# Predation risk increases dispersal distance in prey

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## Abstract

Understanding the ecological factors that affect dispersal distances allows us to predict the consequences of dispersal. Although predator avoidance is an important cause of prey dispersal, its effects on dispersal distance have not been investigated. We used simple experimental setups to test dispersal distances of the ambulatory dispersing spider mite (*Tetranychus kanzawai*) in the presence or absence of a predator (*Neoseiulus womersleyi*). In the absence of predators, most spider mites settled in adjacent patches, whereas the majority of those dispersing in the presence of predators passed through adjacent patches and settled in distant ones. This is the first study to experimentally demonstrate that predators induce greater dispersal distance in prey.

## Keywords

Conditional dispersal, dispersal distance, antipredator behavior, settlement decision, spider mite

## Introduction

Dispersal ecology aims to elucidate how ecological factors affect the dispersal processes of organisms. Although dispersal consists of three distinct phases—departure, transfer and settlement (Clobert et al. 2009)—most theoretical and empirical studies have focussed only on departure

(Bowler and Benton 2005). However, while departure rate is informative, dispersal distances post-departure are necessary to predict the full consequences of dispersal (Travis et al. 2013). The ability of individuals to reach and settle into a suitable habitat patch can determine the fate of their populations, and thus the species (Kokko and Lopez-Sepulcre 2006; Travis et al. 2013), which is especially true when faced with increasing habitat fragmentation and climate change. Therefore, understanding the ecological factors influencing dispersal distance is of crucial importance in changing environments.

Actively dispersing organisms depart their natal patches, making decisions based on dispersal costs and benefits (Bonte et al. 2012). Once individuals have reached a potential patch, they must decide whether to settle or to continue searching for more suitable patches based on the costs and benefits of further dispersal (Bonte et al. 2012). The primary benefit of dispersal is leaving a patch with relatively lower fitness expectations due to resource deterioration and/or kin competition (Hamilton and May 1977). An increasing number of theoretical studies have investigated the influences of these factors on the evolution of dispersal distance (e.g. Rousset and Gandon 2002; Poethke et al. 2011). Furthermore, empirical studies have demonstrated that density and/or kin competition induces plasticity for dispersal distance in actively dispersing organisms such as small mammals (Ims and Andreassen 2005) and herbivorous mites (Bitume et al. 2013).

A further benefit of dispersal is predator avoidance (Lima and Dill 1990). Because individuals dispersing from an invaded patch must avoid being tracked by predators (Lima and Dill

1990), predators may affect not only the probability of departure (e.g. McCauley and Rowe 2010), but also patch settlement decisions and dispersal distances of prey. However, to our knowledge, only a few studies have considered the effects of predators on prey dispersal distances (Tamaki et al. 1970; Weisser et al. 1999; Meng et al. 2012). Tamaki et al. (1970) compared spatial distributions of apterous aphid populations in the presence or absence of parasitoids, and inferred that those aphids dispersed a greater distance if they encountered parasitoids. Similarly, Weisser et al. (1999) demonstrated that predators induced winged offspring in aphids, suggesting predator-induced long-distance dispersal. However, Meng et al. (2012) did not detect increased dispersal distances in adult whiteflies in the presence of predators. The scarcity of studies examining dispersal distances of prey organisms may be due largely to the difficulty in tracking flying organisms that disperse great distances.

To facilitate observation of the prey dispersal process, we used the ambulatory dispersing spider mite *Tetranychus kanzawai* Kishida (Acari: Tetranychidae) and its native predator *Neoseiulus womersleyi* Schicha (Acari: Phytoseiidae). Spider mites in the genus *Tetranychus* are major agricultural pests living in protective webs on leaf surfaces (Saito 1983). In response to plant deterioration, mated females disperse, mainly by walking to a new plant (Brandenburg and Kennedy 1982). However, specialist predatory mites, such as *N. womersleyi*, that can penetrate these webs also promote the dispersal of spider mites (e.g. Bernstein 1984; Grostal and Dicke 1999). Since such predators are used as biological control agents against spider mites (Sabelis and Bakker 1992), understanding their effects on the prey dispersal process is also of economic importance.

Here, we tested the hypothesis that spider mites perceiving a predation risk disperse farther than those dispersing in response to resource deterioration. This is the first experimental demonstration of predators increasing dispersal distances in prey organisms.

## Material and methods

We collected *T. kanzawai* from narrow-leaved vetch (*Vicia sativa* subsp. *nigra* L.; Fabaceae) in Kyoto, Japan. Individuals were maintained on kidney bean (*Phaseolus vulgaris* L.; hereafter “bean”) leaf discs pressed onto water-saturated cotton in Petri dishes (90 mm in diameter, 14 mm in depth). We collected *N. womersleyi* individuals from *Rosa centifolia* L. (Rosaceae) in Nara, Japan. Individuals were reared on bean leaf discs heavily infested with *T. urticae* as prey. All rearing and experiments were conducted under 25°C, 50% relative humidity and an L16:D8 photoperiod.

