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Pesticide-mediated displacement of a phytoseiid predator, *Neoseiulus womersleyi*, by another phytoseiid predator, *N. californicus* (Acari: Phytoseiidae)

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Abstract *Neoseiulus womersleyi* and *N. californicus* are two predators that are frequently used to control spider mites in fruit-tree orchards. *Neoseiulus womersleyi* used to be the dominant predator species in Japan, but since the 1990s in central and southwestern Japan, *N. californicus* populations have been increasing and have displaced populations of *N. womersleyi*. We previously observed the same phenomenon under laboratory conditions when these species were released at a 1:1 ratio, and attributed the displacement to asymmetrical intraguild predation. However, the ratio in fruit-tree orchards could be different from 1:1. Therefore, we hypothesized that differential susceptibilities to pesticides might accelerate species displacement of *N. womersleyi* by *N. californicus*, even if the ratio between these two species was extremely skewed in favor of *N. womersleyi* and no species displacement occurred otherwise. We examined the effects of 21 pesticides on egg-to-adult and adult survivorship in *N. womersleyi* and *N. californicus*. Among these pesticides, two neonicotinoids (acetamiprid and imidacloprid) had much severer effects on *N. womersleyi* than on *N. californicus* and thus could possibly account for the species displacement. When the two species were released onto leaf arenas at an *N. californicus*: *N. womersleyi* ratio of 1:9 in the absence of insecticide, no displacement was observed. However, just after acetamiprid or imidacloprid application, the proportion of *N. californicus* increased, causing *N. californicus* to displace *N. womersleyi*. Our results indicate that displacement in predator complexes of fruit-tree orchards could be due to different degrees of pesticide susceptibility.

Keywords Species displacement · Pesticides · Neonicotinoids · *Neoseiulus womersleyi* · *Neoseiulus californicus* · Phytoseiids

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Introduction

Predatory mites are economically important because of their potential to control mite pest populations and minimize associated economic injury. Among various groups of predators, phytoseiid mites are known to prey mostly on members of the families Tetranychidae (spider mites), Eriophyidae, Tenuipalpidae and Tarsonemidae. They are thus commonly used as natural control agents of spider mites in agriculture (McMurtry et al. 2013). Although biological control has minimal environmental impact compared with the impact of pesticides, competitive displacement of one predatory species by another might result in poorer control of a pest species (Palevsky et al. 2013). The elimination of a formerly established species from a habitat as a result of direct or indirect competitive interactions with a new candidate species is generally referred to as species displacement (DeBach 1966; Reitz and Trumble 2002). Several factors can contribute to species displacement including resource preemption and degradation, competition from other species (Braks et al. 2004; Reitz and Trumble 2002), reproductive interference (Gröning et al. 2007; Hochkirch et al. 2007; Suzuki et al. 2012), intraguild predation (Gotoh et al. 2014), differences in fecundity and foraging ability (Reitz and Trumble 2002) and differences in insecticide susceptibility (Gao et al. 2012).

Several studies have demonstrated that phytoseiid species have cannibalistic and intraguild predatory behaviors (Schausberger 2003; Gotoh et al. 2014; Zhang et al. 2014; Ji et al. 2015). However, it is often difficult to determine whether strong competition and predation result in species displacement. The population densities of some phytoseiid predators [*Phytoseiulus persimilis* Athias-Henriot and *Neoseiulus californicus* (McGregor)] remain stable when they are released alone, but decline when they are released in combination with another phytoseiid predator due to differences of intraguild predation, and differences in cannibalizing severity on conspecifics and heterospecifics (Schausberger and Walzer 2001). In order to predict whether one phytoseiid predator would displace another phytoseiid predator, it is necessary to examine how anthropogenic and other factors affect them differentially.

