith and Cole (1941) stated that daylength was an important factor in controlling the initiation of diapause in *D. variabilis*. However, in the present study, larvae were maintained in darkness, which suggests that the initiation of behavioural diapause in *D. variabilis* larvae is not determined by environmental cues but possibly by an innate mechanism (*i.e.*, a biological clock). Thus, the factors influencing behavioural diapause in *D. variabilis* require further investigation. Furthermore, given the conditions of the present experiments, no photoperiodic cues occurred to trigger a termination of the diapause in the *D. variabilis* larvae, especially for those larvae that survived for more than 200 days. In addition, cessation of behavioural diapause in unfed *D. variabilis* nymphs is triggered by increasing temperatures (Belozero 2009); however, we found that transferring *D. variabilis* larvae to different temperature and relative humidity regimes did not induce questing. Photoperiod, perhaps in combination with increasing temperature, is important to terminate the behavioural diapause and induce questing in *D. variabilis* larvae.

A marked interspecific difference was observed in the behaviour of larvae exposed to the same environmental conditions. The absence of a behavioural diapause in *D. andersoni* larvae is consistent with their seasonal patterns of activity (Wilkinson 1968, 1984) and inability to survive off-host from summer, over winter, through to the next spring (Wilkinson 1968; Sonenshine *et al.* 1976; Owen *et al.* 2014). *Dermacentor andersoni* larvae begin attaching to small mammal hosts in late June, and this activity peaks in July and August and then gradually declines in September (Sonenshine *et al.* 1976; Wilkinson 1984). In a montane population (*i.e.*, collected from Kamloops, British Columbia, Canada), this larval activity extends from May to October (Wilkinson 1968). Unfed *D. andersoni* larvae are less tolerant to water loss than *D. variabilis* larvae are (Knülle 1966; Diyes *et al.* 2021) and are unable to survive more than 10 weeks in summer (Sonenshine *et al.* 1976). This limited off-host survival is consistent with the results of laboratory experiments that show that *D. andersoni* larvae survive for only 3–7 days at constant temperatures of 25 °C and 32 °C and up to 75% relative humidity. Therefore, given these physiological limitations, questing *D. andersoni* larvae must find a suitable host as soon as possible after emerging from the eggs and the hardening of their cuticle.

In contrast, field experiments conducted from summer through to early spring at a site close to Lizard Lake Community Pasture (*i.e.*, near the northern distributional limit of this species) have demonstrated that unfed *D. variabilis* larvae have a very high (95%) survival rate (Diyes *et al.* 2021). This finding would explain the presence of *D. variabilis* larvae on small mammals in March to May in southern Canada (Garvie *et al.* 1978). A second peak of larval activity on hosts also occurs from July to August (Garvie *et al.* 1978; Burachynsky and Galloway 1985). In our lab

experiments, eggs were laid in late June/early July, and the majority of *D. variabilis* larvae emerged by late July, which would be equivalent to the second larval peak on hosts in the field. Interestingly, termination of the questing behaviour of *D. variabilis* larvae in the lab occurred on day 27, which corresponded to mid-August, close to the last time of the year when larvae are found on small mammal hosts (Burachynsky and Galloway 1985). The cessation of questing resulted in clustering of *D. variabilis* larvae at the bottom of the tubes and would represent an adaptation (e.g., reduce their metabolic expenditure and rate of water loss; Fielden and Lighton 1996; Yoder and Knapp 1999; Leal *et al.* 2020) in the field to successfully survive off-host from late summer through to the subsequent spring. *Dermacentor variabilis* larvae retain water more effectively when present in clusters (Yoder and Knapp 1999) and survive longer in moisture-rich environments (Knülle 1966; Sonenshine 1979; Diyes *et al.* 2021). Under laboratory conditions, *D. variabilis* larvae produced by the adults collected from Lizard Lake Community Pasture survived for more than 100 days at constant temperatures of 25 °C and 32 °C and at least 85% relative humidity (Diyes *et al.* 2021).

In summary, the behavioural differences displayed by newly emerged larvae of *D. variabilis* and *D. andersoni* occurred despite being exposed to the same environmental conditions. The continuous host-seeking activity of *D. andersoni* larvae and a long diapause in *D. variabilis* larvae followed by a questing phase are consistent with their respective phenologies. This study represents the first published account of a difference in the behaviour of newly emerged *D. andersoni* and *D. variabilis* larvae produced by females collected from populations at the northern parts of the species' distributional ranges. The behavioural diapause exhibited by *D. variabilis* larvae may represent an important adaptation that is contributing to the northward range expansion by this species; however, this warrants further investigation.

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**Competing interests.** The authors declare they have no competing interests.

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