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Ito and Tamura (2017) is modified as Tamura and Ito (2017).

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Photoperiodic control of reproductive arrest in the oak-inhabiting spider mite *Schizotetranychus brevisetosus* (Acari: Tetranychidae)

Naoya Oda

Katsura Ito

Email : ktr@kochi-u.ac.jp

Faculty of Agriculture and Marine Science, Kochi University, 200 Monobeotsu, Nankoku, Kochi, 783-8502, Japan

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Abstract

Populations of *Schizotetranychus brevisetosus* Ehara (Acari: Tetranychidae), which live on the evergreen oak (*Quercus glauca*), survive the coldest months as either adult females or winter eggs. Adult females comprise the majority of the population in early November and oviposit from late November to early March. Most winter eggs hatch by late March, and adults of the next generation emerge in April. This species is considered an egg-diapausing species, but the environmental cues that regulate female reproductive arrest and resumption are mostly unknown. We investigated the photoperiodic responses of autumn reproductive arrest in 10 populations collected from different elevations in Shikoku, Japan. All populations showed long-day responses to critical daylength (CDL) around 12.2 h light (12.2L) at 20 °C, though there was no linear relationship between CDL and altitude. This result explains the steep decline in the proportion of summer eggs in November. Nonreproductive females developed under 10L at 20 °C commenced oviposition 14.3–20.6 days after transferring to 15L. This long pre-oviposition period explains the reduction in eggs before winter reproduction and suggests shallow adult diapause. Eggs thus obtained hatched in 12.9–15.3 days, similarly to summer eggs. Therefore, egg diapause in *S. brevisetosus* is much shallower than in species on deciduous hosts, which lay their winter eggs in early autumn to hatch at leaf flush in spring. The reproductive arrest and short hatching period may be an adaptation allowing egg-laying in midwinter, when predation pressure is low.

Keywords

Egg diapause
Evergreen host plant
Host phenology
Quercus glauca
Web-nesting

Introduction

Overwintering is a central theme of terrestrial arthropod life-cycle evolution (Dingle 1976; Tauber et al. 1986). Overwintering stages vary even among closely related species (Tauber et al. 1986), and this fact suggests that strong selection pressures are acting on the life cycle. We should understand biotic and abiotic factors that enable various overwintering patterns to know the process of life cycle formation. The main seasonal signals are photoperiod and temperature, and the former is the most reliable cue because daily and yearly fluctuations are

habitat conditions in each population (Dingie 1970). Therefore, geographic variation in this response reflects local adaptation and is an important study subject.

Spider mites (Acari: Tetranychidae) live on leaf surfaces and suck leaf fluids to obtain energy for development and reproduction. In cool or temperate areas, normal development usually stops at the egg or adult female life stage before winter arrives (Veerman 1985). Females of *Tetranychus urticae* Koch reared under short-day and low-temperature conditions stop ovary development (Kawakami et al. 2009) and overwinter in hibernation sites until spring, and this behaviour may affect interactions between predators and prey (Kroon et al. 2005, 2008). It is primarily the photoperiod that induces reproductive arrest or other physiological changes (Lees 1953; Parr and Hussey 1966; Suzuki et al. 2009). To avoid confusion generated by the numerous existing definitions of some of these terms (Leather et al. 1993), here we define *diapause* as a syndrome that enables development to be suspended and involves many physiological changes, such as reproductive arrest or an increase in cold-hardiness (Khodayari et al. 2013; Bryon et al. 2017). *Overwintering* simply refers to passing the winter and resuming activity the next spring, irrespective of whether the animals do this in diapause, in quiescence, or even reproducing as they do in summer.

The overwintering stages of spider mites are loosely restricted by phylogeny (Veerman 1985; Sakagami 2002; Saito 2010) but are modified depending on the availability of the host plants that they use during winter. For example, most *Tetranychus* species enter diapause as adult females. However, females in the temperate populations of *T. urticae* and *T. kanzawai* Kishida climb down from their deciduous hosts and transfer to weed rosettes. Because their diapause is averted on good leaves (Parr and Hussey 1966; Shimizu and Hanaka 1975; Ito 2003), females can reproduce on them and all life stages occur throughout winter (Takafuji and Kamibayashi 1984; Takafuji et al. 1991, 2001, 2003; Morishita and Takafuji 1999a, b). Such phenotypic plasticity is favourable in vegetation composed of plants of different quality according to the model assuming the stochastic rate of diapause (Takafuji and Tsuda 1992; Tsuda et al. 1997). Even in the same phylogenetic clade, species that can use stable hosts tend to overwinter as different life stages (Sakagami 2002). For example, *Oligonychus coffeae* (Nietner), which is in the clade of egg-diapausing species (Matsuda et al. 2014, 2018), is likely to have lost the ability to diapause because all life stages occur in winter (Roy et al. 2014). Similarly, *Tetranychus ludeni* Zacher and *Tetranychus evansi* Baker et Pritchard may have secondarily lost the ability to diapause in the light of phylogeny (Ehara and Gotoh 2009; Matsuda et al. 2014, 2018). These studies suggest that the existence of various winter hosts is essential for mites to employ a range of overwintering strategies.

In extreme cases, several species that feed exclusively on evergreen hosts overwinter in two or more life stages. *Yezonychus sapporensis* Ehara (Saito 2010; H. Yanagida unpublished data) and *Panonychus (Sasanychus) akitanus* Ehara (Gotoh 1986a, b) inhabit evergreen *Sasa* bamboo. Immature individuals complete development by autumn, and emerged females lay winter eggs on the host surface and overwinter themselves. Gotoh (1986b) reported that the winter eggs of *P. akitanus* need chilling for more than 20 days at 5 °C to hatch and regarded this low hatchability as a sign of egg diapause. In contrast, females chilled for 10 days resumed oviposition in only 3 days, showing no clear indication of diapause. Therefore, the relationship between overwintering and diapause is not straightforward at least in this species. Furthermore, *Schizotetranychus shii* Ehara and *Eotetranychus asiaticus* Ehara on evergreen hosts may have lost the capacity for diapause because various life stages exist throughout the winter (Ehara and Gotoh 2009). *Eotetranychus smithii* on semi-evergreen Rosaceae plants shows egg diapause, but adults and eggs coexist inside greenhouses, and this observation suggests the involvement of environmental factors (Nagatomo 1973). The environmental cues that trigger the timing of reproduction and development in these species are unclear, and thus how such multi-stage overwintering is achieved is not elucidated.