In Japan, the phytoseiid predatory mite *Neoseiulus womersleyi* (Schicha) used to be the dominant species among predatory mites in fruit-tree orchards. Populations of the predatory mite *N. californicus* have increased in central and southwestern Japan since the 1990s, both in size and distribution. Consequently, *N. californicus* has become the dominant species in conventionally controlled orchards (Wakabayashi 2000; Amano 2001; Kishimoto 2002). Some growers may have purchased a commercial strain of *N. californicus* (e.g., SPICAL EX®) that had been imported to Japan. The commercial strain was first registered in Japan in 2003 for use in only greenhouses, but in and after 2008 it was used in fruit tree orchards and tea plantations. However, the commercial strain was introduced after the displacement of *N. womersleyi* in fruit-tree orchards, and thus had no role in the displacement. Recently, *N. californicus* was found to eliminate *N. womersleyi* under laboratory conditions, and the cause appeared to be asymmetrical intraguild predation (Gotoh et al. 2014). It was previously found that *N. californicus* competes very strongly with *N. womersleyi*, and there might be a possibility of complete species displacement in fruit-tree orchards in Japan (Gotoh et al. 2014).

A combination of various biological mechanisms or anthropogenic factors, including differential reproductive success or susceptibility to pesticides, might influence species displacement (Kishimoto 2002). Moreover, it was evident that the suppression of natural enemies by application of a pesticide resulted in an outbreak of spider mites (Szczepaniec

et al. 2011). However, the influence of pesticides on the displacement of natural enemies remains unknown in Japanese fruit-tree orchards. To effectively use native natural enemies for pest control in Japanese fruit-tree orchards through integrated pest management (IPM) programs, it is important to elucidate the role of pesticides in species displacement. Amano et al. (2004) examined the effects of 22 pesticides to see whether they could be responsible for the displacement of *N. womersleyi* by *N. californicus* in commercial pear orchards. They found that the two species had very different susceptibilities to milbemectin and pyribaden, which were thus proposed as factors contributing to the displacement, although these two pesticides alone could not account for the displacement. However, their study did not examine the effects of the pesticides on immature stages and did not examine two commonly used pesticides, acetamiprid and imidacloprid. In the present study, we examined the effects of 21 pesticides that were used in Japanese fruit-tree orchards from 1980 to 2000 on both immature and adult stages. Some of these pesticides were not examined by Amano et al. (2004). In addition, in the absence of pesticides, we determined how low the NC:NW ratio had to be to prevent displacement of *N. womersleyi* by *N. californicus*.

Materials and methods

Rearing of predatory and spider mites

An *N. womersleyi* strain was established from mites collected from an apple orchard in Morioka (39°42′N–140°11′E), Iwate Prefecture, northeastern Japan on 1 October 1999, and an *N. californicus* strain was collected from a pear orchard in Ichikawa (35°28′N–140°47′E), Chiba Prefecture, central Japan on 17 August 1995. The mite strains were maintained on excised leaves (ca. 16 cm^2) of common bean *Phaseolus vulgaris* L. that were infested with the two-spotted spider mite *Tetranychus urticae* Koch (green form). *Tetranychus urticae* was collected from a watermelon *Citrullus lanatus* (Thumb.) in Takikawa (43°33′N–141°54′E), Hokkaido, northern Japan on 16 July 2001. Each excised leaf was placed on a water-saturated polyurethane mat in a plastic cup (10 cm ø top × 8 cm ø bottom × 4 cm high) with a perforated lid at 25 ± 1 °C, 60–80 % RH and a 16:8 h light:dark (16L:8D) photoperiod. The leaves were replaced whenever they appeared to dry out or be damaged by feeding mites. The lid of each cup had a 50-mm-diameter hole covered with fine nylon mesh to allow ventilation (Gotoh et al. 2005).

Pesticide bioassays

We used 17 insecticides and four fungicides that were sprayed in Japanese fruit-tree orchards from 1980 to 2000 (Table 1). The chemicals were suspended in distilled water just before treatment. Distilled water was used as a control in all trials.

