

Phenotypic plasticity of reproductive traits in response to food availability in invasive and native species of nematode

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Abstract Invasive species cause severe ecological and economic damage; however, the mechanisms underlying their successful invasion often remain elusive. In the case of *Bursaphelenchus xylophilus*, a global quarantine pest which invaded Asia and Europe, it has been suggested that this species possesses highly competitive abilities, which promotes its establishment and rapid spread. To explore biological traits that may explain its highly competitive abilities, we focused on expression of phenotypic plasticity in response to the food conditions experienced by the females during their development as juveniles in the invasive species *B. xylophilus* and native species *Bursaphelenchus mucronatus*. We report an unexpected significant difference of phenotypic trade-off between egg number and egg size in the invasive species *B. xylophilus* and native species *B. mucronatus*. This leads to superior propagation ability of invasive species, under high and low food conditions in culture. These effects reflect adaptive optimal resource allocation where more eggs

are produced in favorable environments to enhance population viability. Furthermore, we show that *B. xylophilus* eggs hatched earlier than *B. mucronatus* when their parents experienced high food availability. Thus, this study revealed, for the first time, phenotypic plasticity of reproductive traits in *B. xylophilus* which empowers the species a competitive advantage relative to their native counterpart *B. mucronatus* when they are under different range of food availability. These results are a step towards answering the vital question of how an exotic invasive species exclude a native species from its original niche.

Keywords Pinewood nematode · Biological invasions · Maternal effects · Competitive displacement · Blue-stain fungi

Introduction

Biological invasions are serious global threats to biodiversity and ecosystem function (Chapin et al. 2000; Kolar and Lodge 2001; Prenter et al. 2004). Many factors contribute to a successful biological invasion in new environments, including reproductive traits such as parental investment and fecundity, and high phenotypic plasticity of these traits (Drake 2007; Ghalambor et al. 2007; Berg and Ellers 2010). Phenotypic plasticity refers to the capacity of an organism to adopt different phenotypes depending on

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environmental conditions, and can be an important adaptive strategy to the successful colonization of new habitats (Agrawal 2001; Ghalambor et al. 2007; Sommer and Ogawa 2011). Many studies on animals and plants have shown that variation in phenotypic plasticity among introduced and indigenous species play a role in the process of invasion (Agrawal 2001; Richards et al. 2006; Chown et al. 2007; Chun et al. 2007; Hulme 2008). This may be especially true for instances where two similar organisms, one native and one invasive, occupy the same niche. Plasticity gives rise to a wide variety of behavioral, morphological, and physiological traits, and causes the invader to have a higher fitness than its native competitors in the new area (Agrawal 2001; Peacor et al. 2006; Chown et al. 2007; Kajita and Evans 2010). Furthermore, plasticity of an invader increases its ability to displace residents, because higher phenotypic plasticity is advantageous in tolerating novel conditions. A recent study suggests that, in the presence of predators, differences in phenotypic plasticity between nonnative and native species favor the invasive species as the superior competitor (Engel and Tollrian 2009). Therefore, understanding the difference in phenotypic plasticity between nonnative and native species may, in part, explain the invasion success of an invasive species.

Phenotypic trade-off between egg number and egg size has attracted considerable scientific interest over the past decades (Bernardo 1996; Herreras et al. 2007; Olofsson et al. 2009). One determinant of phenotypic quality is egg size, which is generally considered a maternal trait response to variations in environmental conditions experienced by the females and the developing immatures (Bernardo 1996; Herreras et al. 2007; Vijendravarma et al. 2010). Hence, mothers may partition their reproductive effort between egg number and egg size according to the maternal environment (Smith and Fretwell 1974; Einum and Fleming 2000; Olofsson et al. 2009). Phenotypic trade-off is expected between egg number and egg size because energy allocated to producing more eggs cannot simultaneously be used to provide more resources to each egg (Einum and Fleming 2000; Herreras et al. 2007; Olofsson et al. 2009). In several species of fishes, insects, and amphibians, offspring that hatched from larger eggs had higher rates of survival under adverse environmental conditions, while under benign conditions; offspring hatching from smaller eggs survive equally well or even better (Mousseau and Fox 1998;

Segers and Taborsky 2011). Invasive species usually have high propagation capabilities, develop faster, and have increased fitness (Cheng et al. 2009; Burton et al. 2010; Himler et al. 2011). Due to positive density dependence, initially small invading populations may fail to establish and spread. Thus, the successful invasive species is expected to produce many offspring in order to enhance their dispersal ability and extend their range (Burton et al. 2010; Kajita and Evans 2010). Despite these examples, the link between phenotypic plasticity in maternal generations and the success of invasive species in the novel environment remains unknown.