Schizotetranychus brevisetosus Ehara (Ito and Yamanishi 2019) is a **AQ1** specialist of the evergreen Japanese blue oak, *Quercus glauca* Thunb. (Fagaceae, Ehara 1989). This species has a web-nesting lifestyle (the subtype WN-s in Saito 1983), in which developmental stages live socially in a silk-web nest and deposit faeces on the roof of the nest. Adult males engage in lethal combat in the nest, probably for the opportunity to mate (Masuda et al. 2015). Adult and immature mites cooperatively attack predators (Ito 2019), and predator composition is biased towards rove beetles (*Holobus* spp.) and *Anystis* mites, with small numbers of phytoseiid mites (Ito 2020).

The seasonal composition of the developmental stages varies considerably (Ito and Yamanishi 2019). Adult females lay yellowish-white eggs from spring to autumn (referred to as “summer eggs” in Ito and Hamada 2018b; Ito and Yamanishi 2019), which hatch **with** in about 7 days of deposition under 16:8 h light:dark (16L) conditions at 25 °C (Tamura and Ito 2017). All developmental stages are present from May to October. In autumn, all immature mites develop into overwintering adults and females cease oviposition. As a result, the population consists almost exclusively of adult females by late November (there are few males because there is naturally a highly biased sex ratio; see Tamura and Ito 2017). From December to early March, adult females lay bright orange eggs (‘winter eggs’). Thus, only females and eggs are present during the coldest months of the year. The adult females die by late March, and the winter eggs hatch in early March and the hatchlings mature until April. Although this pattern is similar to that of *P. akitanus* or *Y. sapporensis*, it differs in that adults of these species lay winter eggs in September and October and overwinter without reproduction. *Schizotetranychus brevisetosus* has been considered one of the egg-diapausing species because only eggs survive the whole winter (Ito and Hamada 2018b). However, it is not studied whether adults females and winter eggs are in diapause or not. Therefore, the physiological mechanisms that cause this two-stage overwintering pattern are unclear.

In this study, we focused on the fact that the number of *S. brevisetosus* eggs declines steeply in November (Ito and Yamanishi 2019). Predicting that autumnal environments induce female reproductive arrest, we investigated the photoperiodic response and critical daylength (CDL), at which 50% of females arrested oviposition in 10 populations from various altitudes in Kochi, Shikoku District, Japan, to understand adaptations to the local climates. We predicted that females from locations at higher altitudes would tend to cease reproduction earlier (i.e., at a longer CDL), and their eggs would show a deeper diapause as reported in other mites (Koveos et al. 1999) or insects (Batz et al. 2020). Because such climatic differences reflect the characteristics of diapause and associated traits in arthropods (Tauber et al. 1986), we also investigated the variation in the number of days required for the female to start oviposition (latency to oviposition) and for eggs to hatch. Accordingly, we discuss the photoperiodic control of the life cycle of *S. brevisetosus* indicated by our results. Since we concentrated on the effects of daylength, we kept the experimental temperature at 20 °C, which approximated the mean temperature of early October (21.4 °C, Gomen, Kochi in 2020, Japan Meteorological Agency 2021).

Materials and methods

Ten *S. brevisetosus* populations from different elevations (610–530554 m a.s.l.) were collected from roadside *Q. glauca* trees in the Kochi and Tokushima prefectures (Table 1). The laboratory strain of each population was established from at least 200 individuals distributed on several leaves. The mites were reared on detached *Q. glauca* leaves with the abaxial surface facing **AQ2** upwards. These leaves were placed on water-soaked cotton pads in plastic dishes with internal dimensions of 91.3 × 38.2 mm (Insect Breeding Dish; SPL Life Sciences, Gyeonggi-do, Korea). The host leaves used for the rearing and experiments were collected from *Q. glauca* woods in Otani, near Honmura (Table 1). During rearing, the leaf edge was entirely covered with pieces of Kimwipe (Kimberly Clark, Roswell, GA, USA) to prevent the mites from escaping. The leaves used in the experiments to measure CDL were prepared in the same way. Leaves were replaced every 2 or 3 weeks by cutting out the infested sections of the old leaves and placing them on new leaves. The cultures were maintained under a 15:9 h light:dark (15L) photoperiod at 25 ± 0.5 °C. The primary incubator was MIR-154 (Panasonic, Osaka, Japan), but when the humidity became high, a plant-growth chamber (LPH-240S; NK System, Osaka, Japan) was used to keep the relative humidity at 60%. The cultures were maintained for 2–6 months before the onset of experiments to minimise possible effects from maternal experiences in the wild (Danilevskii 1965; Oku et al. 2002). Because the development time of *S. brevisetosus* females is very long (22.6 ± 3.1 days at 25 °C and 16L, Tamura and Ito 2017), the mean generation time might reach one month because it is sometimes longer by 10 days (Gotoh et al. 2003). If so, the rearing period correspond to 2–6 generation times. We considered that such a maintenance period only slightly changed the natural daylength responses, because diapause-related traits are under polygenic control (Kroon and Veenendaal 1998; Ito 2007, 2014; Ito et al. 2012) and genetic variation is stably maintained in a population by genetic drift (Bryon et al. 2017).