Suspensions of the chemicals were gently sprayed onto the leaf disc to result in approximately 4 mg chemical/cm^2. The leaf discs contained either approximately 40 eggs laid over 24 h or 15 mated adult females (3–5 days old) of predatory mites using a rotary spray tower (Mizuho Scientific, Nagoya, Japan) at 266 hPa with four replicates each. The sprayed samples were allowed to dry in the shade and then were maintained at 25 ± 1 °C with a 16L:8D photoperiod. For the bioassays, the company recommended concentrations for each chemical were used (Table 2). To monitor the impact of pesticides, leaf discs with

Table 1 Insecticides and fungicides used in this study on eggs and adult females of *Neoseiulus womersleyi* and *N. californicus*

Common name	Trade name	Formulation[a]	MoA number[b]	Registered company in Japan	Registration year in Japan
Insecticide					
Acetamiprid	Mosplan®	20 % SP	4A	Nippon Soda, Tokyo, Japan	1989
Alanycarb	Orion®	40 % WP	1A	OAT Agrio, Tokyo, Japan	1991
Buprofezin	Applaud®	20 % SC	16	Nihon Nohyaku, Tokyo, Japan	1983
Chlorfenapyr	Kotetsu®	10 % SC	13	BASF, Tokyo, Japan	1996
Clofentezine	Cara®	40 % SC	10A	Nissan Chemical Industries, Tokyo, Japan	1989
Cyhexatin	Plictran®	96 % ai, standard	12B	Kanto Chemical, Tokyo, Japan	1972 (Not available in market)
Etoxazole	Baroque®	10 % SC	10B	Kyoyu Agri, Kanagawa, Japan	1998
Fenpropathrin	Rody®	10 % WP	3A	Sumitomo Chemical, Tokyo, Japan	1988
Fenvalerate	Sumicidin®	3 % EC	3A	Sumitomo Chemical	1983
Hexythiazox	Nissorun®	10 % WP	10A	Nippon Soda	1985
Imidacloprid	Admire®	50 % WP	4A	Bayer CropScience, Tokyo, Japan	1992
Milbemectin	Koromite®	1 % EC	6	Mitsui Chemicals Agro, Tokyo, Japan	1990
Phenthoate	Elsan®	40 % WP	1B	Nissan Chemical Industries	1963
Pymetrozine	Chess®	50 % WP	9B	Syngenta, Tokyo, Japan	1998
Silafluofen	Mr. Joker®	20 % WP	3A	Bayer CropScience	1995
Tebufenpyrad	Pyranica®	10 % EC	21A	Nippon Soda	1993
Thiometon	Ekatine®	95.3 % ai, standard	1B	Kanto Chemical	1961 (Not available in market)
Fungicide					
Iprodione	Rovral®	50 % WP	2	Bayer CropScience	1979
Kresoxim-methyl	Storoby®	50 % SC	11	BASF	1997
Maneb	M-dipher®	75 % WP	M3	Kumiai Chemical Industry, Tokyo, Japan	1956
Myclobutanil	Rally®	10 % WP	3	Dow Chemical, Tokyo, Japan	1990

[a] *EC* Emulsifiable concentrate, *SC* suspension concentrate, *SP* water soluble powder, *WP* wettable powder

[b] MoA number represents Mode of Action (MoA) Classification as determined based on either the IRAC International MoA Working Group (IRAC 2015) or fungicide resistance action committee (FRAC 2016)

eggs were gently sprayed and then hatchlings were kept on the sprayed leaf discs until adulthood. Egg-to-adult mortality was then determined based on the number of hatched eggs and dead immature stages from hatchlings. Mortality was evaluated by gentle probing

Table 2 Mean (±SE, after Abbott's correction) mortality (%) of egg-to-adult-stage and adult female *Neoseiulus womersleyi* and *N. californicus* to 17 insecticides and four fungicides used in Japanese pear orchards from 1980 to 2000

