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Diversity in life types of spider mites

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Phytophagous spider mites, belonging to the subfamily Tetranychinae, have diverse lifestyles. Life type is an important concept for understanding spider mite diversity. There are three basic life types: little web (LW), non-systematic and complicated web (CW), and woven nest (WN), which are characterised by silk production, silk usage patterns, faeces defaecation patterns, and other behavioural outcomes. In this review, we first address the diversity of life types and then discuss the functions of life types as reported by several studies. The primary function of the CW type is to provide a firm footing for residing on the underside of host leaves and to protect mites from the deleterious effects of solar radiation. Next, we discuss how spider mites have evolved various defence mechanisms through life types to avoid their natural enemies. We observed that the life type can affect the results of interspecies competition. Faeces manipulation behaviours observed in the CW and WN type mites may be an adaptation to keep a clean habitat. The CW species showed a significantly higher intrinsic rate of natural increase (r_m) than LW and WN species, and such differences may be associated with host plant stability. Although there was no apparent relationship between sex ratio and life type, the extremely female-biased sex ratio in several WN species appears to contribute to local mate competition. In contrast, WNs strongly affect the aggressiveness of males because they provide a recognisable domain that they should defend. Furthermore, the WN type enhances mite aggregation in nests, and their iteroparous reproduction causes generation overlapping. Such traits may lead some WN species to develop advanced sub-sociality (cooperative sociality).

KEYWORDS

Tetranychinae, Phytoseiidae, Tetranychus, *Panonychus*, *Stigmaeopsis*, *Typhrodromus*

1 Introduction

The class Arachnida, including spiders, are widely known for their silk production and used in various industries. In the related superorder Acariformes, silk producers are found in several taxa, such as Bdellidae, Cheyletidae, Anystidae, and Tetranychidae (Walter and Proctor, 1999). Spider mites, belonging to the subfamily Tetranychinae, are tiny herbivores that produce silk threads from terminal eupathids (silk glands) present on the tips of their pedipalpi (Jeppson et al., 1975). These silk threads function as lifelines for spider mites, aiding in their movement (Saito, 1977a), as well as in the formation webs and tent-like structures. Saito (1983) recognised three basic lifestyles in spider mites and defined 'life type' as a way of living on host-plant leaf surfaces with silk production and usage patterns (threads and webs), defaecation patterns, and other behavioural outcomes such as positions where eggs are placed and where mites enter quiescent phases. Jeffries and Lawton (1984) defined 'enemy-free space' as a type of prey strategy that reduces or eliminates vulnerability to natural enemies. They stressed that the struggle for enemy-free space in natural communities is an important component of the divergent evolution of phytophagous species. Thus, we hypothesised that the life types of spider mites reflect an approach to avoid natural enemies. Here, we introduce the diversity of life types of spider mites and the functions of silk threads. We then discuss the relationships between life types and prey-predator interactions, interspecific competition, faeces management to maintain a clean habitat, life history, sex ratio, sexual selection, and social behaviour. The aim of this review is to understand the diversity and evolution of spider mites from the perspective of life types.

2 Diversity of life types

2.1 Little web type

The simplest of the three life types is the little web (LW) type. LW type is found in the genera *Aponychus*, *Eutetranychus*, *Panonychus*, and *Yezonychus* (Saito, 1983; Mushtaq et al., 2023). *Aponychus firminae* does not produce silk threads (LW-f hereafter, where the lowercase letter refers to sub-category; see Saito (1983) and Saito (1995b) for more details). *Aponychus corpuzae*, on the other hand, produces silken webs for covering the eggs, which is the simplest example of a silken structure (LW-j) in Tetranychinae. *Panonychus citri* and *Panonychus ulmi* always produce silk threads while walking (Saito, 1977a) but they do not construct any web structures other than 'guy ropes' extending from their slender stalks on eggs to the leaf surfaces (Figure 1, LW-c; Beament, 1951).

2.2 Complicated web type

Most *Tetranychus* species and some *Eotetranychus*, *Oligonychus*, and *Schizotetranychus* species have another life type called the CW (non-systematic and complicated web) type (Saito, 1983, 1995b, 2010; Mirza et al., 2018; Mushtaq et al., 2021). Saito (1977a) showed that *Tetranychus urticae*, a well-known pest spider mite in various crops, always spins silk threads while walking. Because females tend to aggregate on leaf depressions (e.g. along leaf midribs), the silk threads produced by them accumulate there and form a web structure. They frequently walk on the web to deposit eggs and faeces (Hazan et al., 1974; Saito, 1983; Gerson, 1985; Mirza et al., 2018) and also use the web for their quiescent phase (CW-u, Figure 1). Leaf depressions over which CW webs accumulate are sometimes created by *Tetranychus* spp. themselves (Oku et al., 2006; Oku and Yano, 2007).

Sasanychus akitanus forms two to three layers of fine webs over depressions on the leaf undersurfaces of the host plant *Sasa senanensis*. The webs do not form the complicated structure like CW-u species and rather appear a stratified structure. The mites walk on these layers and deposit eggs and faeces, as well as enter a quiescent phase in these layers (CW-a, Saito, 1983). Thus, CW type is not just a product of accumulated silk threads but is constructed for specific functional reasons.

2.3 Woven nest type

Many species of spider mites build systematic nest-like web structures on the leaf surfaces of their host plants, which is defined as the woven nest (WN) type (Saito, 1983). *Eotetranychus suginamensis*, *Schizotetranychus shii*, and *S. brevisetosus* construct nests with dense webs over leaf depressions and always deposit their faeces on the roofs of WNs; therefore, their nests are coated with faeces (WN-s).

Among the species forming the WN life type, *Stigmaeopsis* species show the most sophisticated nesting behaviour (before the study by Saito et al. (2004), they were classified as *Schizotetranychus*). Most species of this genus have a sub-life type, WN-c, which is characterised by solid WNs on leaf undersurfaces with faecal deposits at particular locations near the nest entrances (Figure 1). A similar life type has been reported in *Oligonychus perseae* infesting avocado trees, although faeces are not always deposited at specific locations (Aponte and McMurtry, 1997).

Neonidulus tereotus forms a WN-n type, in which the faecal deposition pattern is largely different from that of WN-s and WN-c (Saito et al., 2016). The mites build dense WNs alongside the main vein of the leaf undersurfaces and live there gregariously. The faeces deposited within the nest form a concentric circle (similar to a low-clay rampart) around the nest periphery. Most eggs are laid inside the faecal circle, where immature mites also reside (Saito et al., 2016).

In contrast to previous WN types, *Schizotetranychus recki* with WN-r does not live in groups but instead creates individual nests (like compartments) using two or three leaf hairs on the undersurfaces of the host plant, *Sasa* spp. The mites make private nests, feed, and enter quiescent stages in these nests. The females also weave dense webs around individual eggs (Saito, 1983, 1995b, 2010).