The pinewood nematode *Bursaphelenchus xylophilus* is the causal agent of the destructive pine wilt disease. Native to North America, this nematode has been introduced to Japan, South Korea, China, Portugal and Spain where it has caused irreparable damage to forested ecosystems (Mota et al. 1999; Jones et al. 2008; EPPO 2010; Fonseca et al. 2010). It is considered one of the most important invasive species in the world and is listed as a quarantine pest in more than 40 countries (Tóth 2011). In contrast, *Bursaphelenchus mucronatus* has been known as a non-pathogenic nematode, widely distributed in Eurasian pine forests, and regarded as a native species in China (Mamiya and Enda 1979; Iwahori et al. 2002; Cheng et al. 2009). This species is very similar to *B. xylophilus* in morphology and biology (De Guiran and Bruguier 1989), and occupies the same niche in their ecosystem. *B. mucronatus* has weaker propagation potential and competitive ability than *B. xylophilus* (Cheng et al. 2009). Although the successful invasion of *B. xylophilus* is attributed to its ability to displace other nematode species (Cheng et al. 2009), its underlying mechanisms remain unclear.

Bursaphelenchus species are fungal feeding (Jones et al. 2008), the ecosystem in which they are found harbors many microbes, predominantly Ophiostomatoid fungi, which have positive effects on reproduction in *B. xylophilus* (Maehara and Futai 2008; Niu et al. 2012). The widespread geographically unique suite of Ophiostomatoid fungi, such as *Ophiostoma ips*, *O. minus*, *Sporothrix* sp., and *Ceratocystis* sp., have been reported from wood infested with the *B. xylophilus* in Japan, Korea, and America (Hyun et al. 2007; Kobayashi et al. 1974; Wingfield 1987). Three species of Ophiostomatoid fungi including two new species *Sporothrix* sp.1, *Sporothrix* sp.2 and one shared native

species *Ophiostoma ips* are identified in China. The blue-stain fungus *Sporothrix* sp.1 grew fastest and generated the highest population growth of *B. xylophilus* among them (Niu et al. 2012).

To explore biological traits that may explain its successful invasion, we focused on expression of phenotypic plasticity of egg number and size in response to variation in food availability in the invasive species *B. xylophilus* and native species *B. mucronatus*. During the invasion process, such phenotypic plasticity may play a role in the successful invasion of *B. xylophilus*. To simulate conditions under which these maternal effects operate, we manipulated the availability of food offered to juveniles by utilizing a well-established, optimized reduced fungi feeding protocol in which nematodes were maintained on rigidly rationed fungal food for different amounts of times (e.g., Sutphin and Kaerberlein 2008; Greer and Brunet 2009); after these juveniles became adults, we measured the following maternal reproductive traits: egg size, number, and hatch time.

Materials and methods

Nematode cultures, population dynamics, and establishment of maternal groups with different feeding experience

Two species, *B. xylophilus* and *B. mucronatus*, were obtained from Zhejiang Province, China and cultured with the fungus *Sporothrix* sp.1 on 2 % malt extract agar (MEA, 7 g Biolab malt extract, 7 g Biolab agar and 350 ml deionised water, pH = 5.75). Prior to experiments, *B. xylophilus* and *B. mucronatus* were inoculated on separate plates of the fungus *Sporothrix* sp.1, incubated at 25 °C for the next experiment.

To measure general population dynamics, three hundred juveniles of *B. xylophilus* and *B. mucronatus* were inoculated on separate plates of *Sporothrix* sp.1 cultures. They were kept at 25 °C in the dark, the living nematodes were destructively sampled and extracted from each plate by the Baermann funnel technique at 7, 14, 21 days. Nematodes were recorded under a dissecting microscope (Cheng et al. 2009).

To establish maternal groups with different feeding experience, we reared juveniles to adulthood under three food conditions that followed a well-established, optimized reduced fungi feeding protocol (e.g., Sutphin and Kaerberlein 2008; Greer and Brunet 2009).