Chemicals	Treated (=recommended) concentration (mg/L)	Egg-to-adult					Adult females				
		n	*N. womersleyi*	n	*N. californicus*	NW versus NC[a]	n	*N. womersleyi*	n	*N. californicus*	NW versus NC[a]
Acetamiprid	67	114	93.7 ± 2.0	114	40.5 ± 1.9	***	56	19.3 ± 3.5	59	10.2 ± 1.8	ns
Alanycarb	400	116	3.8 ± 2.2	126	99.2 ± 0.7	***	56	1.8 ± 1.5	56	100 ± 0.0	***
Buprofezin	200	138	0.0 ± 0.0	131	9.6 ± 2.8	***	57	0.0 ± 0.0	60	1.6 ± 1.4	ns
Chlorfenapyr	50	127	93.2 ± 2.3	149	100 ± 0.0	**	60	8.3 ± 1.2	59	100 ± 0.0	***
Clofentezine	160	120	37.5 ± 9.9	123	66.6 ± 10.7	***	58	0.0 ± 0.0	62	0.0 ± 0.0	ns
Cyhexatin	330	131	0.6 ± 0.6	133	23.2 ± 4.8	***	58	12.4 ± 3.2	62	42.8 ± 3.1	***
Etoxazole	50	135	100 ± 0.0	135	100 ± 0.0	ns	57	0.0 ± 0.0	58	5.0 ± 1.4	ns
Fenpropathrin	50	149	100 ± 0.0	142	100 ± 0.0	ns	60	100 ± 0.0	60	100 ± 0.0	ns
Fenvalerate	100	145	100 ± 0.0	175	100 ± 0.0	ns	59	100 ± 0.0	62	100 ± 0.0	ns
Hexythiazox	50	119	35.7 ± 4.9	109	48.9 ± 5.7	*	58	0.0 ± 0.0	59	0.0 ± 0.0	ns
Imidacloprid	50	107	61.6 ± 4.5	76	44.5 ± 3.7	***	56	58.6 ± 4.0	55	70.8 ± 2.9	ns
Milbemectin	10	160	99.4 ± 0.5	124	92.2 ± 2.5	***	58	98.3 ± 1.4	56	80.4 ± 2.8	**
Phenthoate (PAP)	330	130	52.2 ± 9.6	102	100 ± 0.0	***	59	100 ± 0.0	58	100 ± 0.0	ns
Pymetrozine	100	156	7.5 ± 2.2	114	17.9 ± 12.6	***	58	0.0 ± 0.0	59	0.0 ± 0.0	ns
Silafluofen	95	136	100 ± 0.0	115	82.6 ± 2.6	***	53	94.4 ± 3.0	50	87.7 ± 2.3	ns
Tebufenpyrad	50	156	99.5 ± 0.4	139	100 ± 0.0	ns	60	100 ± 0.0	60	100 ± 0.0	ns
Thiometon	330	132	17.0 ± 2.3	92	100 ± 0.0	***	53	15.3 ± 2.9	45	95.0 ± 4.3	***
Iprodione	500	154	0.0 ± 0.0	127	0.0 ± 0.0	ns	59	0.0 ± 0.0	56	0.0 ± 0.0	ns
Kresoxim-methyl	146	153	2.1 ± 1.2	125	9.6 ± 2.9	**	60	0.0 ± 0.0	59	0.0 ± 0.0	ns
Maneb	1500	118	100 ± 0.0	91	100 ± 0.0	*	61	60.8 ± 4.8	59	52.5 ± 2.5	ns
Myclobutanil	40	135	15.4 ± 4.5	121	8.3 ± 1.5	*	60	0.0 ± 0.0	60	0.0 ± 0.0	ns

[a] χ^2-test or Fisher's exact test; ns: $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

with a fine brush. For the adult bioassay, we counted the *N. womersleyi* and *N californicus* prior to and 2 days after application.

For experiments with mixed species, we did not examine chemicals that had similar harmful effects or no effect, or caused nearly 100 % mortality in *N. womersleyi* or *N. californicus* for egg-to-adult-stage individuals and adult females.