Our experimental setup contained three connected leaf patches (Fig. 1a). We introduced a mated 2-day-old female spider mite onto a 10 × 10 mm bean leaf square (initial patch) and allowed her to build webs for 24 h. We then introduced an adult female predatory mite onto the initial patch (predator present), while setups without a predator served as controls (predator absent). Since we intended to examine spider mite dispersal in response to a predator staying in the initial patch, predators were fed only water for the previous 48 h, as they remain in the initial patch containing abundant spider mite eggs longer than predators with previous access to food (SY, unpublished data). After allowing the predators to acclimate for 30 min, we connected the initial patch to two other consecutive leaf squares (second and third patches) with 10 × 30 mm Parafilm bridges. This setup was surrounded by water-saturated cotton to prevent mites from escaping.

We recorded the location and state of spider mites every 24 h until each had dispersed to either of the two consecutive patches. We identified which patch each spider mite first settled; we considered a patch as settled if it contained webs, injury scars, eggs and faeces of spider mites, regardless of the mites' presence. We excluded the data when predatory mites intruded into consecutive patches.

To confirm that female spider mites were not attracted to bean leaves at a distance of 30 mm (as examined above), we connected a leaf and a Parafilm square (10 × 10 mm each) with a T-shaped Parafilm pathway (Fig. 1b) and introduced a female spider mite ($N$=60) at the bottom of the pathway. The number of females that moved in each direction from the T-junction did not significantly differ from equality (leaf:control, 28:32; binomial test, $P$=0.70) (Fig. 1b). Therefore, dispersing spider mites were considered to have abandoned the previous patch, as opposed to having been attracted to adjacent patches, and that dispersal between patches connected with nonfood substrates could simulate ambulatory mite dispersal between remote patches.

## Results

The mean time (day±SE) before spider mites began dispersing was significantly shorter in the presence of predators (1.3±0.11) than in their absence (5.8±0.30; Mann–Whitney *U*-test, $P<0.0001$), suggesting that spider mite dispersal is dependent on predators. If predators are absent, dispersal is seemingly triggered by resource deterioration, but if predators are present, they become important dispersal motivators. This was consistent with results of previous studies reporting higher spider mite departure rates in the presence of specialist predatory mites (e.g. Bernstein 1984; Grostal and Dicke 1999). Furthermore, we showed that most spider mites dispersing in the absence of predators settled in adjacent (second) patches, whereas the majority of those dispersing in the presence of predators settled in distant (third) patches (Fisher's exact test, $P=0.0020$) (Fig. 2). Thus, we experimentally demonstrated that predators increase prey departure rate and dispersal distance.

## Discussion

In general, dispersing organisms adjust their behaviours based on the costs and benefits of dispersal (Bonte et al. 2012). That is, an individual that has reached a potential patch has the option to remain or to continue dispersing. Our results, showing that most prey individuals settled in adjacent patches in the absence of predators, support published theoretical research (Poethke et al. 2011). These authors predicted that dispersing individuals should settle in adjacent patches unless the cost of between-patch dispersal is extremely low because the costs of resource competition should sufficiently decrease after one dispersal step. Although dispersal costs were not simulated in our experiments, the average costs of between-patch dispersal that spider mites should incur in the wild may be considerable because their webs serve as refuges from numerous predators (Yano 2012) and spider mites in the open are extremely vulnerable. Our results imply that ignoring the first encountered patch is disadvantageous for spider mites when the predation risk by specialist predatory mites is low. Conversely, prey individuals dispersing greater distances in response to predators may benefit from escaping predators, not only because they move farther away from the invaded patch, but also because the probability of being tracked by predators substantially decreases with every between-patch dispersal event in the wild, where multiple dispersal directions are available. We showed that the majority of spider mites dispersing in the presence of specialist predatory mites passed through adjacent patches without settling, which implies that the benefits of greater dispersal distances under predation risk may outweigh the average costs of dispersal.

In contrast to departure rate, the ecological factors that influence dispersal distance are less understood. This is the first empirical study to demonstrate that predators induce greater dispersal distance in individual prey. Thus, both the departure rate (Bowler and Benton 2005) and dispersal distance appear to be affected by predation risk. Fronhofer et al. (2014) empirically and theoretically demonstrated that spatially correlated local extinctions select for long-distance dispersal. Contrary to unpredictable extinction events such as disease outbreak (Muller-Landau et al. 2003) and habitat fragmentation (Kallimanis et al. 2006), extinctions of local spider mite populations by specialist predators should be predictable because individuals can perceive intruding predators (e.g. Bernstein 1984; Grostal and Dicke 1999); therefore, conditional dispersal strategies in response to the presence of predators, as observed in our study, would be more advantageous than fixed strategies insensitive to predation risk.