For both food restriction (low food) and food rich (high food) conditions, nematodes were cultured on the fungus *Sporothrix* sp.1. Under low food condition nematodes were grown on same *Sporothrix* sp.1 plate for 21 days, whereas under food rich condition, nematodes were transferred to fresh plates with food every 7 days to ensure a sufficient source of food for maintenance of the nematode colony and progeny development. For low to high food, second stage juveniles from low food parents were transferred to fresh plates for growing up into adults. This design resulted in three different experimental groups of adults for measuring maternal effects, which were denoted as L, H and LH. A possible fourth group of high to low feed adults (HL) could not be established as second stage juveniles from well fed parents transferred to low food do not complete development into adults.

Egg number and size assays

To investigate the effect of food availability on the number and size of egg production of different types of parents (L, H, LH). Two hundred fourth stage juveniles (female : male = 40:160) were inoculated on the fungal mats (1 female, 4 males per plate, n = 40 plates) and kept at 25 °C for 2 days, then transferred to fresh plates. Old plates were stored at 25 °C for 2 days and then scored for number of nematodes present. Transfers and scoring continued until all nematodes failed to produce progeny for two consecutive days (Sutphin and Kaerberlein 2008). Eggs and all of the hatched larvae from each Petri-dish were recorded as total number of eggs produced by a female. In each Petri-dish, pictures were taken of eggs with an Olympus BX51 microscope (Olympus America Inc., Melville, NY) and a digital imaging system Olympus DP2-BSW software at 40× magnification. The area (A) and perimeter (P) of each egg was measured automatically using Olympus DP2-BSW software. The egg shape is approximate prolate spheroid, using estimated semi-major axis a and semi-minor axis b for each egg, we calculated the egg volume V_{EGG} as: $V_{\text{EGG}} = 4/3\pi ab^2$. In subsequent analyses V_{EGG} was used as input value for egg size (Gutteling et al. 2007). The eggs are collected before first stage larvae (L1); we aimed to measure five eggs from each female, which would result in 200 measurements. The actual

number measured per treatment varied depending upon image quality and the current age structure of the population resulting in variable data range (*B. xylophilus*: L, n = 150; H, n = 191; LH, n = 190; *B. mucronatus*: L, n = 123; H, n = 200; LH, n = 227).

Female size assays

Fifty females of *B. xylophilus* and *B. mucronatus* from experimental groups of parents (L, H, LH) were used in the experiment. When the nematodes reached the adult stage, they were cultured for 2 days (Zhao et al. 2007). In order to calculate body volume, digital pictures were taken of the bodies at 20× magnification. Area (A) and perimeter (P) of each nematode were measured digitally (see above for equipment used). Assuming that the body of a nematode resembles a cylinder, we calculated the volume by: $V_F = \pi A^2 / 2P$. In subsequent analyses V_F was used as input value for female body size (Gutteling et al. 2007).

Hatching time and rate assays

To measure hatching time, ten (female: male = 1:1) adults of both *B. xylophilus* and *B. mucronatus* were randomly picked from experimental groups of parents (L, H, LH), then transferred to fresh plates kept at 25 °C for 48 h. The average hatching time was calculated as the proportion of unhatched eggs to total eggs laid multiplied by the experimental time (T = 48 h): $N_{\text{egg}} / (N_{\text{egg}} + N_{\text{juv}}) \times T$ (Muschiol et al. 2009). Where N_{egg} refers to unhatched eggs, N_{juv} refers to hatched juveniles.

To measure hatching rate, one hundred adults and stage 4 juveniles of both *B. xylophilus* and *B. mucronatus* were randomly picked from experimental groups of parents (L, H, LH), then transferred to fresh plates (90 mm diameter × 20 mm high) with *Sporothrix* sp.1 (*Sporothrix* sp.1 grown on 2 % MEA for 10 days) kept at 25 °C for 12 h. Under sterile conditions, 25 eggs were washed out and placed in a small Petri-dish (35 mm diameter) using a 20 µl syringe, and 2 ml sterilized water was added to the dish. Four Petri-dish cultures for each treatment were used. Experiments were kept at 25 °C for 72 h. To obtain hatching rates, the proportion of newly hatched nematodes (out of 25 eggs) in each Petri-dish were counted under a microscope (Zhao et al. 2007).

