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Nocturnal activity in the arboreal Collembola *Willowsia japonica* (Folsom, 1987)

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Abstract

The diel cycle of *Willowsia japonica* was studied using traps on the tree trunk during the summer months. *W. japonica* was more active during nighttime than daytime on the trunk of *Quercus crispula* throughout summer, regardless of body size. The difference was, however, blurred by precipitation, which activated *W. japonica* even during daytime. However, precipitation increased diurnal activity levels and decreased the difference between daytime and nighttime abundance. Although other springtails such as *Desoria spatiosa, Subisotoma* sp., and *Tomocerus aokii*, as well as woodlice were more sensitive to respond to moisture than *W. japonica*, *W. japonica* is considered relatively tolerant to desiccation among springtails. Its diel cycle of activity still appears to be shaped by environmental moisture. We also found that the proportion of individuals with discernible gut contents did not significantly differ between night and day, but smaller individuals were more likely to have filled guts, suggesting that juvenile *W. japonica* feed at a higher rate than adults. In conclusion, the physiology of Collembola necessitates a relationship between activity levels and environmental moisture, even in species considered desiccation-tolerant such as *W. japonica*.

Keywords *Willowsia japonica* | nocturnal activity | precipitation | tree trunk | baiting technique

1 Introduction

Collembola are principal members of the soil animal communities (Bellinger et al. 1996–2024). Their behavior is likely to be affected by diurnal environmental fluctuations such as daylight and moisture, as their cutaneous respiration necessitates a thin and porous cuticle (Davies 1927). Ample studies on diurnal activity have been made on winter-active Collembola on the snow surface, showing their enhanced activity during daytime (e.g., Uchida & Fujita 1968, Fox & Stroud 1986, Hågvar 2000, Nekhaeva et al. 2024). However, studies in other habitats such as litter and soil are limited (Frampton et al. 2001). In these habitats, the level of disturbance is milder, and diurnal fluctuations are indirect compared to exposed environments. In contrast, the tree trunk represents a habitat where environmental conditions fluctuate regularly, and our trapping method, a non-destructive approach, facilitates investigations into Collembola ecology in this environment (Shaw 2015). We employed this technique to study diurnal activity of the arboreal collembolan, *Willowsia japonica* (Folsom, 1897), including in the context of precipitation, as moisture is critical for the survival of Collembola (Choi et al. 2006; Kaneda & Kaneko 2011).

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Willowsia japonica (Entomobryidae) is an arboreal species that seasonally migrates between the ground and trees. In Hokkaido, northern Japan, *W. japonica* overwinters on the ground under snow (Matsumoto et al. 2018), climbs up tree trunks just after snowmelt in April, and breeds from June to August (Matsumoto & Suma 2023). Our recent systematic surveys revealed that *W. japonica* was never found in the litter (Suma *et al*. 2025) but was abundant on trunks of *Quercus crispula* during summer months (Matsumoto *et al*. 2025).

In the present study, we aimed to reveal the difference in day *vs.* night activity of *W. japonica* during the summer months. Circumstantial evidence has implied that the difference is ascribed to moisture, though to a lesser extent than for other Collembola. Indeed, we found that precipitation increased diurnal activity, reducing the difference in diurnal and nocturnal activity levels. There was no difference in feeding activity in terms of day *vs.* night comparison, but small individuals were more feeding-active than large individuals.

2 Materials and methods

A block of forest (ca. 60 × 30 m) in a park in Chitose, Hokkaido, Japan (42°78′N, 141°60′E) as an experimental site – in a cool, temperate region with deep, long-lasting snow cover – was selected as an experimental site. The block was sub-divided into five, and investigations were made weekly, rotating around the sub-blocks, and repeated 11 times in 2024 and 15 times in 2025. The dominant tree was *Q. crispula*, alongside *Acer* spp., *Cerasus* spp., *Tilia japonica*, and others. The ground was covered with thick litter and had little undergrowth. A piece of jute mesh cloth (7 × 7 cm) folded into half was put in a plastic mesh bag (20 × 10 cm) to constitute a trap. Traps were fixed with plastic string onto the trunk of *Q. crispula* (20 to 40 cm diameter at chest height, Figure 1). Care was taken not to examine the same trees within a month. Data on precipitation were retrieved from the Meteorology Agency of Japan (https://www.data.jma.go.jp/stats/etrn/index.php).