Table 1

Summary of the experimental populations

Code	Label	Locality	GPS coordinates	Date	Altitude (m a.s.l.)
1	Usa	Usa-cho, Tosa	N33°25'36.7" E133°27'07.6"	28 Apr 2019	6
2	Hidakamura	Iwameji, Hidakamura	N33°31'22.1" E133°19'54.5"	19 Jul 2020	20
3	Honmura	Noichi-cho, Konan	N33°34'50.0" E133°43'36.6"	24 Jun 2019	37
4	Yamada	Tosayamada-cho, Kami	N33°37'48.1" E133°42'43.5"	18 Dec 2018	89
5	Sakagawa	Tosayamada-cho, Kami	N33°36'39.4" E133°44'19.5"	12 Mar 2020	90
6	Kahoku	Birafu, Kahoku-cho	N33°38'41.2" E133°47'09.4"	12 Mar 2020	139
7	Sameura dam	Kagami, Tosa-cho	N33°45'04.3" E133°31'41.2"	1 Mar 2019	348
8	Nakamura-daiou	Nakamura-daiou, Otoyō-cho	N33°44'21.9" E133°40'46.3"	24 Jul 2019	417
9	Oriu	Kito-mura, Naka-cho	N33°46'17.8" E134°08'38.7"	30 Mar 2019	423
10	Kajigamori	Nakamura-daiou, Otoyō-cho	N33°44'32.8" E133°40'35.4"	12 May 2019	530

The populations were collected from Kochi Prefecture, Japan, except for population 9, which was from Tokushima

Exp. I. Photoperiodic response

In each treatment, 60 adult females randomly sampled from the culture were transferred onto one or two detached host leaves (when two leaves were used, 30 females were placed on each leaf; populations 2, 4, 5, and 6 in Table 1). These dishes were kept for 2 days under 15L and 25 °C to obtain eggs. After the females had been removed, these dishes were incubated under five different daylength conditions (10L, 11.5L, 12L, 12.5L, and 13L) at 20 ± 0.5 °C using a multi-incubator (HPK-8R3; Fukushima Galilei, Osaka, Japan). The photoperiods of 10L and 13L approximated the hours of daylight on the winter solstice (9 h 56 min) and 1 September (12 h 52 min) in Kochi, respectively (National Astronomical Observatory of Japan 2021). To prevent leaf deterioration, all mites were transferred onto new leaves every 2 or 3 weeks from the start of mass rearing. Infested parts of old leaves were cut out using a razor blade and placed onto new leaves. Mites that did not move to the new leaf surface within a day were transferred using a fine brush. Not all daylength treatments were represented in all populations because in some cases the mites developed too slowly.

Daily, the females that emerged were individually placed, using a fine brush, onto 1.5 × 1.5 cm leaf fragments that included midribs. The dishes containing these pieces were maintained under the same daylength conditions under which the mites had developed. These females were likely to be fertilised because the females of spider mites copulate with males immediately after their emergence. This inference is because *S. brevisetosus* males approach preimaginal females and engage in mortal combat, and sperm competition must be intense (Masuda et al. 2015).

Females that had not oviposited within 9 days were regarded as non-ovipositing (possibly laying winter eggs in the future). The criterion was determined by the fact that 90% of Tosayamada females in the culture deposited summer eggs within 9 days of emergence when maintained at 20 °C and under 15L in preliminary experiments (n = 18). The proportion of non-ovipositing females out of the total was calculated for each daylength treatment.

The CDL for each population was estimated using logistic regression, assuming a binomial error distribution. The fitted model was as follows:

$$\log\left(\frac{\widehat{p}_i}{1 - \widehat{p}_i}\right) = a_i + b_i x_i, \quad 1$$

where \widehat{p}_i was the estimated proportion of non-ovipositing females in the i -th population, x_i was daylength (fixed effect), and a_i and b_i were constants. The analyses were conducted using the *glm* command in R version 3.5.1 (R Core Team 2018). The CDL $x_{i,0}$ was obtained by replacing \widehat{p}_i with 1/2:

$$\log\left(\frac{1/2}{1 - 1/2}\right) = a_i + b_i x_{i,0}. \quad 2$$

Since the left side is zero, this comes to

$$x_{i,0} = -\frac{a_i}{b_i}. \quad 3$$

The error distribution and residual deviance were investigated to verify the assumptions of logistic regression (Crawley 2005). Furthermore, the CDL estimates were regressed against the elevations of the collection sites (Zar 2010) to determine whether the timing of reproductive arrest was associated with the variation in climatic conditions typically associated with variation in altitude.

The photoperiodic response of all populations was estimated using generalised linear mixed models (GLMM) with the *glmer* command in the *lme4* package in R. Three statistical models were compared. In the first model, both intercept (a_i) and slope (b_i) could vary among populations (the full model). In the second model, all populations had a common slope, but intercepts could vary (the random intercept model). In the third model, populations had a common intercept but different slopes (the random slope model). The model with the lowest Akaike information criterion (AIC) value was selected. The fixed or random effects in intercept and slopes, as well as other statistical parameters such as deviances and likelihood, were estimated. The *common* CDL, which was based on the fixed factors of the model selected above, was calculated using Eq. (3).

Exp. II. Number of days required for females to initiate oviposition and eggs to hatch

The period of ovipositional arrest was measured in populations 1, 3, 4, and 7–10 (Table 1) to investigate geographic variation. The non-ovipositing females from the 10L treatment were transferred immediately after checked for oviposition (day 9) to the 15L, 20 °C conditions, which promote oviposition (Ito and Hamada 2018b). The number of days that elapsed before the first oviposition occurred was recorded. After oviposition, the female and all eggs except one were removed with a fine brush. The number of days required for this egg to hatch was recorded. The reason for checking only one egg was to avoid a possible bias due to a difference in the offspring number per female.

The number of days required for oviposition and hatching were both analysed using one-way analysis of variance (ANOVA), and pairwise comparisons among populations were conducted using Tukey's honestly significant difference (HSD) test. The assumptions for the ANOVAs were checked using a normal Q–Q plot and a leverage plot (Zar 2010). Additionally, the average number of days required for each event were regressed against the elevation of the collection sites to determine whether there was an association.