Statistical analyses

Statistical analyses for this study were performed using SPSS 17.0 for Windows (SPSS Inc., Chicago, IL, USA). Effects of original maternal environment on egg size and female size was assessed using one-way ANOVA, followed by the Tukey's multiple comparison tests. Population dynamics and hatching time were analyzed by independent samples *t* test. Consequently, in order to examine how egg number and size variations related to maternal food environments, we used linear regression analysis to analyze the corresponding data between egg number and egg size. Data were log-transformed if needed to meet the assumptions of normality. Relationships between variables were evaluated using Pearson's correlation coefficients.

Results

Population dynamics

To assess food restriction and food rich conditions, we performed population dynamics experiments through different feeding times. Nematode population dynamics are feeding time dependent. Total number of *B. xylophilus* and *B. mucronatus* increased from 7 to 14 days (*B. xylophilus*, $t = -5.888$, $df = 16$, $P < 0.001$; *B. mucronatus*, $t = -5.821$, $df = 16$, $P < 0.001$), but decreased at 21 days (*B. xylophilus*, $t = 8.210$, $df = 16$, $P < 0.001$; *B. mucronatus*, $t = 4.867$, $df = 16$, $P < 0.001$) (Fig. 1). Furthermore, *B. xylophilus* produced more offspring than *B. mucronatus* at the start of the experiment, there was a significant difference between them at 7 days ($t = 2.306$, $df = 16$, $P = 0.035$) and 14 days ($t = 3.018$, $df = 16$, $P = 0.008$).

Egg number and size

Evidence for a phenotypic trade-off between egg number and egg size was only found in the population of *B. xylophilus* (Fig. 2). There was a significant negative correlation between egg number and egg size in *B. xylophilus* regardless of food availability (L, $r = -0.418$, $P = 0.033$, $n = 26$, Fig. 2a; H, $r = -0.579$, $P = 0.001$, $n = 30$, Fig. 2c; LH, $r = -0.597$, $P < 0.001$, $n = 32$, Fig. 2e); however, we found no significant relationship between egg number and egg

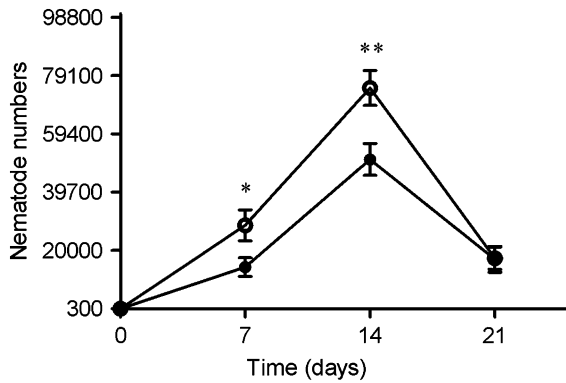


Fig. 1 The change of nematode numbers associated with feeding day. Represented values are mean \pm SE (error bars). Asterisks indicate statistically significant differences between *Bursaphelenchus xylophilus* and *Bursaphelenchus mucronatus* on 7 and 14 days (independent samples *t* test, * $P < 0.05$; ** $P < 0.01$). Open circles, *Bursaphelenchus xylophilus*; filled circles, *Bursaphelenchus mucronatus*

size in *B. mucronatus* under different feeding protocols (L, $r = 0.344$, $P = 0.099$, $n = 24$, Fig. 2b; H, $r = -0.175$, $P = 0.353$, $n = 30$, Fig. 2d; LH, $r = -0.284$, $P = 0.128$, $n = 30$, Fig. 2f).

Egg size was significantly affected by juvenile food experience in both *B. xylophilus* ($F_{2, 509} = 70.102$, $P < 0.001$; Table 1) and *B. mucronatus* ($F_{2, 542} = 84.142$, $P < 0.001$; Table 1). Likewise, the two groups did not differ in plasticity; eggs laid by poorly fed parents (L) were larger than eggs laid by well fed parents (H) (*B. xylophilus*, $P < 0.001$; *B. mucronatus*, $P < 0.001$). For the LH group, second stage juveniles from poorly fed parents, females adjusted their egg size and produced smaller eggs compared to those that experienced low food availability (*B. xylophilus*, $P < 0.001$; *B. mucronatus*, $P < 0.001$), but *B. xylophilus* eggs were larger than that from juveniles that experienced high food