2.4 Multiple life types

Life types are not always fixed in certain species. As reported by Saito (1983), one species can sometimes exhibit different life types depending on the leaf structure of the host plant. *Eotetranychus tiliarium* forms a CW-r type on *Alnus hirsuta* and a WN-t type on *Alnus japonica*. Additionally, the physical features of the leaf are sometimes pivotal for spider mites, e.g. *S. recki* to achieve their life types. However, Mushtaq et al. (2023) observed that *T. urticae* (CW-u), *Eutetranychus orientalis* (LW-j), and *E. palmatus* (LW-j) exhibit a consistent life type, even in different host plants. The authors concluded that these spider mites are highly adapted to the resources of different host plants for survival, with slight variations in some important life type characteristics.

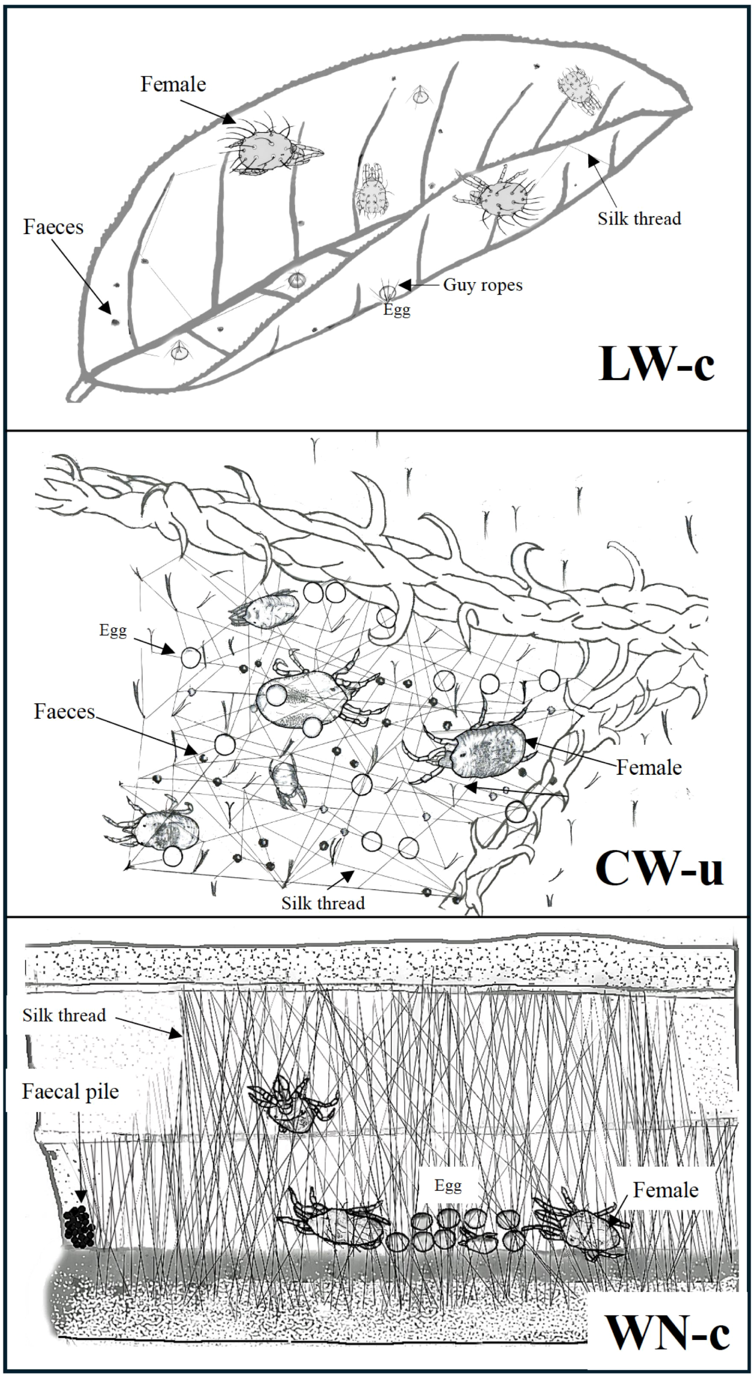

FIGURE 1
Sketches of three life types in spider mites: LW-c (*eg. Panonychus citri*) representing LW, CW-u (*eg. Tetranychus urtiace*) representing CW and WN-c (eg. *Stigmaeopsis longus*) representing WN. These drawings do not reflect actual body sizes.

3 Functions of life types

3.1 Primary function of CWs and WNs

It is difficult to determine the 'function' of a certain character in the evolutionary sense (Williams, 1966). In this review, we adopt a practical usage of the term 'function', i.e. if there is evidence that a particular life type aids spider mites in overcoming any adverse conditions, such as gravity, climatic conditions, predators, competitors, and diseases, we consider such a case to be indicative of the function of the life type.

However, before considering life type functions, we should address the fundamental question of why most spider mites prefer to live on the undersurface of host plant leaves (Table 1). This preference is considered an adaptation to avoid rainfall (Jeppson et al., 1975) and ultraviolet B (UVB) radiation (Barcelo,

TABLE 1 Intrinsic rate of natural increase (r_m), life type and sex ratio for species of Tetranychinae.