Single versus mixed species experiment

To determine whether *N. californicus* excludes *N. womersleyi* under laboratory conditions, 3- to 5-day-old mated females of each species were placed in each arena (Gotoh et al. 2014). An arena consisted of a 4×4 cm section of a bean leaf surrounded by a 'fence' of wet cotton (5-mm high), which prevented the mites from leaving. The bean leaf, including its petiole, was placed on wet cotton to keep it fresh. Subsequently, about 700 *T. urticae* prey individuals of all stages were placed in each arena. The leaf arenas were placed in individual plastic cups (12 cm ø top $\times$ 10 cm ø bottom $\times$ 6 cm high) and maintained at 25 °C, 60–80 % RH and a 16L:8D photoperiod. Under these conditions, the leaves remained fresh for at least 30 days.

For the initial release, each experimental arena received one or two mated adult females of *N. californicus* alone, and there were 10 replicates. For *N. womersleyi*, eight or nine mated adult females were released alone, and there were five replicates. In other arenas, we released both predators at NC:NW ratios of either 2:8 (2 *N. californicus* and 8 *N. womersleyi* adult females/leaf disc) or 1:9 (1 *N. californicus* and 9 *N. womersleyi* adult females/leaf disc), with five replicates per ratio. When the number of prey individuals in an arena fell below about 500, additional prey individuals from the stock culture were brushed onto the arena with a fine brush. The mites were observed every 3 days for 30 days. At each observation time, the adult females of each species were counted under a stereomicroscope. Adult females of the two species could be easily distinguished by the lengths of their dorsal setae.

Neonicotinoids application on mixed species

Chemicals were applied to combinations of *N. californicus* and *N. womersleyi* at an NC:NW ratio of 1:9 in an arena, with five replicates. The mites were observed at 3-day intervals for 30 days. Both pesticides were applied on day 9. At each observation time, the adult females of each species were counted under a stereomicroscope.

Data analysis

The mean numbers of adult females in mixed species arenas were compared with paired *t* tests. The percentage of dead mites was corrected using Abbott's (1925) formula. The mortality of both species using different chemicals was compared using Fisher's exact test or Chi square test. All tests were performed with IBM SPSS version 22 (IBM, Armonk, NY, USA).

Results

Pesticide bioassays

The bioassays indicated that *N. womersleyi* and *N. californicus* had significantly different responses to most of the chemicals in the egg-to-adult stage but had significantly different responses to only a few of the chemicals in the adult stage (Table 2). Four of the chemicals (acetamiprid, imidacloprid, milbemectin and silafluofen) had more harmful effects on *N. womersleyi* than *N. californicus*. However, silafluofen had similar negative effects on adult females of both species and milbemectin caused more than 99 and 98 % mortality of *N. womersleyi* in the egg-to-adult and adult stages, respectively. Thus, only acetamiprid and imidacloprid had substantially different effects on *N. womersleyi* and *N. californicus*. Both of them were more harmful to *N. womersleyi* than to *N. californicus* in egg-to-adult stage (Table 2). After acetamiprid application, egg mortality was 50.5 % for *N. womersleyi* and 0.8 % for *N. californicus* (data not shown), whereas after imidacloprid application, egg mortality was 37.8 % for *N. womersleyi* and 38.6 % for *N. californicus* (data not shown). Acetamiprid caused much higher mortality of eggs and egg-to-adult stage individuals in *N. womersleyi* than in *N. californicus*, while imidacloprid caused slightly higher mortality in egg-to-adult stage individuals in *N. womersleyi* (Table 2). However, alanycarb and thiometon had more severe effects on *N. californicus* than on *N. womersleyi* (Table 2).

Single and mixed species experiments in the absence of pesticides

Changes in the populations of *N. californicus* and *N. womersleyi* females when released alone or in combination are shown in Fig. 1. Initially, gravid females of a single species of predator mite were released into an arena containing *T. urticae*. For each predator species, the number of females (males were not counted) increased to about 100 in the 30-day experimental period, even though the starting numbers of *N. californicus* were lower (Fig. 1a–d).