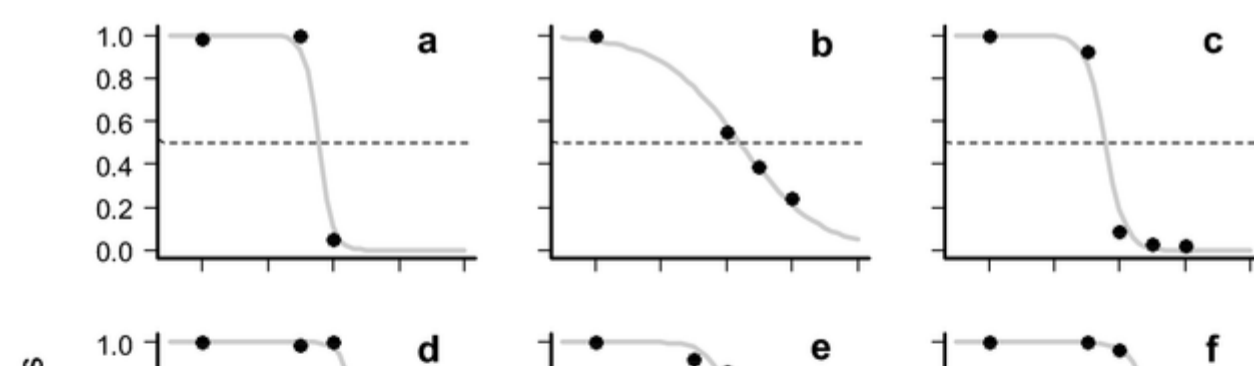
Results

Exp. I. Photoperiodic response

Figure 1 shows the proportion of non-ovipositing females. Response curves were sigmoidal in all populations. The variation among populations was largest at 12L and 12.5L (standard deviation [SD]: 0.37 h and 0.25 h, respectively), while the variation was < 0.1 h in all other daylength treatments. The CDL (50%) lay between 12 and 12.5L, except for the two lowland populations (from Usa and Honmura), which had a CDL of 11.8L (Table 2). Despite this fact, no linear relationship was detected between CDL and altitude (Fig. 2; $F_{1,8} = 3.182$, $r^2 = 0.195$, $P = 0.112$ for the regression). The Q–Q and leverage plots revealed no outliers in the regression. Several populations showed overdispersion in the logistic regression of CDL; that is, the residual deviance was greater than the degree of freedom (Table 2).

Fig. 1 This figure seems a little blurring (probably due to low resolution?). If needed, please use the figure attached (fig1_re.docx)

Photoperiodic response, in terms of the proportion of non-ovipositing females, at 20 °C. **a–j** Populations 1–10, respectively (Table 1). **k** The common curve estimated by the generalised linear mixed model (black line). The gray lines show the curves of the 10 populations