Species	Leaf side infested	Life-type +subtype	Source of life-type	r_m	Source of r_m	Sex (male) ratio	Source of sex ratio
Aponychus corpuzae	underside	LW-j	Saito and Ueno, 1979	0.181	Saito and Ueno, 1979	0.33	Saito and Ueno, 1979
Panonychus citri	both sides	LW-c	Saito, 1983	0.209	Gotoh et al., 2003	0.25	Saito, 1979
Panonychus ulmi	both sides	LW-c	Saito, 1983	0.193	Gotoh et al., 2003	0.17	Gotoh et al., 2003
Eutetranychus orientalis	both sides	LW-j	Saito, 1995b	0.143	Elhalawany, 2019	0.24	Elhalawany, 2019
Panonychus mori	both sides	LW-c	Saito, 1995b	0.198	Gotoh et al., 2003	0.21	Gotoh et al., 2003
Yezonychgus sapporensis	underside	LW-s	Saito, 1983	0.126	calcu. from Saito, 2010	–	–
Sasanychus akitanus	underside	CW-a	Saito, 1983	0.214	Saito, 1992	0.11	Gotoh, 1987b
Tetranychus cinnabarinus	underside	CW-u	Saito, 1983	0.237	Hazan et al., 1973	0.43	Hazan et al., 1973
Tetranychus desertorum	underside	CW-u	Saito, 1983	0.290	Nickel, 1960*	0.33	Nickel, 1960*
Tetranychus evansi	underside	CW-u	presumed from Sarmento et al., 2011	0.277	Gotoh et al., 2010	0.12	Gotoh et al., 2010
Tetranychus piercei	underside	CW-u	Saito, 1995b	0.275	Ullah et al., 2014	–	–
Tetranychus kanzawai	underside	CW-u	Saito, 1983	0.268	Kondo and Takafuji, 1985	0.34	Kondo and Takafuji, 1985
Tetranychus urticae	underside	CW-u	Saito, 1983	0.336	Shih et al., 1976	0.31	Saito, 1979
Amphitetranychus vienensis	underside	CW-u	Saito, 1983	0.172	Gotoh, 1986	0.18	Gotoh, 1986
Schizotetranychus bambusae	underside	CW-b	Saito, 1983	0.221	calcu. from Saito, 2010	0.21	Saito, 2010
Eotetranychus tiliarium	underside	WN-t	Saito, 1983	0.178	Gotoh, 1987a	0.21	Gotoh, 1987a
Eotetranychus uncarus	underside	WN-u	Saito, 1983	0.198	Gotoh, 1987a	0.16	Gotoh, 1987a
Oligonychus castaneae (ununguis)	upperside	WN-u	Saito, 1983	0.178	Saito, 1979	0.47	Saito, 1979
Oligonychus perseae	underside	WN -c	Aponte and McMurtry, 1997	0.160	Imbachi-Loípez et al., 2017	0.08	Imbachi-Loípez et al., 2017
Stigmaeopsis longus	underside	WN -c	Saito, 1995b	0.162	Saito and Takahashi, 1982	0.13	Saito and Takahashi, 1982
Stigmaeopsis takahashii	underside	WN -c	Saito et al., 2004	0.135	Saito and Takahashi, 1982	0.16	Saito and Takahashi, 1982
Stigmaeopsis miscanthi	underside	WN -c	Saito, 1995b	0.144	Saito et al., 2013	0.13	Saito et al., 2013
Stigmaeopsis celarius	underside	WN -c	Saito et al., 2004	0.092	Mori, 2000, see Saito, 2018	0.28	Mori, 2000
Stigmaeopsis sabelisi	underside	WN -c	Saito et al., 2018	0.115	Saito et al., 2013	0.12	Saito et al., 2013
Stigmaeopsis nanjingensis	underside	WN -c	Saito and Zhang, 2017	0.090	Zhang, 2002	–	–
Stigmaeopsis saharai	underside	WN -c	Mori and Saito, 2005	0.113	Mori, 2000, see Saito, 2018	0.21	Mori, 2000, see Saito, 2018
Stigmaeopsis tenuinidus	underside	WN-p	Saito et al., 2016	0.080	Zhang, 2002	0.15	Zhang, 2002
Schizotetranychus cercidiphyli	underside	WN-u	Saito, 1983	0.160	Gotoh, 1983	0.25	Gotoh, 1989
Schizotetranychus lespedezae (leguminosus)	underside	WN-t	Saito, 1983	0.173	Gotoh, 1983	0.28	Gotoh, 1983
Schizotetranychus schizopus	underside	WN-t	Saito, 1983	0.206	Gotoh, 1983	0.17	Gotoh, 1989

(Continued)

TABLE 1 Continued

Species	Leaf side infested	Life-type +subtype	Source of life-type	r_m	Source of r_m	Sex (male) ratio	Source of sex ratio
Schizotetranychus recki	underside	WN-r	Saito, 1983	0.156	calcu. from Saito, 2010	–	–
Schizotetranychus brevisetosus	underside	WN-s	Saito, 1995b	0.062	Tamura and Ito, 2017	0.12	Tamura and Ito, 2017

-, data was unavailable, * under 25±2°C.
The literatures reported the maximum value of r_m were referred. The life history and sex ratio data were obtained under 25±1°C.

1981). Ohtsuka and Osakabe (2009) supported the latter idea by demonstrating that egg hatching and juvenile development were significantly suppressed on the upper side of leaves exposed to sunshine or on leaves placed under a UV-transparent film. Plant leaves serve as selective sunscreens for small arthropods on the undersurfaces of leaves (Lavola et al., 1998). Thus, as they lack resistance to solar radiation, spider mites often select leaf undersurfaces to reside (Osakabe, 2021). Sakai et al. (2012) tested the fecundity of *T. urticae* using kidney bean leaf discs with their adaxial or abaxial sides facing upward or downward under laboratory conditions. They revealed that the adaxial leaf surfaces rather have a nutritional advantage over abaxial surfaces. Then these nutritional factors did not explain the biased distribution of *T. urticae* to leaf sides. Therefore, the deleterious effects of solar UVB radiation and heat on spider mites may explain why most spider mites live on leaf undersurfaces.

Even if spider mites can thrive equally well on both leaf sides, they may still choose to reside on the underside to escape from the deleterious effects of solar radiation. However, this escape strategy comes with the risk of falling. Saito (1977a) observed that *T. urticae* occasionally lost their footing while walking on the underside of downward-facing smooth (webless) leaf surfaces. These mites rely on silk threads to suspend themselves and subsequently ascend the leaves by climbing the threads, underscoring the significance of silk threads as lifelines during locomotion (Saito, 1977a). This phenomenon also suggests that *T. urticae* (and most *Tetranychus* spp.) has an insufficient structural apparatus (empodia) to walk around smooth leaf undersurfaces that face downward. Saito (2010) stressed the importance of empodium morphology in facilitating the movement of *T. urticae* on dense CWs. The empodium of *T. urticae* consists of three pairs of fine hairs (proximoventral hairs) that open radially, which may enable mite legs to firmly grasp the thin and disordered web threads (Gutierrez and Helle, 1985). Conversely, the clawless empodia of this species, with low efficiency for gripping the leaf substratum, may make their movement on the undersides of downward-facing smooth (non-web) host difficult. Consequently, *T. urticae* and related species (with clawless empodia) should have developed other ways to compensate for such limitations and live stably on the leaf undersides. Saito (1977b) reported that the silk threads (silk segments) of *T. urticae* females are distributed aggregately on leaf undersides (facing downward) for a day after introduction, indicating that the females first move around frequently in a confined area to accumulate silk threads (see also Saito, 1985).

These results suggest that *T. urticae* needs to immediately produce dense webs on newly invaded leaf undersides to avoid the negative effects of solar radiation and gravity. Thus, the primary functions of CWs accumulated on the leaf underside include ‘footing’ (Saito, 1985) and/or ‘safety net’. Several studies have reported heterospecific web sharing in *Tetranychus* spp (Yano, 2012; Sato et al., 2016), and this phenomenon may be explained by the primary function of CW: mites should enter webs pre-produced by either conspecifics or heterospecifics to avoid falling off from the leaves and to avoid solar radiation. Meanwhile, Yano (2008) found that dispersing females of *T. urticae* follow the trails left by preceding females. This behaviour is thought to be due to the movement of a new colony within a group. However, the phenomenon may also stem from their aversion to walking on webless surfaces and preference to walk on the silk threads left by preceding females, as webless surfaces are considerably dangerous. The WN life type, characterised by nesting behaviour with silk, undoubtedly saves mites from the force of gravity as a safety net, considering that almost all species live on the leaf underside.

3.2 Life types as predator avoidance devices

The CW produced by *Tetranychus* spp. on leaf surfaces impedes the entry of generalist and specialist predators in different manners (Putman, 1962; McMurtry and Scriven, 1964; McMurtry and Johnson, 1966; McMurtry et al., 1970; Gerson, 1979; Sabelis, 1981; Gerson, 1985; Sabelis and Bakker, 1992; McMurtry and Croft, 1997; Yano, 2012; McMurtry et al., 2013). If specialist predators such as *Phytoseiulus persimilis*, *Neoseiulus womersleyi*, and *Neoseiulus californicus* can cope with the webs (Sabelis and Bakker, 1992; Shimoda et al., 2009), spider mites may change their oviposition and/or quiescent sites from leaf surfaces to webs to avoid (or mitigate) predation (Oku et al., 2003; Otsuki and Yano, 2017). Oku and Yano (2007) observed that female *Tetranychus kanzawai* (CW-u) and *T. urticae* tend to deposit their eggs on webs immediately after encountering predators (also see Murase et al., 2017). Furthermore, Lemos et al. (2010) reported that *Tetranychus evansi* eggs laid on webs were less frequently preyed upon by the predatory mite *Phytoseiulus longipes* than those laid on leaf surfaces. These results suggest that the shift in oviposition and quiescent sites from leaf surfaces to webs is a strategy to reduce predation risks (Grostal and Dicke, 1999).