When the two predator species were introduced together in an NC:NW ratio of 2:8, *N. californicus* began to displace *N. womersleyi* after about 15 days (Fig. 1e), although the number of *N. californicus* females was less than when *N. californicus* was released alone (Fig. 1a, b). On the other hand, when the initial NC:NW ratio was 1:9, the *N. californicus* population grew more slowly than, and did not displace, the *N. womersleyi* population (Fig. 1f).

Effects of neonicotinoids on mixed species

Because the two neonicotinoid insecticides (acetamiprid and imidacloprid) were more harmful to *N. womersleyi* than *N. californicus*, their influence on species displacement was examined in mixed species arenas. Nine days after *N. californicus* and *N. womersleyi* were released in an NC:NW ratio of 1:9 (1 *N. californicus* and 9 *N. womersleyi* adult females/ leaf disc), acetamiprid and imidacloprid were individually applied (Fig. 2a, b, respectively). Just before addition of the insecticides, the number of *N. womersleyi* adult females was higher than the number of *N. californicus* adult females, in agreement with the results shown in Fig. 1f. After application of the insecticides, the numbers of *N. womersleyi* adult females declined sharply, while the numbers of *N. californicus* adult females immediately increased (Fig. 2). These results are consistent with the lower mortalities the pesticides
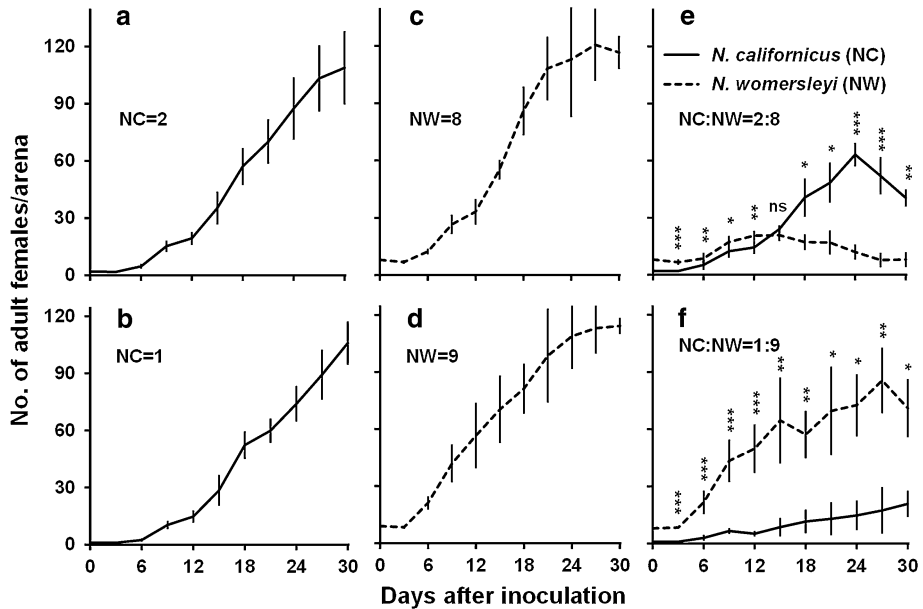
Fig. 1 Changes in the number of adult females per arena after the following releases of *Neoseiulus californicus* (NC) and *N. womersleyi* (NW). **a** 2 NC; **b** 1 NC; **c** 8 NW; **d** 9 NW; **e** 2 NC and 8 NW; **f** 1NC and 9 NW. The conditions were 25 °C and a 16L:8D photoperiod. Paired *t* test; ns: $P > 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. *Vertical lines* indicate standard deviation

caused in immature *N. californicus* than in immature *N. womersleyi* (Table 2). Finally, *N. womersleyi* was nearly completely displaced by *N. californicus*.

Discussion

The present results clearly show that pesticides could accelerate the displacement of *N. womersleyi* by *N. californicus* even though, in the absence of pesticides, no displacement was observed when the two species were released at an NC:NW ratio of 1:9. This finding, based on laboratory experiments, suggests that the use of some pesticides, such as acetamiprid and imidacloprid, can promote species displacement of *N. womersleyi* by *N. californicus* in Japanese fruit-tree orchards.