Each investigation was conducted over three days, and eight trees each were examined (Table 1). A trap was installed twice on each tree, once for daytime and once for nighttime sampling, with a 36 hour interval between the sampling periods. The first daytime sampling was made from trees 1–4 between 06:00 and 18:00 (day 1) followed by the first nighttime sampling from trees 5–8 between 18:00 and 06:00 (days 1–2). Trees 1–4 were again examined for the nighttime period between 18:00 and 06:00 (days 2–3), and trees 5–8 for the daytime period between 06:00 and 18:00 (day 3).

Traps were subjected to the Tullgren extraction method to collect Collembola in 100 % isopropanol. *W. japonica* was identified, according to Ichisawa (2015), selected and counted under a dissecting microscope (Olympus SZ60, Tokyo) for each trap to preserved in 70 % ethanol. Specimens were randomly mounted in Hoyer's medium on glass slides to determine body length and feeding activity. The proportion of specimens from each trap mounted ranged from 40–100 %. Mounted specimens were photographed along with a ruler with a digital camera (Olympus Stylus SH-1, Tokyo), and enlarged photos were used to precisely determine body lengths.

Figure 1. A trap set on a tree trunk.

Table 1. Investigation scheme of *Willowsia japonica* on Quercus crispula trunks

Daytime (06:00-18:00)		Nighttime (18:00-06:00)	
Day 1	trees 1, 2, 3, and 4	Days 1–2	trees 5, 6, 7, and 8
Day 3	trees 5, 6, 7, and 8	Days 2–3	trees 1, 2, 3, and 4

Specimens were divided into eight size classes with an interval of 0.21 mm. Individuals with visible gut contents were regarded as feeding-active, and those with no visible gut contents as feeding-inactive. Other species such as *Desoria spatiosa, Subisotoma* sp., and *Tomocerus aokii* and woodlice (Isopoda) were also captured.

T-tests were first used to compare daytime *vs.* nighttime activity levels per weekly investigation, and the results were then fortified by the generalized linear mixed model (GLMM). To ascertain the relationship between the time of day, precipitation, and activity levels, a generalized linear mixed model (GLMM) was fitted using the *glmmTMB* package in R v. 4.4.3 (Brooks et al. 2017, McGillycuddy et al. 2025, R Core Team 2025). This model had the formula:

$$\textit{individuals} \sim \textit{time of day} * \textit{precipitation} + (1 \mid \text{Date}) + (1 \mid \text{Date:Tree.ID})$$

and a negative binomial error distribution to account for overdispersion. The statistical relationships between time of day, body size, and the presence of gut contents were determined using a binomial GLMM with the formula:

$$\textit{cbind(Full,Empty)} \sim \textit{time of day} * \textit{body size} + (1 \mid \text{Date})$$

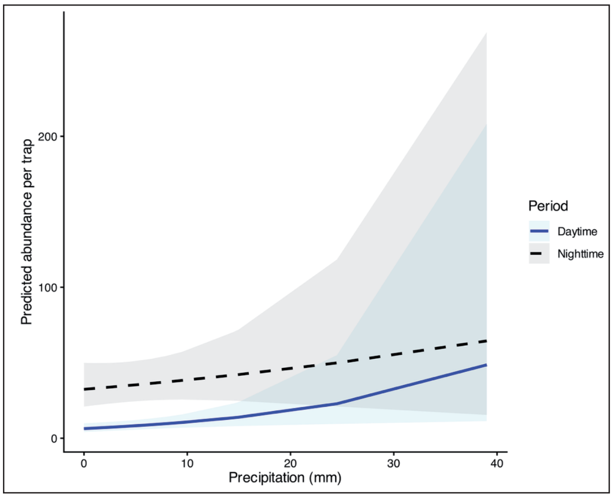

Figure 2. Predicted abundance of *Willowsia japonica* in tree-trunk traps with increasing precipitation, for both daytime and nighttime sampling periods.