Dittmann and Schausberger (2017) showed that *T. urticae* females aggregate more closely and are more active in the presence of predator cues. The benefit of tighter aggregation arises from the encounter and dilution effects, the combination of which is called attack abatement (Schausberger et al., 2021). Here, the CWs may provide a refuge and landmark for individual mites to aggregate.

However, Okada and Yano (2021) reported that rainstorms had a negative effect on *T. kanzawai* eggs deposited on webs, as strong rainstorms can easily remove the eggs deposited on CWs. They hypothesised that there is a trade-off in selecting the oviposition sites by *T. kanzawai*—the eggs on webs are advantageous for escaping predation but disadvantageous for survival under adverse climatic conditions.

To understand the additional functions of the WN life type, 'removing' and 'non-removing (intact)' life type experiments have proven to be useful. Horita et al. (2004) removed the webs covering *S. recki* eggs and compared the probability of predation between eggs with and without web protection. The WN-r type nests effectively protected the eggs from four species of sympatric predators (Table 2). An exception was *Agistemus summersi*, which exhibited a preference for preying on eggs contained within web nests than on those without nests. In this case, the web is likely a cue for the predator to locate the prey eggs. The WN-r type in *S. recki* functions as a refuge for spider mites from predators; however, in the case of *A. summersi*, WN exposes spider mites to danger.

Mori and Saito (2004) addressed the functions of the WN-c type by observing three species, *Stigmaeopsis longus*, *Stigmaeopsis takahashii*, and *Stigmaeopsis saharai*, inhabiting *Sasa senanensis* and having different-sized nests. Several females of each species were introduced onto detached *S. senanensis* leaves. After the females had constructed their web nests and deposited a sufficient number of eggs within them, the females were removed, and the 'web-removal' and 'web-intact' treatments were conducted. Several predator species that occur sympatrically on *S. senanensis* were introduced individually into each experimental arena. The results clearly showed that the nests had strong protective effects on the eggs (Table 2). The key points from these results are that the protective effect of the WN type is positive but varies among nests of different sizes and among predator species.

Another function of the WN-c type has been observed in *S. takahashii* (and probably *S. saharai*), which builds many small separate nests during its lifetime. Randomly scattered nests have an indirect effect by creating void nests after predation, effectively decreasing predator-searching efficiency (Saito et al., 2008).

Life types involve not only the web structure, but also the behavioural outcomes of spider mites on host leaves (Saito, 1983, 1995b). *Yezonychus sapporensis* deposits its eggs and spends its quiescent stages on the tips of leaf hairs (this species is categorised into the LW-s type, Saito, 1983). Yanagida et al. (2001) investigated whether eggs deposited on the tips of leaf hair (*S. senanensis*) are safer than those deposited on leaf surfaces. Seven predator species which occur on *S. senanensis* were examined. The feeding rates of several predator species decreased when prey eggs were positioned on the tips of leaf hairs. However, among the predators tested, the feeding rates of *Phytoseius tenuiformis* and *A. summersi* were equal regardless of egg position (Table 2).

The spider mite *A. corpuzae* has an extremely flat body. Furthermore, it feeds in a typical posture (lying flat) and completely spreads its body and legs on *S. senanensis* leaf surfaces. Chittenden and Saito (2006) used quiescent deutonymphs, which normally assume a flat posture on leaf surfaces. Half of them were tipped on their sides and the other half were left untouched in their natural positions. Additionally, webs covering eggs were removed to determine their function. The feeding abilities of the four predator species that usually co-occur with *A. corpuzae* were tested. *Amblyseius orientalis* and *Typhlodromus bambusae* showed increased egg consumption rates when the egg webs were removed. All tested predators consumed more deutonymphs that were tipped compared with normally positioned deutonymphs. Therefore, the egg-covering webs and quiescent posture with a flat body help *A. corpuzae* to avoid predation from at least two predator species (Table 2). Osakabe (1988) reported a similar function of egg webs (guy ropes), in which guy ropes surrounding the eggs of *P. citri* prevented *Amblyseius sojaensis* from touching the eggs. Furthermore, Yano and Shirotsuka (2013)

TABLE 2 Relationships between spider mite life types and their natural enemies on *Sasa senanensis*.

Spider mites	Predators Life type +subtype	*Typhlodromus bambusae*	*Amblyseius orientalis*	*Amblyseius* sp.1	*Phytoseius tenuiformis*	*Agistemus summersi*	*Agistemus iburiensis*	References
Stigmeopsis longus	WN-c	+	No data	++	+	+	=	Mori and Saito, 2004
Stigmeopsis takahashii	WN-c	-	No data	++	++	++	=	Mori and Saito, 2004
Stigmeopsis saharai	WN-c	-	No data	++	++	+	=	Mori and Saito, 2004
Schizotetranychus recki	WN-r	+	+	+	=	-	+	Horita et al., 2004
Yezonychus sapporensis	LW-s	+	+	+	=	=	+	Yanagida et al., 2001
Aponychus corpuzae	LW-j	=	+	No data	+	=	No data	Chittenden and Saito, 2006

Whether life type is effective to protect mites from predation, ++, highly effective ; +, effective ; =, ineffective ; -, rather increase predation.

reported that the dorsal setae and resting posture of *P. citri* (LW-c type) function as anti-predator defence mechanisms. Adult *P. citri* females lie on citrus leaf surfaces, with their dorsal setae (hair) oriented upwards. Compared with normally lying females, both manipulated non-lying females and hair-removed females experienced higher predation risks. When a predator approached the body surface of a lying female, the setae inevitably created elasticity upon contact, eventually repelling the predator from the female.

The above three examples show that not only the outcomes of spider mite behaviour but also the morphology itself has a predator avoidance (or elimination) function.

3.3 Function of silk threads

Next, we discuss that the silk threads themselves function as a predator avoidance tool. Even if spider mites with the CW type (e.g. *Tetranychus* spp.) produce more silk in the presence of predator cues (Oku et al., 2003; Schausberger et al., 2021), it may be challenging to discern whether they actively use silk threads as a defensive tool or whether it is simply a by-product of increased walking activity, because these mites continuously produce silk while walking (Saito, 1977a).

Saito and Zhang (2017) reported that female *Stigmaeopsis nanjingensis* strongly reinforce their nests after recognising predator cues. Note that this species does not produce silk except for weaving nests or egg covers (Saito and Zhang, 2017). The females heavily reinforce the nest (Figure 2) after considerable spinning movement and then close almost all the nest openings. This robust nest structure force *T. bambusae* immatures to be locked out, resulting in most of them starving to death outside the nest. Thus, reinforcing web nests with silk in response to predatory cues provides direct evidence that silk protects spider mites from predators.