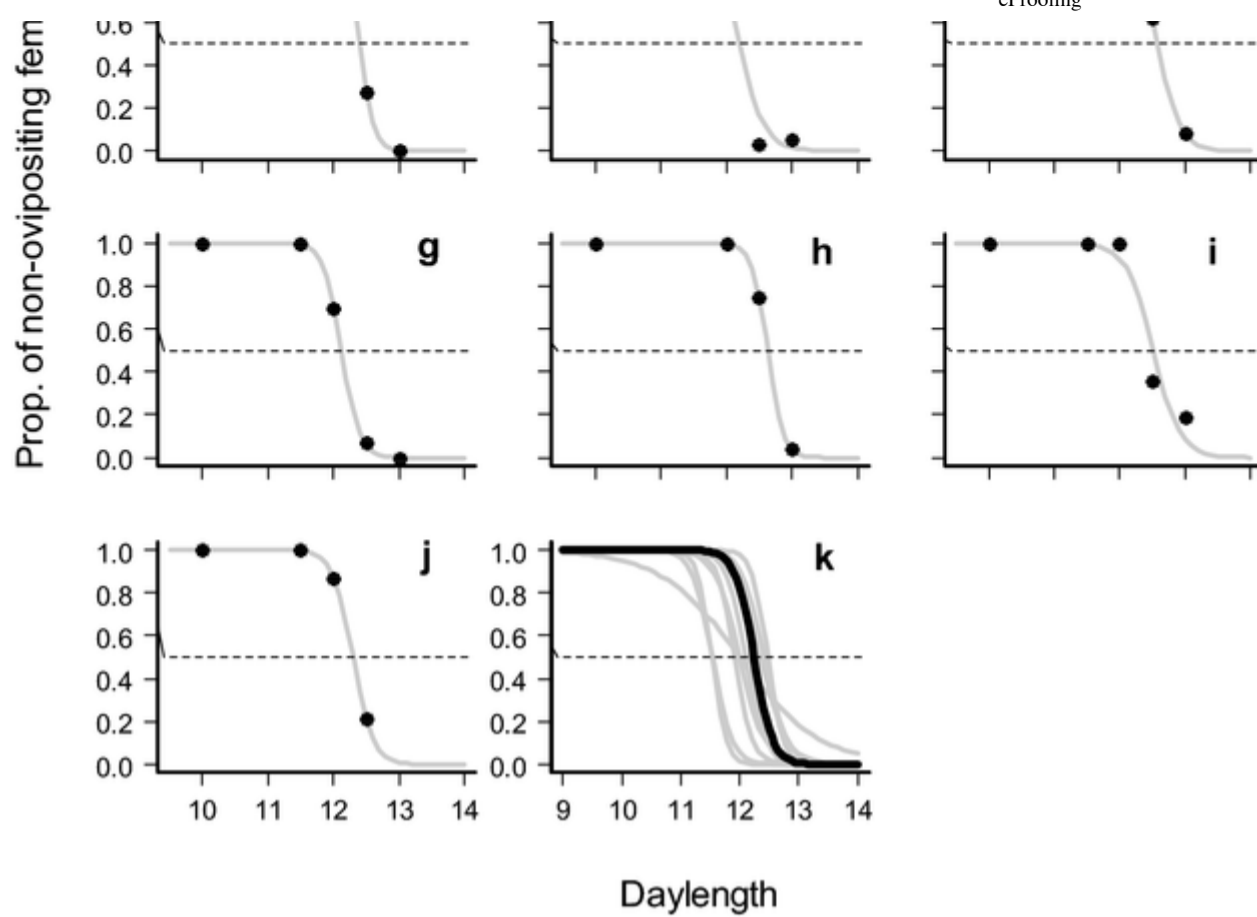


Table 2

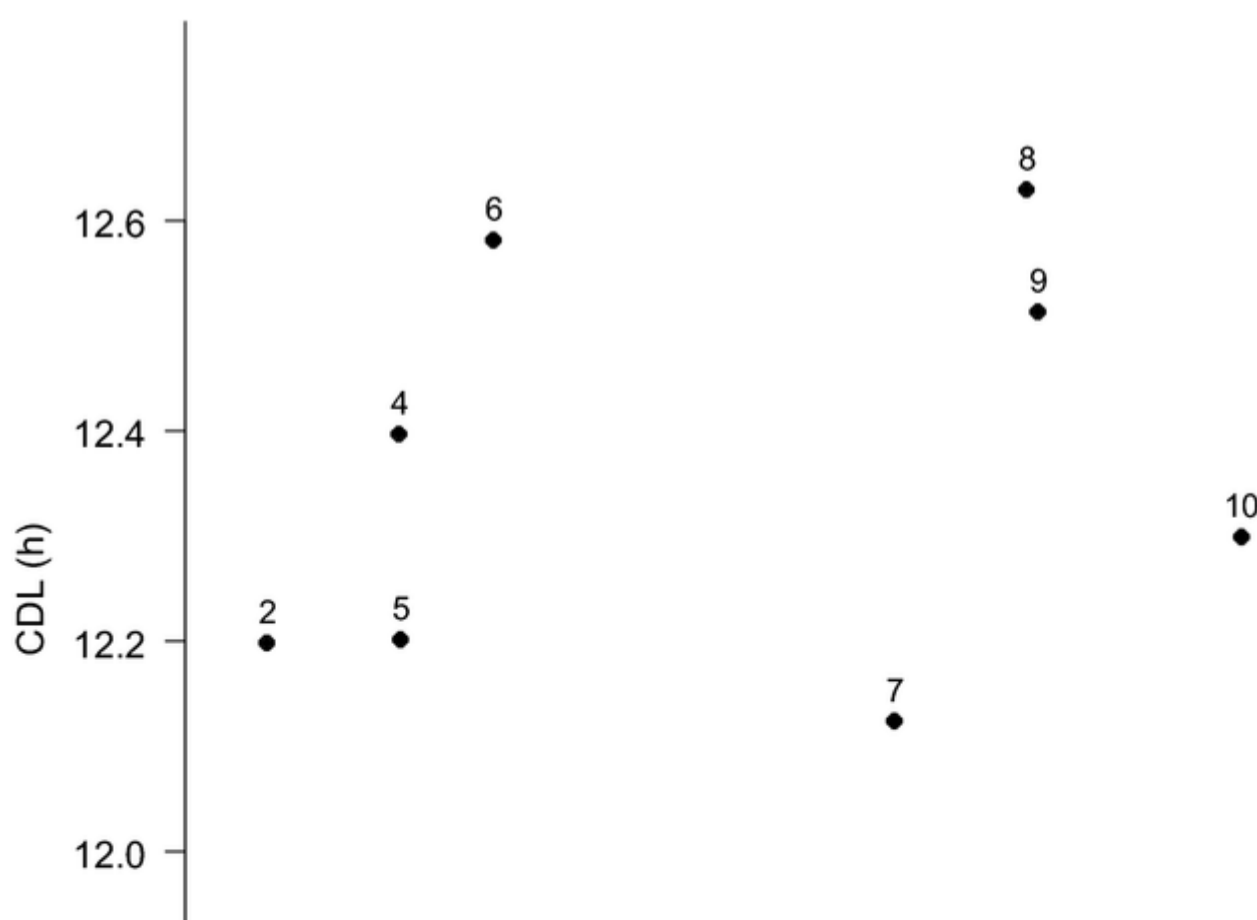
Estimated critical daylength (CDL) and fitted values of fixed effects

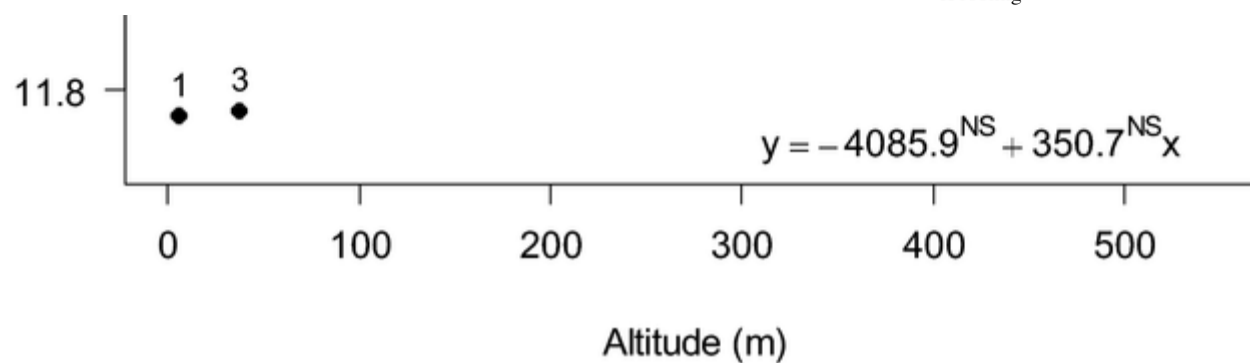
Code	CDL	<i>a</i>	<i>b</i>	Res. dev.	<i>df</i>
1	11.78	111.23	- 9.45	33.68	1
2	12.20	20.11	- 1.65	2.40	2
3	11.78	79.13	- 6.72	15.11	3
4	12.40	115.17	- 9.29	9.98	3
5	12.20	64.30	- 5.27	29.92	3
6	12.58	74.20	- 5.90	0.26	3
7	12.13	89.62	- 7.39	1.60	3
8	12.63	109.43	- 8.67	0.56	2
9	12.51	61.30	- 4.90	20.42	3
10	12.30	80.73	- 6.56	0.70	2

Residual deviance (Res. Dev.) and the degrees of freedom (*df*) are indicated. See Table 1 for the population details

Fig. 2 If the figure 2. and 3. are the final versions, we can provide the original PDF figures with higher resolution. Please disregard if it is not the case.