Fig. 2 Relationship between log-transformed egg number and log-transformed egg size. The food conditions parents experienced as juveniles were: **a, b** low food; **c, d** high food; **e, f** low-high food

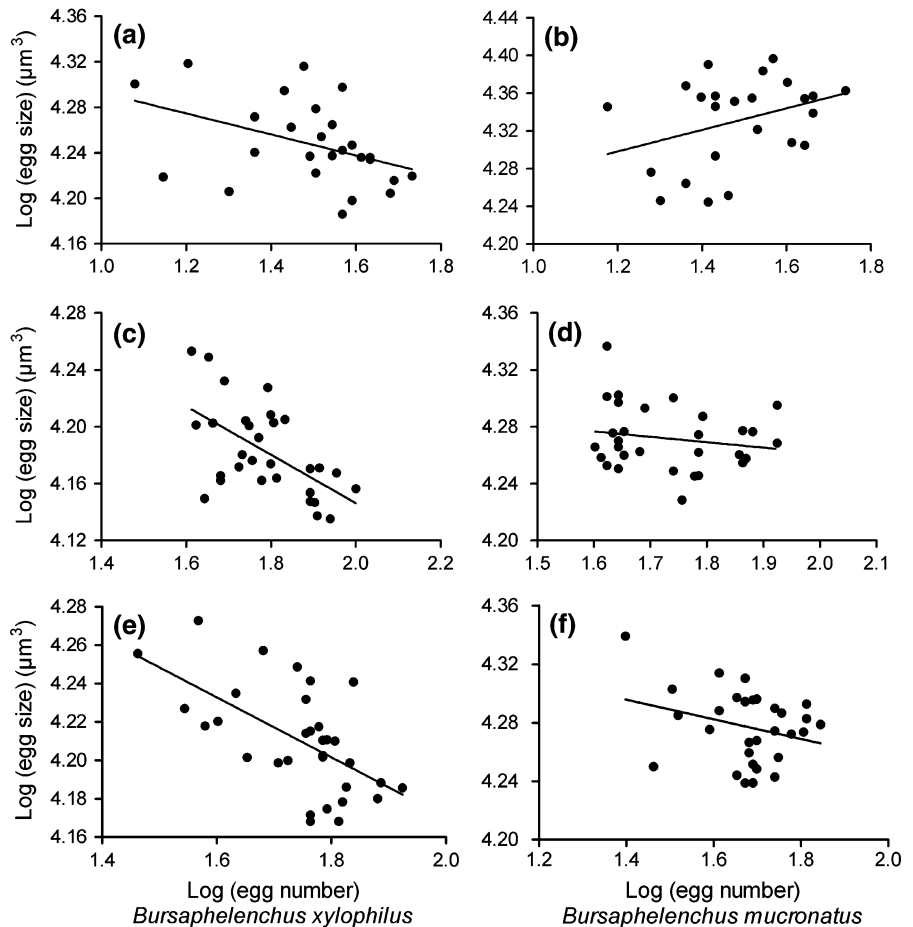


Table 1 Effects of different food conditions on egg size and female size

Food	Egg size (μm^3) [mean \pm SE]		Female size (μm^3) [mean \pm SE]	
	<i>B. xylophilus</i>	<i>B. mucronatus</i>	<i>B. xylophilus</i>	<i>B. mucronatus</i>
L	17,555.4 \pm 176.7a	21,514.0 \pm 247.0a	235,152.7 \pm 6,331.71c	267,086.8 \pm 8,426.5c
H	15,076.8 \pm 134.6c	18,716.7 \pm 105.7b	360,521.4 \pm 13,115.1a	330,274.8 \pm 7,365.9a
LH	16,363.1 \pm 137.3b	19,121.2 \pm 129.3b	286,318.8 \pm 6,984.8b	303,023.3 \pm 8,030.9b

Means in a column followed by different letter are significantly different at $P < 0.05$, data were analyzed by Tukey's multiple comparison test

L low food, H high food, LH low-high food

availability ($P < 0.001$), and were not significantly different from *B. mucronatus* ($P = 0.085$).