Kanazawa et al. (2011) used artificial dust to experimentally determine that females of *S. longus* use adhesive silk threads to perform regular cleaning of the nest space and eggs. They first learned that silk-weaving behaviour is not a by-product of nest building (nest reinforcement); rather, it is actively performed as a function of cleaning the living space and eggs. As such, they have discovered an extraordinary new role of silk threads as devices for cleaning the nest space and/or eggs. These strongly indicate that special adaptations for maintaining clean habitats are essential for animals to evolve aggregative social lives.

3.4 Counterattack and life types

Life types may sometimes become prerequisites for spider mite defence 'behaviours', as WN-type nests provide 'domains' for predator-prey interactions.

Counterattack behaviours of *S. longus*, *S. miscanthi*, and *S. nanjingensis* against the specific phytoseiid predator *T. bambusae* have been reported (Figure 3; Saito, 1986a; Mori and Saito, 2005; Yano et al., 2011; Saito and Zhang, 2017). For example, approximately 30 and 80 precent of *T. bambusae* larvae were killed when they intruded a nest defended by eight *S. longus* females for two days and two *S. longus* males, respectively (Saito, 1986b). Ito (2019) also reported a similar phenomenon in another WN-type species, *S. brevisetosus*. He found biparental counterattack behaviour in this species against insect predators, such as midge (*Feltiella* sp.), within and around nests. Thus, the WN type appears to play a crucial role in supporting spider mite counterattack behaviour, i.e. WN nest provides sufficient group (family) living space and landmarks (such as a fort or domain) for defence.

3.5 Counter response of predators

From the perspective of predators, they must evolve some ways to overcome spider mite defence (life types, counterattacks, and so on) to maintain their ecological niches.

Sabelis and Bakker (1992) investigated whether the morphology of phytoseiid predators aids in coping with the CWs of spider mites. They tested a functional hypothesis on how the seta patterns (chaetotaxy) of phytoseiids contribute to protection in sticky environments, specifically focusing on their impact on the foraging

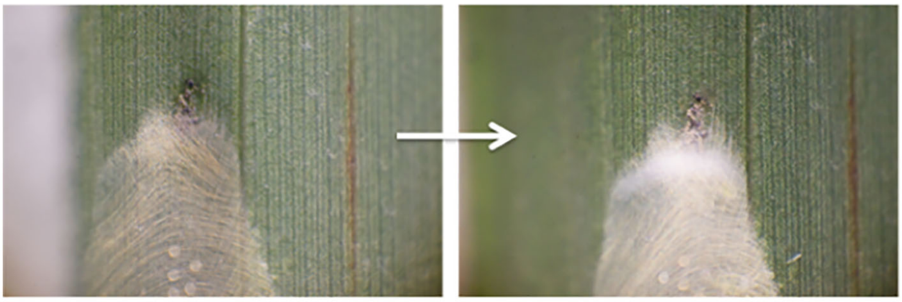

FIGURE 2
Left, *Stigmaeopsis nanjingensis* nest before introduction of predator larva. Right, 72 hours after the introduction (larva was already excluded from the nest). From Saito and Zhang (2017).

FIGURE 3
Adult male of *Stigmaeopsis nanjingensis* counterattacking against adult male of *Typhlodromus bambusae*.

success in the CWs of *Tetranychus* species. They concluded that the seta patterns of phytoseiids influence their ability to cope with webs (seta protection hypothesis). In line with this, Shimoda et al. (2009) reported that specialist predatory mites *P. persimilis*, *N. womersleyi*, and *N. californicus* cope with the CWs of *T. urticae* using chelicerae and palps—they can cut the threads and move easily inside the web.

Another interesting example is *T. bambusae*. As previously stated, *S. nanjingensis* adults exhibit a strong counterattack against *T. bambusae* (Saito and Zhang, 2017). Direct counterattacks (killing) and locking out predators using reinforced web nests would be more efficient when both sexes defend their nests together. The mortality of *T. bambusae* immatures due to *S. nanjingensis* counterattack is extremely high, suggesting that these immature predators find it difficult to survive alone in nests with several prey adults. However, *T. bambusae* can still maintain its status as the main predator of *S. nanjingensis* populations (Zhang et al., 2000, 2004; Tsuji et al., 2011). Adult predators exhibit three types of behaviours (ripping dense nest webs, excluding adult prey, and killing them) to cope with the counterattacks of adult preys. Almost all immature predators can survive and feed on prey eggs when accompanied by their mothers, who can invade nests by ripping the web and killing or purging dangerous prey adults (Saito and Zhang, 2017).

Aponte and McMurtry (1997) observed that phytoseiids such as *Galendromus helveolus*, *Galendromus annectens*, and *N. californicus* can enter nests of *Oligonychus perseae* exhibiting a WN-u type by ripping webs and then feed on the adults. Other species, such as *Euseius hibisci* and *Iphiseius degenerans*, are unable to enter the nests, probably because of their larger size, but feed on mites found outside the nests. Furthermore, Montserrat et al. (2008) reported that *N. californicus* females can rip open the nests of *O. perseae*.

3.6 Life type and interspecies competition

Life type can sometimes induce competition among spider mite species. It is well-known that *Panonychus ulmi* is abundant in apple orchards in the early season and is replaced by *T. urticae* in the late season (Foott, 1963; Tanigoshi et al., 1979). Morimoto et al. (2006) and Osakabe et al. (2006) confirmed that *T. urticae* excludes *P. ulmi* under both experimental and field conditions and suggested that CWs constructed by *T. urticae* may influence the outcome of their competition. As mentioned earlier, *T. urticae* has a CW life type, whereas *P. ulmi* has an LW life type. *T. urticae* can move on dense and complex webs with the help of their special empodia. In contrast, the hooked empodial claws of *P. ulmi* are expected to be functional for grasping leaf surfaces but must get hooked on threads when walking on the *T. urticae*'s CWs (Saito, 2010). *P. ulmi* may have difficulty living on leaf surfaces with accumulated webs, leading to their displacement by *T. urticae*.

A similar phenomenon has been observed in two *Tetranychus* species with CW type infesting tomato plants. *Teteranychus evansi* can downregulate plant defence, which is usually induced by mite infestation, whereas *T. urticae* cannot (Sarmento et al., 2011). The plant leaf surface under *T. evansi* webs is attractive for *T. urticae* not only in terms of a safety net and protection against predators, but also in terms of suitable feeding areas where plant defences are not induced. However, *T. urticae* has difficulty reaching the leaf surface to feed when the leaf is covered with dense webs produced by *T. evansi*, as the webs of *T. evansi* are much thicker than those of *T. urticae*. Furthermore, *T. evansi* produces more silk when exposed to damage or other cues associated with *T. urticae*. Thus, the silken webs produced by *T. evansi* prevent competitors from profiting from downregulated plant defences (Sarmento et al., 2011).