The relationship between critical daylength (CDL) and the altitude of *S. brevisetosus* populations. The slope of the linear regression was not significant ($P = 0.112$)





In the GLMM results for the common response, the full model was selected as the best model based on AIC, and this model indicated a large variance in intercept (Table 3). The common CDL was estimated as 12.2L from the estimated coefficients of the fixed effects ($\log p/(1-p) = 78.36 - 6.40x$). The other two models performed similarly poorly due to high AIC and inflated deviances; that is, these random effects did not improve the model fitting and were not considered further.

Table 3

Summary of the model selection from three potential models

Model	AIC	logLik	Dev	df	SD (intercept)	SD (slope)
Full	301.0	-145.5	291.0	40	24.952	2.047
Intercept	382.4	-188.2	376.4	42	1.569	-
Slope	382.3	-188.2	376.3	42	-	0.130

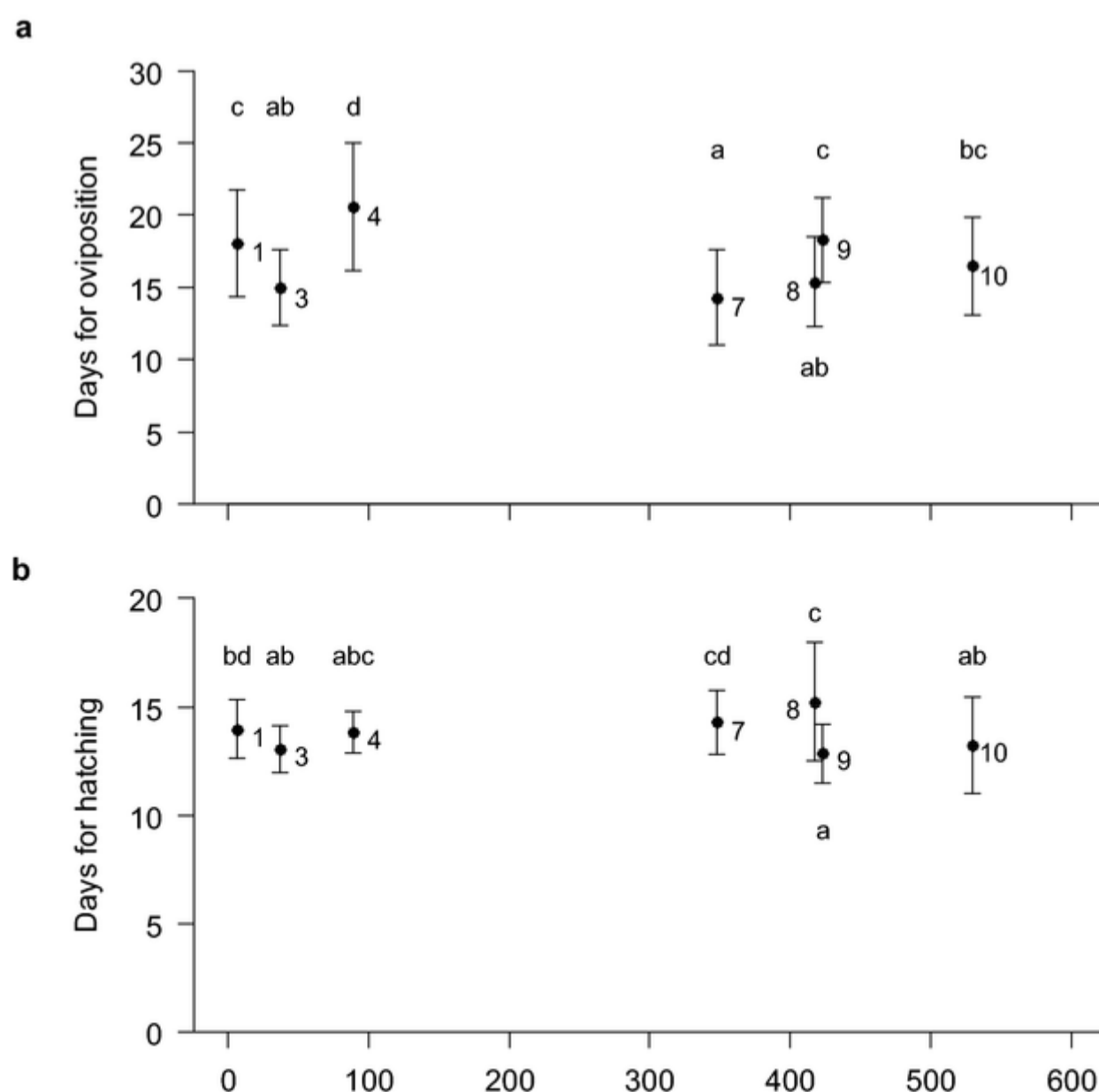
Random effects are included in both the intercept and slope (full model), intercept only (intercept model), and slope only (slope model). For each model, the Akaike information criterion (AIC), log likelihood (logLik), deviance (Dev), the degrees of freedom of residuals (*df*), and standard deviations of random effects (SD) are shown

Exp. II. Number of days required for female oviposition and egg hatching

In the populations examined, 14.3–20.6 days on average were required for oviposition under 15 L, 20 °C conditions (after 9 days at 10L) ($n = 34-65$, Fig. 3a). The number of days before oviposition occurred differed among the populations (one-way ANOVA, $F_{6,356} = 18.52$, $P < 0.001$), and there was a significant difference between some pairs (Tukey's HSD test, $P < 0.05$), but there was no linear effect of source-population altitude ($F_{1,5} = 0.491$, $P = 0.515$).