Female size

Female size of *B. xylophilus* and *B. mucronatus* at maturity exhibited very similar affects under different feeding protocols. Low food availability inhibited female growth, causing a decline in size, whereas high food availability leads to an increase in size (Table 1). Females that experienced high food availability were larger than the females that experienced low food availability (*B. xylophilus*, $P < 0.001$; *B. mucronatus*, $P < 0.001$). For the LH group, second stage juveniles from poorly fed parents that were given high food exhibited females that were significantly larger than those receiving low food (*B. xylophilus*, $P < 0.001$; *B. mucronatus*, $P = 0.005$), but smaller than those receiving high food (*B. xylophilus*, $P < 0.001$; *B. mucronatus*, $P = 0.044$).

Hatching time and rate

To understand how maternal food environments elicit the hatching time phenotypes, we examined its impact on *B. xylophilus* and *B. mucronatus* eggs (Fig. 3). Eggs from poorly fed parents (L) of both species had similar hatching time ($t = 0.442$, $df = 18$, $P = 0.664$). However, for eggs produced from well fed parents (H), hatching time were significant difference in both species, *B. xylophilus* eggs hatched earlier than that for *B. mucronatus* ($t = -5.227$, $df = 16$, $P < 0.001$). For the LH group, second stage juveniles, the hatching time for *B. xylophilus* eggs was also earlier than that for *B. mucronatus* ($t = -3.177$, $df = 8$, $P = 0.013$). Moreover, there was no observable variation in egg hatching rates with change in food level of the parent nematode *B. xylophilus* (all $P_s > 0.05$; L, 99 %; H,

100 %; LH, 100 %) and *B. mucronatus* (all $P_s > 0.05$; L, 98 %; H, 100 %; LH, 100 %).

Discussion

Our results are consistent with the expectation that phenotypic plasticity in reproductive traits increased superior competitive ability of invasive species *B. xylophilus* to utilize food resources over native species *B. mucronatus*, based on several lines of evidence: (1) *B. xylophilus* exhibited phenotypic trade-off between egg number and egg size (Fig. 2a, c, e). This result suggests that *B. xylophilus* may well be at an advantage relative to their native *B. mucronatus* counterparts when they are under a wide range of food availability. (2) Shorter hatching time (Fig. 3),

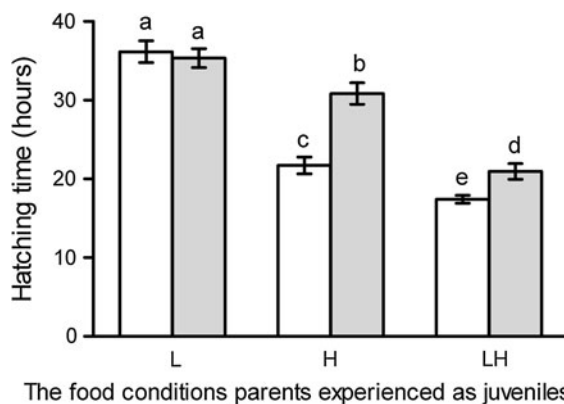


Fig. 3 Effects of the food conditions parents experienced as juveniles on egg hatching time. Each bar represents the mean \pm SE different letters above the bars indicate statistical significance differences were calculated with independent samples t test ($P < 0.05$). L low food, H high food, LH low-high food. Open bar, *Bursaphelenchus xylophilus*; filled bar, *Bursaphelenchus mucronatus*

gives *B. xylophilus* numerical advantage, suggesting *B. xylophilus* will become dominant in a mixed population with *B. mucronatus* under benign environmental conditions. (3) Population dynamics analysis revealed that high food availability led to the production of more *B. xylophilus* offspring than *B. mucronatus* (Fig. 1). Competition for resources is one of the most important interactions an invasive species faces in a new environment (Ings et al. 2006; Engel and Tollrian 2009). The result provides support for previous work which suggested that female fecundity is another mechanism that can lead to displacement of one population by another (e.g., Reitz and Trumble 2002; Cheng et al. 2009).

We have also investigated potential effect of maternal food environments on egg size, using different types of parents from experimental groups. Females exposed to low food availability as juveniles produced larger eggs than that females exposed to high food availability (Table 1). However, it is not the extent of phenotypic plasticity that differs between two species of nematode. Perhaps the large egg size reflects enhanced ability to compete with conspecifics and better suited to poor conditions (e.g., Marshall et al. 2006; Harvey and Orbidans 2011). When competition among juveniles for resources is intense, mothers that increase egg size can improve expected fitness (Segers and Taborsky 2011). If mothers respond to reduced food availability by producing larger eggs, then this environmental maternal effect may represent adaptive plasticity (Mousseau and Fox 1998). Therefore, food-associated variation in egg size within populations of *B. xylophilus* and *B. mucronatus* represents an adaptive maternal effect in which females adjust egg size depends strongly on the conditions their offspring are likely to experience.