3.7 Life type and faeces manipulation

Faeces manipulation is an important behavioural element in life-type recognition (Saito, 1983). Many species with WN and CW life types exhibit faeces manipulation behaviours to different degrees.

Tetranychus urticae lays many faecal pellets on CW webs (Hazan et al., 1974; Gerson, 1985); hence, Hazan et al. (1974) used the pellets on the webs as an indicator of web density. However, little information is available on why *Tetranychus* spp. deposit their faeces on CW webs. Saito (1995b) suggested that such faecal deposition behaviour may keep living and feeding spaces (leaf surfaces) clean. If one of the functions of the CW type is to enhance group formation and cohesion (Le Goff et al., 2010; Schausberger et al., 2021), the leaf surfaces where mites aggregate and feed should be kept clean.

This hypothesis appears to be true for several WN-type species which deposit faeces on the roof, inner margin of nests, or on other sites (Saito, 1995b). In particular, a relationship between faeces manipulation and group size has been found in the genus *Stigmaeopsis*. *S. miscanthi*, *S. longus*, *S. takahashii*, and *S. saharai* share a common feature in that they construct tunnel-like nests and create faecal piles near the nest entrances. However, faecal manipulation is slightly different among these species. Sato et al. (2003) and Sato and Saito (2006) found that *S. miscanthi* and *S. longus* defaecate at sites where faecal piles already exist by using volatile chemical cues from faecal piles, whereas *S. takahashii* and *S. saharai* defaecate near nest entrances using only tactile cues. *S. miscanthi* and *S. longus* build larger nests by extending their nests continuously to live gregariously for a long time; therefore, minimising the locations of faecal piles must be an adaptive strategy to decrease the risk of disease. Volatile chemical cues are convenient for this purpose. Although the exact nature of volatile chemical cue remains unidentified, it is known to be an ether-soluble substance originating from host plants, since mites change their defaecation site in response to these substances (Sato and Saito, 2008).

4 Life type and life history

Sabelis (1991) conducted a comprehensive review on spider mite life history and concluded that interspecific comparisons of life-history data reported to date do not provide evidence for trade-offs between developmental rate, body size, silk production, and egg production.

Since this review, life history studies on various spider mite species have increased, but information about their life types remains scarce. Here, we collected life history data, including life type-related descriptions and analysed the relationship between life history and life type (Table 1). The maximum intrinsic rate of natural increase (r_m) of each species under 25 ± 1 °C was considered to be one of the important parameters that describe its life history. We plotted the r_m data by life type and detected a clear tendency for the r_ms of CW-type species to be consistently higher than those of WN-type (Figure 4, $P < 0.001$) and LW-type species ($P < 0.05$). The r_ms values of the LW-type species were intermediate between those of the CW- and WN-type species (Figure 4).

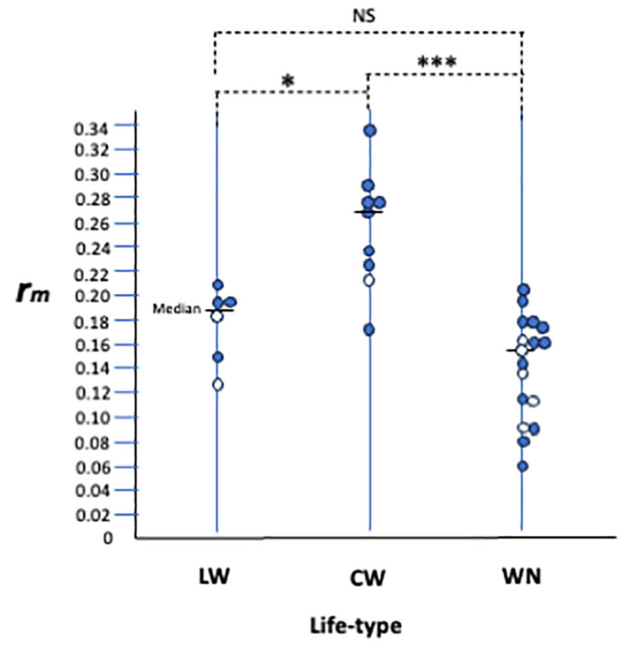

FIGURE 4
Relationships between life-type and life-history parameter, r_m. Each circle represents a single spider mite species. Open circles are species on *Sasa senanensis*. Life-history and life-type data appear in Table 1. NS, insignificant, *P <0.05, ***P<0.001 by Wilcoxon signed rank test with Rice (1989) adjustment for post hoc multiple comparisons.

Species with higher r_m values are supposed to be able to adapt to their relatively unstable habitats (Mitchell, 1973; Southwood, 1977; Saito, 1979). *Tetranychus* spp. having the CW type showed higher r_m and mainly inhabited herbaceous hosts. As mentioned previously, the CW type is supposed to be an outcome of establishing footing webs on the leaf undersides, which are free from solar radiation and gravity. 'Walking around with silk threads' is crucial for constructing CW webs, and it must be indispensable for mites, such that it may be performed at a low cost.

In contrast, the habitats of WN-type species, such as bamboo and woody plants, appear to be comparatively stable because of their longevity (stability in time) and large stock (tree) sizes (stability in space). This stability may help the species survive for several generations in the same habitat. The longer a colony persists in the same habitat, the greater the risks associated with the accumulation of natural enemies (predators and diseases, Southwood, 1977; Saito and Ueno, 1979). As described previously, the WN type functions as an effective defence mechanism (shelter) against predators. Thus, the low r_m of the WN-type species may be related to their sophisticated defence mechanisms which are inevitably accompanied by higher costs.

However, there is an exception to the above reasoning of host plant stability. As shown in Figure 4, different life type species with various r_m values (open circles) occur on the same host plant (*S. senanensis*). It appears that unstable habitats are only available for CW-type species, but stable habitats may be open for species of all life types. Does a relatively stable host plant allow mite species with different life types and r_m s to coexist together, or are there unknown factors at play? In any case, the host plant stability does not entirely explain the relationship between life type and life history. Hence, it remains unclear why there is a relationship between life type and life history.

5 Life type and sex ratio

As a life history parameter, r_m is higher in the CW type than in the LW and WN types; thus, some relationship between life type and sex ratio is also expected. In spider mites, the sex ratio is often female-biased (Table 1), with the degree of bias varying largely among species.

Local mate competition (LMC) theory (Hamilton, 1967) has been broadly accepted as an explanation for female-biased sex ratios. In most animals, the sex ratio is 1:1, which is explained by frequency-dependent selection, with the assumption of panmictic populations (Fisher, 1930). However, in animals distributed in patches due to low mobility or other reasons, mating occurs within local patches (Hamilton, 1967). In such animals, intra-male competition for access to females often occurs among brothers. Consequently, mothers may produce more daughters than sons to reduce the unnecessary competition between their sons.