Fig. 3 We attached file of a higher resolution (fig3_re.dox). If this is needless ignore this file.

a Interpopulation variation in the number of elapsed days until female oviposition occurred at 20 °C and 15L (excluding the first 9 days at 10L; Fig. 1). **b** Variation in the number of days before the hatching of the egg. See Table 1 for explanation of population codes. Pairs with different letters were significantly different according to Tukey's HSD test ($P < 0.05$). The regression of each trait with altitude was not significant ($P = 0.515$ and 0.874 , respectively)



Altitude (m)

The results of the number of days that elapsed before the eggs hatched were similar to those for the number of days required for oviposition (12.9–15.3 days on average) under 15L, 20 °C conditions (Fig. 3b). The numbers of eggs recorded hatching per population varied between 13 and 60 (41.3 ± 15.7 , $n = 7$ populations), because some eggs died during incubation. Hatchability differed among populations ($\chi^2_6 = 66.541$, $P < 0.001$) but was not correlated with altitude (Pearson's $r = -0.021$, $t_5 = -0.047$, $P = 0.96$) or with the number of days for eggs to hatch ($r = -0.345$, $t_5 = -0.835$, $P = 0.442$). The number of days that elapsed before the eggs hatched differed significantly among populations (one-way ANOVA, $F_{6,282} = 10.04$, $P < 0.001$), but again, no linear relationship with altitude was found ($F_{1,5} = 0.028$, $P = 0.874$).

Discussion

Daylength

We demonstrated that photoperiod governs autumnal reproductive arrest in *S. brevisetosus*. All populations followed sigmoid response curves (Fig. 1a–j), and thus it is a long-day species (Tauber et al. 1986). The results agree qualitatively with the field observation that the proportion of eggs to the total individuals on the infested leaf decreases in late October or early November when daylength shortens (Ito and Yamanishi 2019), the actual population size could not be estimated because the distribution of *S. brevisetosus* was highly clumped). Several populations showed overdispersion in the logistic regression of CDL (Table 2), probably because each population contained females with different genotypes governing their photoperiodic response. In other words, the probability of reproductive arrest was variable even within each population. Such heterogeneity violates the assumption of the logistic analysis, so a mixed model was required instead (see below). Nevertheless, the coefficients estimated by the logistic model sufficiently explained the responses in all populations (Fig. 1a–j), so the effect of overdispersion on estimating coefficients may be negligible.

The response curves varied among populations, as reported for other egg-diapausing species (Morimoto and Takafuji 1983). Notably, the response curve of the Hidakamura population had an exceptionally gradual slope due to the population containing 24% and 39% nonreproductive females at 12.5L and 13L ($n = 41$ and 50 , respectively; Fig. 1b). The reason for this unusual pattern is uncertain, but the leaves used in the experiment may not have been suitable and may have affected the response. Spider mites adapt rapidly to local hosts without apparent costs (Gotoh et al. 1993; Tajima et al. 2007; Malagnini et al. 2012; Sousa et al. 2019), and the incidence of diapause tends to be lower on more favourable hosts under moderate conditions (Ito and Saito 2006; Ito 2010). The genetic composition of *Q. glauca* varies among localities (Xu et al. 2015), and thus leaf quality may differ among populations. If the leaves provided during the experiment were unsuitable for the development of Hidakamura females, the photoperiodic curve may have been skewed upward. We should test this hypothesis by clarifying the association between leaf suitability and the occurrence of reproductive arrest (Ito and Saito 2006), and elucidate why only one population exhibited a unique response curve. Another possibility is that in early autumn (12–13L), some of the females continue laying summer eggs while others stop oviposition. Such dimorphism may be advantageous in fluctuating environments (Seger and Brockmann 1987; Bradford and Roff 1993; Roff 2002). Further empirical studies are needed to test these possibilities.

The variation in the proportion of nonreproductive females was greater at 12L and 12.5L than in the other treatments, and the common CDL was estimated to be 12.2L (Fig. 1k). These estimates explain the stage structure in the field reasonably well. The proportion of eggs is still high in early October because adult females continue reproducing (Ito and Yamanishi 2019). These females may have developed from mid-September (average temperature 24.5 °C) to late September (22.9 °C, Gomen in 2020; Japan Meteorological Agency 2021), because females require 3 weeks to develop at 25 °C (Tamura and Ito 2017). This development period may be roughly a week longer at 20 °C, based on the concept of degree-days (the total amount of heat above the threshold temperature t_0 required for development), if t_0 is assumed to be around 10 °C like other spider mites in Japan (Kiritani 2012).

Daylength in mid-September is 12.5L, excluding civil twilight, and this shortens rapidly toward the autumnal equinox (Japan Meteorological Agency 2021). Thus, some females may not oviposit in October, while others continue to do so. The proportion of eggs declines steeply after early October (11.5L), and oviposition in females from all populations stopped at this daylength (Fig. 1a–j). Civil twilight does affect CDL in some species. Uchida (1982) estimated the CDL of *Panonychus* species in pear orchards as 13L, including 20 min of illumination at > 3.5 lx at dawn and dusk. This value fitted with the production of diapausing eggs in mid-September. Shinkaji (1975) also attributed the difference between the actual season of egg production (late September) and the estimates of CDL based on laboratory experiments (12.5L, corresponding to mid-September) in an *Oligonychus* species on chestnut trees (Ehara and Gotoh 2007; Arabuli and Gotoh 2018) to 30 min of civil twilight. However, such effects may be negligible for *S. brevisetosus* because *Q. glauca* grows in hillside forests that receive inadequate sunshine to produce these effects. Most of the infested leaves are in the dark at dawn and dusk (K. Ito, personal observation).

Pre-oviposition period

Most of the females that developed under the 10L or 11.5L conditions did not oviposit for 9 days, and required a further 2 or 3 weeks to oviposit after they were transferred to 15L (Fig. 3a). Such an extremely long day, which corresponds to the daylength in the summer solstice in Kochi (14.5 h), strongly promotes oviposition in spider mites (Veerman 1985; Ito and Hamada 2018b). Thus, the cessation of oviposition in autumn may be longer than the present results. Oviposition after this ovipositional arrest may correspond to winter-egg deposition in late November, long after reproductive arrest in late October (Ito and Yamanishi 2019). This cessation also suggests a possibility of shallow reproductive diapause in adult females.