3 Results

In 2024, a total of 13 investigations yielded 5934 individuals of *W. japonica* (daytime 2684, nighttime 3250) (Table 2). When comparing nocturnal and diurnal activity levels for each weekly investigation using t-tests, numbers of individuals collected per trap were larger during nighttime than daytime sampling periods in 11 investigations; in eight of them, differences

Table 2. Number of *Willowsia japonica* collected per trap during daytime and nighttime in 2024. t-tests were conducted to determine whether the means of two groups were significantly different from each other at the 0.05 (*), 0.01(**), and 0.001 (***) levels, or not significant (ns). Precipitation represents the sum of the three-day investigation period, including the intervals between samplings. Data from the Meteorology Agency of Japan. https://www.data.jma.go.jp/stats/etrn/index.php

Investigation start date	Daytime mean ± sd	Nighttime mean ± sd	t-test	Precipitation (mm)
June 17	1.1 ± 2.1	21 ± 30.6	ns	15
26	1 ± 1.7	3.7 ± 2.7	ns	0
July 1	5.9 ± 3.9	34.4 ± 21.4	**	3
9	4.5 ± 5.5	26.4 ± 9.1	***	0.5
Aug. 6	241.8 ± 361.2	76.5 ± 75	ns	14.5
11	33.9 ± 10.6	21.1 ± 17.4	ns	9.5
16	6 ± 7.1	13 ± 0.7	*	0
Sept. 6	8 ± 9.9	27.6 ± 4.2	***	3.5
9	7.8 ± 7	78.5 ± 35	***	2.5
12	1.5 ± 2.1	22.3 ± 12.2	**	1
15	18 ± 15.5	38.3 ± 18.9	ns	39
19	1.5 ± 2.7	22.4 ± 15.8	**	0.5
24	4.6 ± 5.1	21.3 ± 17.1	**	4.5

Table 3. Number of *Willowsia japonica* collected per trap during daytime and nighttime in 2025. t-tests were conducted to determine whether the means of two groups were significantly different from each other at the 0.05 (*), 0.01(**), and 0.001 (***) levels, or not significant (ns). Precipitation represents the sum of the three-day investigation period, including the intervals between samplings. Data from the Meteorology Agency of Japan. https://www.data.jma.go.jp/stats/etrn/index.php

Investigation started from	Daytime mean ± sd	Nighttime mean ± sd	t-test	Precipitation (mm)
May 8	0.6 ± 0.7	45.5 ±36.7	*	9.5
13	1.1 ± 1.1	9.6 ± 6.2	**	0
21	0.8 ± 0.9	6 ± 6.5	ns	0
June 4	3.4 ± 3.5	18.1 ± 18.3	ns	0.5
16	11.5 ± 14.7	38 ± 50.1	ns	4
23	18.4 ± 8.6	29.3 ± 12.1	ns	0
July 6	10.4 ± 10.1	80.9 ± 43.3	**	0
13^d	20.7 ± 20.1	50.4 ± 46.8	ns	5
21	13.4 ± 6.3	86.6 ± 42.8	**	0
Aug. 13	15.1 ± 15.9	110 ± 97.4	*	4.5
20	22.5 ± 19.2	25 ± 25.4	ns	8
28	7.53 ± 3.7	13.83 ± 8.5	ns	24.5
Sep. 4	5.4 ± 2.7	26 ± 21.4	*	0
10	7.6 ± 7.3	28 ± 31.8	ns	6.5
18	2.1 ± 3	3.6 ± 2.4	ns	0

were significant, but not in three (Table 2). In the investigations started from August 6th and 11th, more animals were captured during daytime sampling. The August 6th investigation, collected a total of 1934 and 612 individuals for daytime and nighttime samplings, respectively. During the daytime, a single trap collected 1126 individuals, and 1092 (97.0%) were juveniles; this outlier may explain the opposing trend. Regardless of sampling time, a large number of ants, presumed to be *Pristomyrmex* sp., was trapped along with with numerous juveniles. Similar results were obtained in 2025 (Table 3). Across 15 investigations, 5322 individuals were captured (daytime 949, nighttime 4373). Nighttime samplings always yielded larger numbers of individuals per trap than daytime samplings, and the difference was significant in six investigations out of 15.

Our GLMM (Figure 2) revealed that nighttime abundance was approximately five times greater than daytime abundance (estimate = 1.62 on a log scale, $p < 2e\text{-}16$) and, controlling for time of day, precipitation increased by a factor of about 1.05 per mm (estimate = 0.0521, $p = 0.0154$). The interaction term showed that precipitation increased diurnal activity levels more than nocturnal activity levels (estimate for periodNighttime:precipitation = -0.0344, $p = 0.00221$).