The dispersal of tiny, wingless spider mites is relatively limited; therefore, the occurrence of LMC is highly probable. Indeed, regulating the offspring sex ratio by females according to the number of foundresses, as predicted by the LMC model, has been observed in the CW type, *T. urticae* (Young et al., 1986; Roeder, 1992; Roeder et al., 1996; Macke et al., 2011) and *T. cinnabarinus*

(Wrensch and Young, 1978), as well as in the WN type, *S. longus* and *S. miscanthi* (Sato and Saito, 2007). The CW and WN type species live in groups (colonies) inside webs and rarely leave when there is no habitat deterioration and/or the danger of predation. If mating frequently occurs within a colony, LMC is expected to be stronger in the CW and WN types than in the LW type. In addition, as previously discussed, WN type species may inhabit more stable environments than CW type species. This suggests that LMC is stronger in the WN type than in the CW type. Therefore, the bias in the sex ratio towards females is expected to be highest in the WN type, followed by the CW and LW types.

However, no significant relationship between life type and sex ratio was detected ($P > 0.10$; Figure 5); in each life type, the sex ratio largely varied among the species. There are several possible explanations for the unclear relationship between life type and sex ratio. First, factors other than LMC, such as temperature (Margolies and Wrensch, 1996; Roy et al., 2003) and changes in population density (Weerawansha et al., 2022), may also influence sex ratio. Life history data are often obtained from individual females; that is, females that are kept alone. Therefore, the sex ratio obtained from life history experiments may not always reflect sex ratios in the field, especially in species with sex-ratio control abilities. Additionally, the ability to control sex ratios varies among species. Macke et al. (2011) reported that the lines of *T. urticae* exposed to strong LMC lost the ability to control offspring sex ratio and consistently produced offspring with a female-biased sex ratio, whereas those exposed to mild LMC retained the ability to control offspring sex ratio. WN-type species are predicted to be consistently exposed to stronger LMC conditions than LW- and CW-type species. The degree of sex ratio changes in *S. longus* and *S. miscanthi* of the WN-c type is smaller than that predicted by LMC (Sato and Saito, 2007). Even though the expected relationship between sex ratio and life type could not statistically supported, a female-biased sex ratio has been consistently observed in the WN type, suggesting that the sex ratio is also related to life type.

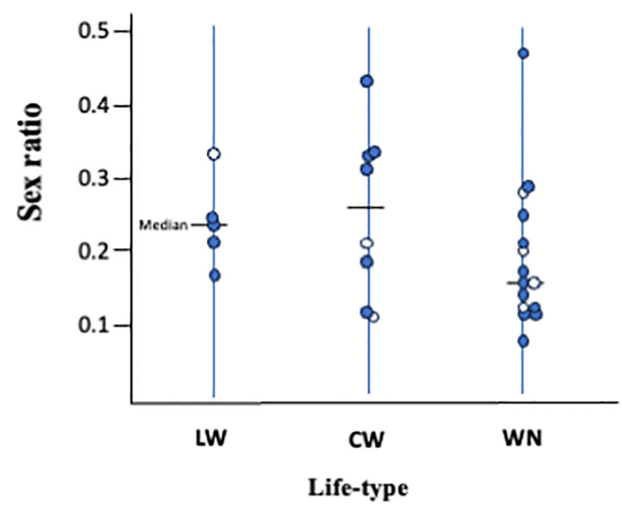

FIGURE 5
Relationships between life-type and sex ratio (male ratio). Each circle represents a single spider mite species. Open circles are species on *Sasa senanensis*. Life type and sex ratio data appear in Table 1. There is no significant difference ($P > 0.10$) between three life types.

6 Life type and sexual selection

Life types inevitably influence the probability of encountering mates, as the distribution of individuals is associated with whether they live alone or in groups. Male spider mites can deliver enough sperm in a single mating to fertilise all the eggs produced by a female during her lifetime (Helle, 1967). In addition, if mating is completed successfully without any interruptions, the sperm of the first male is used to fertilise the eggs, even if the female mates with multiple males (the first male sperm precedence, Helle, 1967; Potter and Wrensch, 1978; Satoh et al., 2001; Oku, 2008; Morita et al., 2020; Rodrigues et al., 2020). In such situations, males actively seek out quiescent females nearing adulthood (and occasionally virgin females) and guard them by mounting on their dorsum (known as precopulatory mate guarding = precopula, Ridley, 1983). If other males disturb the guarding male, they engage in physical combat to get mating priority over the females (Potter et al., 1976a). Then, searching, guarding, and fighting are three basic elements of male mating behaviour in spider mites.

Precopula and fighting behaviours of males have been reported in several spider mite species with different life types (Potter et al., 1976a; Saito, 2010). Although the reproductive behaviours of spider mites have been investigated in many studies, including mating durations (Potter and Wrensch, 1978; Takafuji and Fujimoto, 1985; Ozawa and Takafuji, 1987; Kunimoto et al., 1991; Oku, 2008; Sato et al., 2014a, 2015; Kobayashi et al., 2022), male fights over females (Potter et al., 1976a, 1976b), alternative male reproductive tactics (Sato et al., 2013b, 2014b), female choice (Vala et al., 2004; Oku, 2009; Tien et al., 2011), the cost and benefit of multiple mating (Oku, 2010; Rodrigues et al., 2020), and the influence of predators on reproductive behaviour (Murase et al., 2017; Oku et al., 2018; Rocha et al., 2020), these studies only focused on *Tetranychus* species and a few other genera. Hence, sufficient data is not available to address the relationship between mating systems and life types.

However, fatal (lethal) male fights have been observed in several WN type species, such as *S. miscanthi* species group and *S. brevisetosus* (Saito, 1990a; Masuda et al., 2015). In fatal male fights, a male thrusts its stylets, usually used for sucking the juice of host plants, into the other male's body, thereby killing the competitor by sucking its body fluids, i.e. cannibalism (Figure 6, Saito, 1990a; Masuda et al., 2015). Intra-sexual competition for access to females is a common phenomenon observed across many animal taxa (Andersson, 1994) and is not restricted to spider mites. However, killing rivals in male fights is rare in the animal kingdom because the cost of such a fight is extremely high relative to the resource (mate) value. Thus, the conditions under which a fatal fight evolves are limited (Maynard Smith and Price, 1973). It is important to note that the males of *S. miscanthi* engage in fatal fights not only for access to females but also to defend their 'nests'. Nests of the WN type may prepare recognisable domains that make it easy for males to defend against competitors (and predators). There is evidence that the closely related species *S. longus* (WN-c type) can recognise the existence of nests (domains) by its dorsal

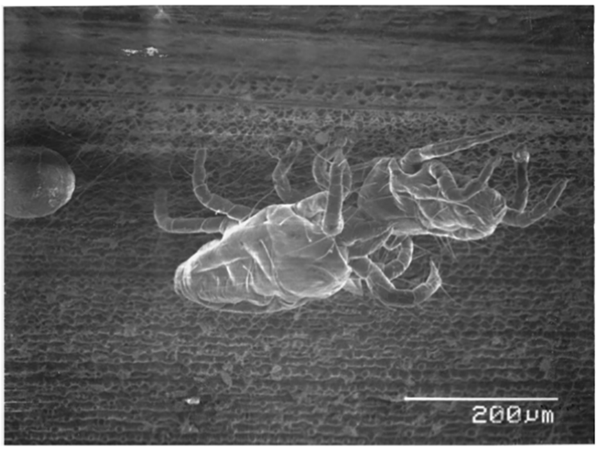

FIGURE 6
Male-to-male fatal combat in *Stigmaeopsis mischanthi*. Photographed by Y. Saito under a scanning electron microscope (with cryosystem, Hitachi S-2100A).

setae (Mori and Saito, 2013). Furthermore, females are packed closely in WN nests (Figure 1), which may make it easy for males to monopolise. These factors appear to be the prerequisites for the evolution of strong male aggression. Thus, we can understand why the males of CW species seldom engage in a fatal fight, even though they often exhibit intra-male competition (Potter et al., 1976a)—because there is no clear border of the domain where the males can recognise the defence. Nevertheless, we could not strictly explain why fatal fights evolved exclusively in males of certain species.