Our results imply that the distribution of dispersal distances (dispersal kernel) measured in the absence of predators (Bitume et al. 2013; Fronhofer et al. 2014) should be significantly different when predators are present. Further empirical studies are required to understand how greater dispersal distances in response to predation risk contribute to the stability of prey populations and how this in turn influences the effectiveness of predators in suppressing prey populations. Addressing these questions would allow us to predict invasion rates of a prey species expanding its range (Kokko and Lopez-Sepulcre 2006), and in particular, insights into these issues regarding mite predator–prey interactions could contribute to the successful biological control of spider mites.

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## Figure captions

**Fig. 1 a** An experimental setup to investigate whether spider mites settle in adjacent (second) patches or continue to distant (third) patches in the presence or absence of predators. **b** An experiment to confirm that female spider mites are not attracted to bean leaves at a distance of 30 mm.

**Fig. 2** The proportion of spider mites that settled in adjacent (second) or distant (third) patches. Significantly more spider mites that encountered predatory mites settled in distant patches than those dispersing in response to resource deterioration (Fisher's exact test). Replicate numbers are shown in bars.

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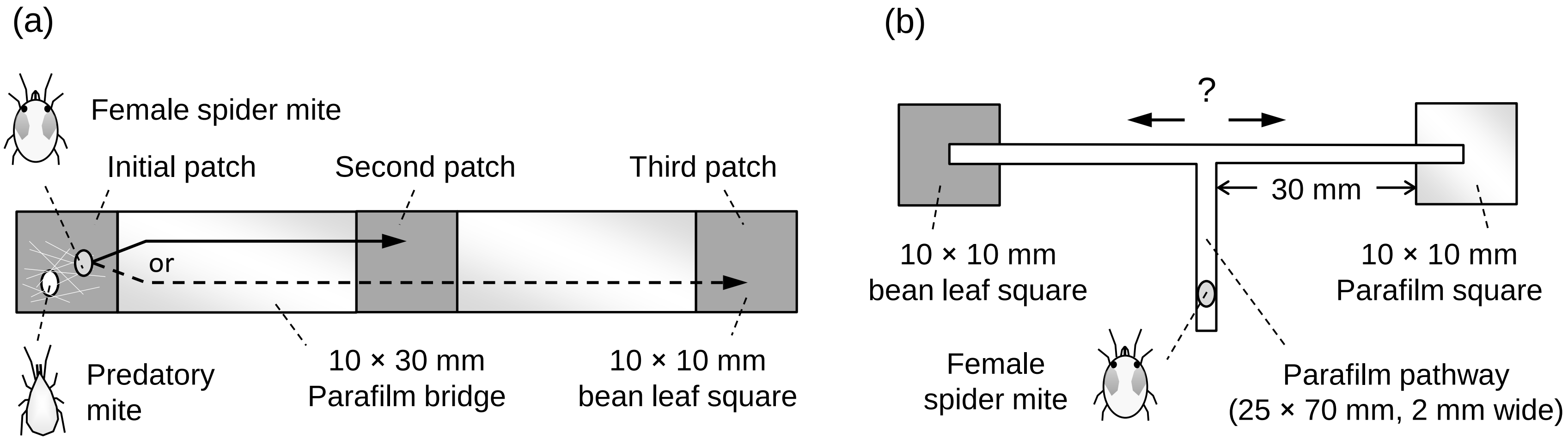
(a)
Female spider mite
Initial patch
Second patch
Third patch
or
Predatory mite
10 × 30 mm Parafilm bridge
10 × 10 mm bean leaf square
(b)
?
30 mm
10 × 10 mm bean leaf square
10 × 10 mm Parafilm square
Female spider mite
Parafilm pathway (25 × 70 mm, 2 mm wide)

**Fig. 1**

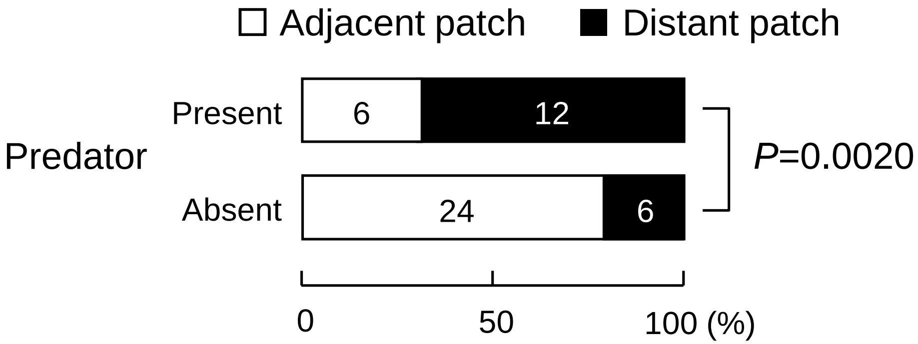
☐ Adjacent patch
■ Distant patch
Predator
Present
Absent
6
12
24
6
P=0.0020
0
50
100 (%)

**Fig. 2**