Analyses of population structure based on body size showed a similar pattern in both 2024 and 2025, and the 2025 data were presented (Figure 3). Pooled data were presented for the May investigations since the number of animals collected during daytime was too small. The size distribution pattern changed with time (Fisher's exact test, $p < 0.0001$ for both day and night). The population consisted exclusively of large individuals in May, and eggs were often recognized within the abdomen of the May 21–23 specimens. In June, juveniles emerged and predominated within the populations, and large individuals almost disappeared. In July and August, juveniles decreased, and large individuals increased within the population. There were no significant differences between the day and night distributions for each month, except for August (Fisher's exact test, $p = 0.0002$), during which the smallest size class was overrepresented at night (chi-square residual = 3.88) and the second-smallest size class was overrepresented during the day (residual = 4.78).

The feeding activity of the populations in June and July 2025 was compared in terms of sampling time and body size (Table 4). This time period was chosen due to the sufficient abundance of both adult and juvenile individuals. The time of sampling did not significantly

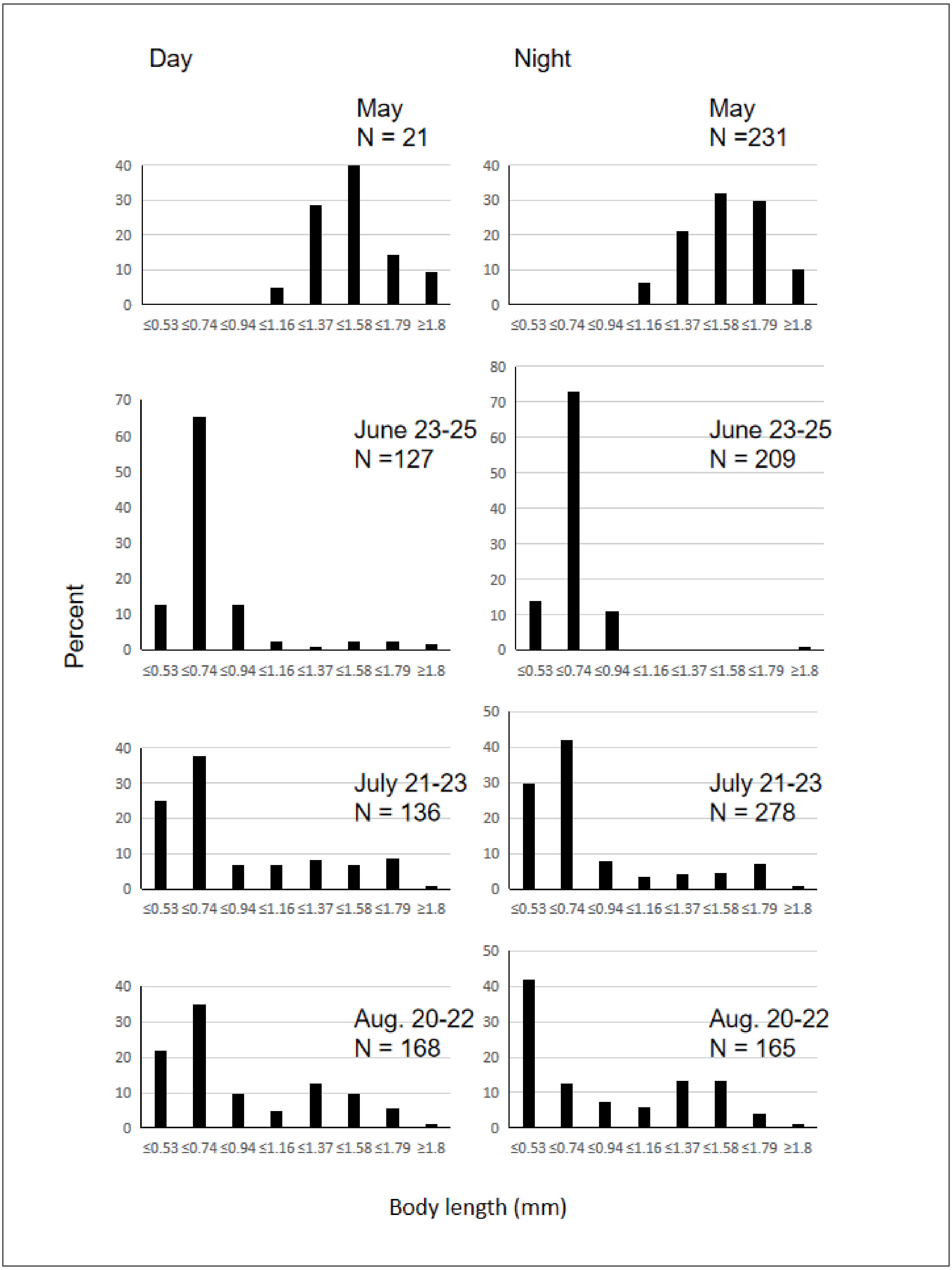

Figure 3. Change in population structure with time in 2025. Specimens collected from May to August were sorted according to body length classes.