Interestingly, *S. longus* males do not engage in fatal fights, even though they show very strong counterattack behaviour against natural enemies (Saito, 1990a, 2010). The reason for such a difference between closely related species may stem from variation in their distribution patterns, as *S. longus* is distributed throughout northern Japan, whereas *S. miscanthi* group (Saito, 1990a) and *S. brevisetosus* are mainly found in southern Japan. In the *S. miscanthi* group (two forms of *S. miscanthi*, *Stigmaeopsis sabelisi* and *Stigmaeopsis continentalis*, and *Stigmaeopsis formosa*), there is geographic variation in the intensity of fatal male fights (Saito, 1995a; Saito and Sahara, 1999; Sato et al., 2013a). Geographical variation corresponds to the difference in average relatedness between nest-mate males which is based on the probability of mother-son mating in early spring through harsh winter conditions (Saito, 1995a, 2010; Sato et al., 2013a). A game-theoretical analysis by Saito and Takada (2009) indicated that the intensity of aggression (frequency of aggressive males) decreases with an increase in relatedness between confronting males when there is sufficient benefit from cooperation. Note that the counterattack of *S. longus* and *S. sabelisi* against predators is more effective when there are multiple males (i.e. cooperation of males, Saito, 1986a; Yano et al., 2011). Therefore, not only WN type but also kin structure is thought to be an important cause of male fight variation (Saito, 1995a, 2010; Saito and Sahara, 1999; Saito and Takada, 2009; Sato et al., 2013a).

As mentioned before, *S. brevisetosus* has the WN-s life type and show male counterattack behaviour (Ito, 2019) and male-to-male fatal combat (Masuda et al., 2015) similar to the species group of *S. miscanthi*. Recent phylogenetic studies have revealed that *S. brevisetosus* is distinct from the monophyletic clade of the genus *Stigmaeopsis* (Matsuda et al., 2018). This means that the fatal male-to-male combat as well as the male counterattack behaviour converged in these two genera (Ito, 2019), again reiterating that WN type provided a strong 'background' for such behaviours.

7 Life type and sociality

The cooperative and/or social behaviours of spider mites have been thoroughly reviewed by (Saito, 1997, 2010) and Schausberger et al. (2021). The simplest sub-social behaviour is maternal egg-covering habit in the LW life type (Saito, 1995b). The construction of shelter-like webs to protect themselves and their young against natural enemies in the CW and WN types is considered a more advanced sub-social behaviour. Such constructions may also promote aggregation (Schausberger et al., 2021). Unlike spiders, which exhibit semelparous reproduction leading to the creation of an egg mass, spider mites, being iteroparous, need specific reasons for aggregating their eggs (or other life stages). The necessity for refuge from predators, footing, and a safety net might have promoted the evolution of web formation, which leads to the aggregation of individuals in a confined space. These might provide important traits for the evolution of sociality, i.e. nesting habits lead to mite aggregation and iteroparous reproduction causes generation overlapping to allow interactions between parents and offspring (Saito, 1997, 2010), which have been considered to be the basic elements of sub-sociality (Wilson, 1975). However, aggregation may increase the risk of rapid habitat deterioration and disease outbreaks. There are at least two ways to avoid such risk. The first is to increase the population rapidly (higher r_m) and disperse it as quickly as possible before the habitat deteriorates and the disease becomes widespread, as assumed in the CW type. The second is to live in spatiotemporally stable habitats. Mites living in stable habitats should invest more in web construction to protect themselves from predators and develop nest sanitation behaviours (faeces manipulation and nest cleaning by silk), which is observed in the WN type.

There are differences in nest size, nest persistence, and intensity of parent-offspring relationships among *Stigmaeopsis* spp. with the WN-c type (Saito et al., 2016; Saito, 2018). Larger nests in *S. longus*, *S. miscanthi*, and *S. nanjingensis* can contain a large number of nest members (mostly kin) and persist for a long period, so that the nest defence (counterattack) against natural enemies by the group becomes effective through cooperation (Mori and Saito, 2004). On the other hand, smaller nests of *S. takahashii* and *S. saharai* only contain a small number of mites and persist for a short period;

therefore, counterattacks are ineffective (Mori and Saito, 2004). However, smaller nests serve as protective refuges that are more effective than larger nests, as they make it difficult for many predator species to search (Saito et al., 2008) and intrude (Mori and Saito, 2004). In short, there might be two strategies against predators, i.e. 'defence by kin group in large nests' and 'protection by smaller and solid nests' (Mori and Saito, 2004). This must be a reason why there is such variation in nest size of *Stigmaeopsis* spp. and the former strategy may be synonymous with 'cooperative sociality' (Saito, 2010).

8 Epilogue

As discussed above, life types provide a fundamental framework for the diversity and evolution of spider mites. In addition, life types can be useful in identifying spider mite species. Many species of the genus *Stigmaeopsis*, one of the main groups discussed in this review, have recently been described based on their life-type characteristics. Before Saito (1990b), only one species, *Schizotetranychus* (at present, *Stigmaeopsis*) *celarius*, was known. Subsequently, differences in life type characteristics, including nest size, defaecation sites, and male behaviour, have been recognised (Saito et al., 2016), and 15 species have been described in the reinstated genus *Stigmaeopsis* to date (Saito et al., 2019). If life types are described in various spider mite species using the method described by Saito (1995b) as a standard method, this will greatly contribute to our understanding of the diversity and evolution of spider mites.

Life type might have evolved through natural selection, as an 'extended phenotype' proposed by Dawkins (1982). This review shows that life type is closely related to the defence mechanisms against natural enemies. This result corresponds well with Jeffries and Lawton's (1984) definition of 'enemy-free space'. Therefore, we supposed that spider mite life types reflect a way to avoid natural enemies.

Descriptions of diversity and global comparisons between species are necessary steps for the development of evolutionary ecological studies. However, there is a great difficulty in studying evolutionary processes solely by such between-species comparisons without accurate phylogenic information (Harvey and Pagel, 1991). Several recent studies on the molecular phylogeny of spider mites revealed important discrepancies in the morphological classification of genera and molecular phylogenetic relationships (Matsuda et al., 2014; Matsuda et al., 2018). Then, attempts to analyse the evolution of life types along with phylogenetic trees should be made, after the molecular and morphological phylogenetic studies on spider mites attain a reasonable position and more robust and comprehensive data on life types are accumulated.

Author contributions

YutS: Writing – review & editing, Writing – original draft. YukS: Writing – review & editing, Writing – original draft.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Publisher's note

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