The question of whether to produce many smaller or a few larger eggs is one of the most important reproductive traits an invasive species faces as food levels vary. Competitively superior invasive species will probably tend to produce more offspring, which facilitate its establishment in a new environment (Burton et al. 2010; Kajita and Evans 2010). There are different theoretical and empirical evidence to explain this phenomenon, one is that mothers can predict good rearing conditions for their young, and thus tend to produce more, but not larger eggs (Smith and Fretwell 1974; Segers and Taborsky 2011). In many cases, fluctuation in food availability elicited phenotypic changes in resource allocation to growth, maintenance and reproduction (fecundity,

offspring size and offspring quality) (Beckerman et al. 2006; Pollux and Reznick 2011). In this work, we interpret maternal effects on the reproductive allocation patterns as an adaptive response to different resource levels. The invasion species *B. xylophilus* can adjust their resource allocation; offspring of parents reared in high food availability environments produced more and smaller eggs than the offspring from parents reared in low food availability environments. There is a significant negative relationship between egg number and egg size in *B. xylophilus* regardless of the food availability they have experienced. However, we did not find this phenomenon in *B. mucronatus* when parents were reared with three different food levels. Further investigation into why *B. xylophilus* apparently sacrifices egg size for increased numbers, but *B. mucronatus* does not remains to be answered.

Bursaphelenchus xylophilus is a pathogenic nematode; it is the causative agent of pine wilt disease. *B. mucronatus* is a non-pathogenic nematode as it usually does not kill pine trees (Cheng et al. 2009), where availability of resources is presumably very high, there may be fewer constraints acting on allocation of resources among the nematodes thereby not having trade off between these two traits. The plasticity in phenotypic traits is more likely to be observed in variable environmental conditions rather than fixed stable conditions (Agrawal 2001; Pollux and Reznick 2011). Such phenotypic trade-off can have profound implications for females as they can allocate resources into egg number and egg size depending on variations in food availability. Hence, we suggest that *B. xylophilus* females invest their stored resources into laying a greater amount of smaller eggs to enhance their dispersal ability under high food availability.

Hatching plasticity allows organisms to respond appropriately to the environment experienced during early development (Warkentin 2011). Previous studies have shown that matching the hatching time to food availability is an important adaptation for rapid population growth (e.g., Koeller et al. 2009; Van Asch et al. 2010). We also found good agreement between food conditions that juveniles experienced and the egg hatching time. Eggs that were laid by high food or low-high food groups, hatched earlier than low food groups (Fig. 3). However under high food conditions *B. xylophilus* eggs hatched earlier than *B. mucronatus* eggs. Early hatching may facilitate *B. xylophilus* to have a greater increase in number and thus become

dominant in a theoretically combined population under benign environmental conditions. These findings therefore suggest that maternal effects can have a profound effect on invasion potential via hatching plasticity.

B. xylophilus and *B. mucronatus* are plant nematodes and thus interact with various plant fungi in their natural habitat. Some fungi that they interact with are less or not suitable as a food source for the *B. xylophilus* (e.g., some *Trichoderma* spp., *Verticillium* spp., etc.) (Mae-hara and Futai 2008). However, our study focused on blue-stain fungus *Sporothrix* sp.1, which is suitable for propagation of both nematodes (Niu et al. 2012), but the specific situation of the field remains worthy of further research.

In conclusion, we have demonstrated that the invasive species *B. xylophilus* show phenotypic trade-off between egg number and egg size, and is different from the native species *B. mucronatus*. Food induces increased maternal effects on egg hatching and size. When *B. xylophilus* juveniles experienced low food availability, the adults produced larger eggs with a prolonged hatching time, whereas when juveniles experienced high food availability, adults tended to produce more eggs that hatched significantly earlier. The ability to have effective phenotypic plasticity promotes competitive ability, especially during times of resource-rich or disturbance conditions, which may represent a key adaptation which leads to displacement of *B. mucronatus* and successful invasion. Our results raise the possibility that such adaptations, at least in part, provide insights into the mechanisms underlying the success of invasive species.

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