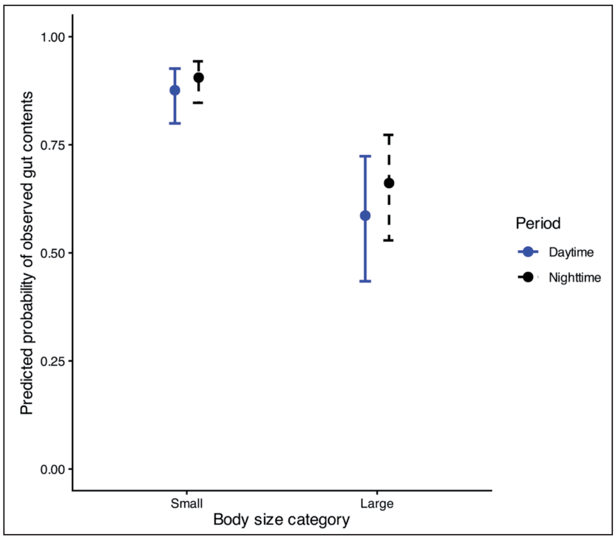

Figure 4. From our binomial GLMM, the predicted probability of an individual having discernible gut contents depending on body size and time of day.

affect feeding activity; the overall activity averaged 79.0 % (65.4 to 87.5 %) for daytime sampling and 80.3 % (56.1 to 99.5 %) for nighttime sampling (binomial GLMM estimate = 0.325 on the log-odds scale, p = 0.150). However, the difference was evident between small (≥ 1.16 mm long) and large (< 1.16 mm long) animals; the former showed 88.5 % of feeding activity (63.5 to 100%) and the latter 58.4 % (0 to 100%). The binomial GLMM (Figure 4) indicated an approximately five-fold increase in the odds of smaller individuals having filled guts (estimate = 1.62, p = 1.98e-11). There was no significant interaction between time of day and body size (estimate for periodNighttime:Body.sizeSmall = -0.0207, p = 0.944).

4 Discussion

Our previous studies have revealed the life cycle and arboreal nature of *W. japonica*. *W. japonica* (=*Himalanura ezoensis*) overwinters and develops in lichen colonies on the ground, and possibly in litter under snow during winter months (Matsumoto *et al.* 2018). This springtail actively feeds on fungal mycelia growing on dead grass under snow in late winter (N. Matsumoto, unpublished). *W. japonica* was the first to climb tree trunks in May (Matsumoto *et al.*, 2025) and appear reproductively active; Matsumoto & Suma (2023) described the reproductive cycle as follows: genital pores were evident in five out of 16 animals (31.3 %) on April 19 and 11 out of 14 (78.6 %) on June 24, and juveniles (smaller than 0.53 mm) first occurred in June. Three quarters of the Collembola populations on the trunk of *Q. crispula* were *W. japonica* (Matsumoto *et al.* 2025), but *W. japanica* was never found on the forest floor in summer (Suma *et al.* 2025). Overall, the mode of its life cycle is similar to *W. platani* in Europe (Shaw 2015). Dense scale coating alleviates damage

Table 4. Percent individuals with filled guts captured during daytime and nighttime. Small: ≥ 1.16 mm long; Large: < 1.16 mm long. Figures indicate percent individuals. Numbers of individuals determined in parentheses.

Investigation started on	Captured during	Body class		Overall mean
		Small	Large	
June 4	daytime	100(4)	50(18)	68.1(22)
	nighttime	87.5(24)	54.8(115)	60.4(139)
16	daytime	84.8(79)	100(6)	85.9(85)
	nighttime	93.6(233)	83.8(18)	92.8(251)
23	daytime	93.2(118)	0(9)	86.6(127)
	nighttime	98.6(206)	66.7(3)	99.5(209)
July 6	daytime	74.6(63)	51.2(41)	65.4(104)
	nighttime	63.5(96)	46.8(77)	56.1(173)
13	daytime	90.8(98)	34.8(23)	80.2(121)
	nighttime	87.2(148)	62.5(64)	79.7(212)
21	daytime	90.3(103)	78.8(33)	87.5(136)
	nighttime	97.8(232)	71.7(46)	93.5(278)
	Mean	88.5	58.4	

from desiccation to help *Willowsia* spp. survive in an arboreal habitat in summer (Shaw 2015).