Differential susceptibility to pesticides has previously been associated with changes in the demographics of arthropod pest complexes. For example, the spirea aphid *Aphis spireacola* Patch displaced *Aphis pomi* De Geer, the predominant aphid pest of apple (*Malus domestica* Borkh.) in eastern and northwestern USA (Hogmire et al. 1992; Brown et al. 1995; Lowery et al. 2006). *Aphis spireacola* was substantially less susceptible than *A. pomi* to a variety of commonly used insecticides, which influenced species displacement.

Similarly, displacement of the B biotype by the Q biotype of the whitefly *Bemisia tabaci* (Gennadius) was attributed to higher resistance of the Q biotype to insecticides, such as pyriproxyfen and some neonicotinoids (Horowitz et al. 2003, 2005; Chu et al. 2010; Dennehy et al. 2010). Similar observations have been made on the B and Q biotypes of *B. tabaci* in Japan (Tsueda and Tsuchida 2011) and in China (Rao et al. 2012). Differences in

Fig. 2 Changes in the number of adult females per arena after application of acetamiprid (**a**) and imidacloprid (**b**) when *Neoseiulus californicus* and *N. womersleyi* were released in a combination of 1:9 ratio at 25 °C and a 16L: 8D photoperiod. *Arrows* indicate acetamiprid and imidacloprid applications. Paired *t* test; ns: $P > 0.05$; **$P < 0.01$; ***$P < 0.001$. *Vertical lines* indicate standard deviation
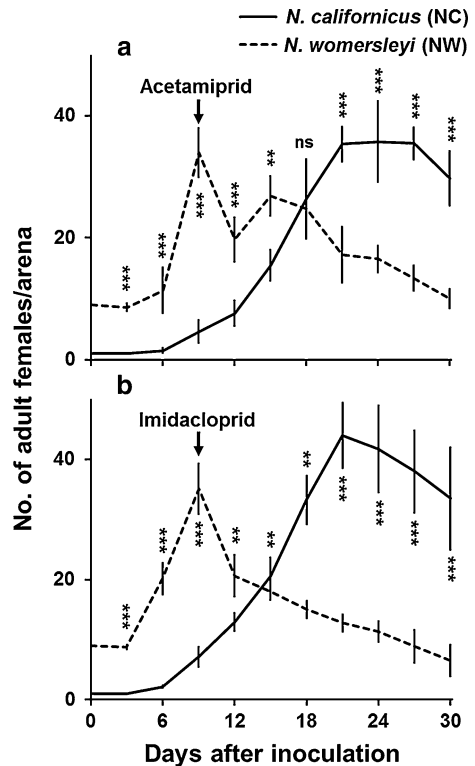
resistance to neonicotinoids was a major factor that affected species displacement of the B biotype by the Q biotype whitefly (Luo et al. 2010; Wang et al. 2010; Rao et al. 2012; Yuan et al. 2012; Sun et al. 2013). These observations indicate that insecticides shifted species competitive interactions effects in favor of the Q biotype across China (Sun et al. 2013). Likewise, the leafmining fly *Liriomyza sativae* (Blanchard) was displaced by *Liriomyza trifolii* (Burgess) in California (Parrella et al. 1984; Reitz and Trumble 2002) and in China (Gao et al. 2012) due to differential responses to pesticides.