In other egg-diapausing species, females reared under short-day conditions begin to lay winter eggs a few days after emergence (Lees 1953; Shinkaji 1975; Gotoh 1986b). This prolonged ovipositional arrest may not be the result of delayed ovary development, because

brevisetosus may instead be an adaptation for reproduction in winter, when predation pressure is low, because rove beetles *Holobus* spp., the main predators, are still active in autumn but are not present from December to February (Ito 2020). Thus, winter is suitable for females to reproduce as long as they can tolerate the winter climates. Our understanding of the physiological mechanisms of traits related to overwintering in spider mites is restricted to only a few model species (Khodayari et al. 2012, 2013; Bryon et al. 2017). Multi-stage overwintering in these species may provide valuable materials to study the evolutionary changes in the overwintering patterns during adaptation to novel hosts.

Furthermore, the hatching time of eggs laid by females that had developed in the 10L treatment was about 2 weeks in all populations examined (Fig. 3b). Though this egg period is longer than in the summer eggs of other egg-diapausing species such as *P. ulmi* (5–7 days at 23–25 °C, 15–16L; Gotoh et al. 2003; Yin et al. 2013), this is much shorter than their diapausing eggs (Lees 1953). Broufas and Koveos (2000) estimated the degree-days required for 50% hatching of *P. ulmi* winter eggs in apple orchards in northern Greece to be 129.4 ± 4.5 (mean \pm SE, based on a developmental threshold of 7.4 °C) from 10 February. On this basis, 10.3 days may be needed at a constant 20 °C after this date, but winter eggs are laid in early autumn, so the actual egg period should be much longer. For *S. brevisetosus*, the number of days required for summer-egg hatching is 7.0 ± 0.4 (mean \pm SD, $n = 22$) at 25 °C and 16L (Ito and Tamura 2017) and 11.7 ± 1.0 ($n = 33$) at 20 °C and 15L (in preparation). These periods are similar to the estimates for all the sample populations in the present study (Fig. 3b). There was also no significant difference in the proportion of unhatched eggs associated with altitude, which is often the case in egg diapause (Koveos and Broufas 1999). Therefore, the diapause of the eggs observed in this study was considered very weak. Although we observed that the eggs of females reared under 10L were orange like natural winter eggs, the eggs in the lab did not produce a robust cuticle like winter eggs do in the field (Ito and Yamanishi 2019). We hypothesise that exposure to short daylengths is insufficient to fully induce egg diapause, at least at 20 °C, even though the colour of the eggs did change. Since the experiments in our study were performed at a relatively high temperature (20 °C), a lower temperature may be needed to induce strong egg diapause. *Eotetranychus smithii*, which lives on semi-evergreen Rosaceae hosts, produces diapausing eggs at < 17.5 °C regardless of photoperiod (Gotoh and Kameyama 2014). We should investigate the effects of temperature further in *S. brevisetosus*.

Association with elevation

Generally, the seasonal period available for development and reproduction is shorter at higher altitudes because there are fewer days when the effective temperature is above the threshold for these activities. Therefore, the timing of diapause initiation and termination in insects and mites is usually correlated with altitude (Tauber et al. 1986). For example, diapause intensity, which governs diapause duration, is positively correlated with altitude in *T. urticae* (Koveos et al. 1993, 1999; Broufas and Koveos 2000; Saito et al. 2002). In the present study, the daily minimum temperature at the sampling sites around 300 m regularly fell below 0 °C in January (22 days in 2021 at Motoyama, 252 m a.s.l.; Japan Metrological Agency 2021), but this frequency was lower in the lowlands (15 days in 2021 at Gomen, 12 m a.s.l.). Nevertheless, we found no significant altitudinal cline in CDL, although the CDLs of the two populations from lower elevations were lower (11.5L, Fig. 2). Similarly, there were no altitudinal patterns in the number of days required for oviposition (Fig. 3a), egg hatching (Fig. 3b) and hatchability. A simple interpretation of these results would be that populations at different altitudes have similar timings of reproductive arrest and resumption (Fig. 3a) and a similar depth of diapause (Fig. 3b). It is probable that effective temperature, which is the sole selection pressure on the timing of reproductive arrest, is a weak pressure in the evergreen leaf environment (Shimazaki et al. 2019). Defoliation in autumn would also provide a selection pressure on the reproductive season of herbivorous arthropods (Komatsu and Akimoto 1995), but this factor does not affect *Q. glauca*.

The seasonal timing of a female's reproductive arrest influences offspring survivorship (Cohen 1970; Taylor 1986a, b; McNamara 1994). If all offspring are killed by low autumnal temperatures in mountainous areas, mothers should cease the deposition of summer eggs earlier to avoid the total loss of those offspring, which could instead be produced as winter eggs, to be part of the next year's population. However, if the cold-hardiness of mites at high altitudes is high, the optimal timing for reproductive arrest is rather complicated. Ito and Chae (2018a) found that the survival rates of late nymphal stages preserved at 4 °C for 30 days were moderate to high in the Kochi population of *Stigmaeopsis longus*, which inhabits evergreen bamboo leaves. If *S. brevisetosus* also has such a high level of cold-hardiness, temperature may not be the factor that limits the timing of the reproductive arrest. The cold-hardiness of each life stage of *S. brevisetosus* should be further explored.

Conclusion

The overwintering of *S. brevisetosus* is characteristic in that females completely stop ovipositing in response to short daylengths, and this arrest is maintained for several weeks before ovipositing resumes. These results are compatible with the observation that *S. brevisetosus* females cease oviposition in autumn and resume in winter. This period before they resume oviposition is much longer than that of the females of most other egg-diapausing species, and such a life cycle has not been previously reported. This pattern is possible only on evergreen hosts, which provide a stable habitat throughout the year. We could not find any indication that the CDL, the long pre-oviposition period, or the time required until egg hatching are correlated with elevation, unlike in previous studies in other species. These results support the occurrence of very weak egg diapause. In addition, an extended period of female oviposition arrest suggests the possibility of adult diapause. The above traits are related to adaptation in which females oviposit in winter when predator pressure is low. The adaptation to evergreen hosts in temperate zones may encourage the evolution of a range of overwintering patterns. These evolutionary pathways should be clarified using molecular phylogenetic analyses.

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