The arboreal habitat is characterized by diel changes in temperature and moisture. We found that *W. japonica* was more active during nighttime. This may apply to both male and female animals, since they were both present on the tree (Matsumoto & Suma 2023). Although color pattern is claimed to characterize sexual dimorphism (Yoshii 1992), Hisamatsu & Itoh (1997) did not refer to color pattern dimorphism in their breeding experiments, and we were unable to distinguish the sexes. Increased nocturnal activity levels could be explained by the cooler temperatures and reducing rates of water loss through cuticular transpiration.

Our circumstantial evidence further indicates a role of moisture in determining the activity levels of *W. japonica*; precipitation increased overall activity levels, and the distinction between activity levels in the daytime and nighttime appeared was blurred on rainy days. These results resemble previous studies on other species of Collembola which demonstrate the importance of moisture on activity. Rainfall is known to stimulate the climbing activity of *Entomobrya nivalis* and *Orchesella cincta* (Bowden *et al*. 1976). Further, an isotomid collembolan migrates vertically after a short spell of heavy rain (Farrow & Greenslade 1992). In the case of another arboreal species, *Xenylla brevispina*, eggs are deposited in the litter to avoid desiccation, and juveniles subsequently climb trees (Ito 1991). However, *W. japonica* does differ from these cases in that it appears to reproduce in the dry environment of the trunk, rather than migrate upwards only after rain, given its absence from the forest floor during summer (Suma et al. 2025). This implies that *W. japonica* is relatively tolerant to desiccation. Our trapping results also suggest moisture may be more crucial to the Collembola other than *W. japonica*; miscellaneous springtails such as *D. spatiosa, Subisotoma* sp., and *T. aokii* appeared to respond more sensitively to precipitation. This would corroborate previous results showing that different species of Collembola reacted differently to moisture on the tree trunk (Bauer 1979).

How predation affects *W. japonica* in the arboreal habitat remains yet to be elucidated. The ant, *Pristomyrmex* sp. was present in large numbers on almost every tree during both daytime and nighttime but very seldom captured with the sole exception of the August 6th, 2024 sampling―the climax of breeding season (Matsumoto & Suma 2023). Spiders were very seldom trapped. Further studies are necessary to elucidate the effect of predators in the arboreal habitat of *W. japonica* during the summer months..

We failed to show any difference in the activity between daytime and nighttime in terms of age of *W. japonica* individuals, as determined by body length. Change in population structure over the summer months agreed with our previous observations (Matsumoto & Suma 2023). Difference in feeding activity was also as predicted; smaller individuals were more feeding-active than larger individuals during June and July. The degree to which juveniles feed at a significantly higher rate than adults may be even greater than our statistical analyses indicate. This is because juveniles with empty guts were, in many cases, molting or had just molted as identified by their hyaline appearance, and feeding activity is likely to be reduced at such stages given their greater vulnerability to biotic and abiotic stressors. Only considering non-moulting individuals would likely increase the difference in feeding activity between juveniles and adults.

5 Conclusion

Willowsia japonica migrates to the arboreal habitat in summer (Matsumoto et al. 2025) and is entirely absent from the litter on the ground (Suma et al. 2025). Arboreal behaviour may be a means of escape from competition and predation in the litter. The arboreal habitat is under the influence of diurnal fluctuations in temperature and moisture. We here demonstrated this species' nocturnal activity on the tree trunk; this may be driven primarily by moisture levels, given the apparent reduction in the difference in daytime and nighttime activiy levels following precipitation. This is despite circumstantial evidence implying that *W. japonica* is relatively tolerant to desiccation; its dense scale coating, typical of corticolous species, should protect it from desiccation and allow it to dominate in summer, as is the case with *Willowsia platani* (Shaw 2015). Therefore, the physiology of Collembola necessitates a relationship between activity levels and environmental moisture, even in species considered desiccation-tolerant.

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