Pesticides have different impacts on different species of spider mites and their predators. In the present study, the number of *N. womersleyi* adult females was higher before acetamiprid and imidacloprid application, whereas the proportion of *N. californicus* immediately increased after application (Fig. 2). Thus, the species displacement of *N. womersleyi* by *N. californicus* in Japanese fruit-tree orchards (Wakabayashi 2000; Amano et al. 2004; Gotoh et al. 2014) might have resulted from their differential susceptibilities to these neonicotinoids. An *N. womersleyi* population in several Japanese pear orchards was affected negatively by different pesticides including imidacloprid (Izawa et al. 2000). In the present study, the egg-to-adult stage of *N. womersleyi* was strongly affected by acetamiprid and imidacloprid. Although Amano et al. (2004) did not examine acetamiprid and imidacloprid, they reported that milbemectin and pyribaden were more lethal to adults of *N. womersleyi* than to adults of *N. californicus*. However, they were unable to determine to what degree these differences were responsible for the species displacement. In our study, milbemectin caused more than 90 % mortality in the egg-to-adult stages of both *N. womersleyi* and *N. californicus*. Because the mortalities were very high for both species,

these pesticides probably did not affect the species displacement. In apple orchards in Washington State, the predatory mite *Galendromus occidentalis* (Nesbitt) outnumbered the predatory mite *Zetzellia mali* (Ewing; Beers et al. 1993), but after several treatments of acetamiprid, *Z. mali* outnumbered *G. occidentalis* (Beers et al. 2005). In the phytoseiids *Amblydromella caudiglans* (Schuster) and *G. occidentalis*, imidacloprid caused adult female mortalities of 85 and 78 %, respectively (Schmidt-Jeffris and Beers 2015). In *G. occidentalis*, acetamiprid and imidacloprid were moderately toxic to larvae and had moderate to severe effects on fecundity (Beers and Schmidt 2014). Thus, these chemicals are not only detrimental to adults but also to the fecundity and immature stages of phytoseiids. In this study, we used only one strain of each species, although strains of *N. womersleyi* and *N. californicus* were found to vary in susceptibility to pesticides (Amano et al. 2004; Mochizuki 1990). Therefore, in future studies, we plan to test susceptibilities to chemicals in different strains of these two species.

Neonicotinoids have been used for insect and mite pest management for approximately 25 years in Japan. The population density of *N. californicus* has been increasing since the 1990s (Amano 2001). Acetamiprid and imidacloprid were first registered in Japan in 1989 and 1992, respectively. According to the spray calendar maintained by Chiba Prefecture, farmers started using acetamiprid and imidacloprid in fruit-tree orchards in Chiba Prefecture, in 1993 and 1997, respectively. The spraying period roughly corresponds with the time of displacement of *N. womersleyi* by *N. californicus*. Furthermore, the laboratory bioassays showed that the two pesticides are less harmful to *N. californicus* than to *N. womersleyi*. The failure of *N. californicus* to displace *N. womersleyi* even when the NC:NW ratio at the time of release was 1:9, together with the observation that *N. womersleyi* was displaced after the application of acetamiprid and imidacloprid, suggest that these two pesticides caused the displacement of *N. womersleyi*. These results indicate that the different modes of action of pesticides at different life stages have a role in phytoseiid mite species displacement.

Because of the increasing use of natural enemies in IPM programs, growers must understand how the natural enemies are affected by pesticides. It is likely that spider mite pest management programs with neonicotinoids need to be adjusted, as *N. californicus* exhibits dominance over *N. womersleyi* in Japanese fruit-tree orchards and displacement might occur. Continued use of either acetamiprid or imidacloprid at the recommended dose might lead to complete displacement of *N. womersleyi* by *N. californicus*. On the other hand, alanycarb and thiometon were more lethal to *N. californicus* than to *N. womersleyi* (Table 2), so that continued use of these pesticides might cause *N. californicus* to completely disappear from fruit-tree orchards. The *N. womersleyi* populations in Japanese fruit-tree orchards might rebound if changes are made in the pesticides that are used. For example, diamides suppress the growth of *N. californicus* more than they suppress the growth of *N. womersleyi* (Hirotsuna Hoshi, pers. comm.). Finally, this research provides new insights into the side effects of acetamiprid and imidacloprid (i.e., causing predatory species displacement of *N. womersleyi* by *N. californicus*) and highlights the importance of considering these side effects in Japanese fruit-tree orchards.

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