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Behavioural, morphological, and life history shifts during invasive spread

Monica A. Mowery · Cor Vink · Andrew C. Mason · Maydianne C. B. Andrade

Abstract Invasive species are common around the world, but we still do not know which traits are most important for successfully establishing in new environments. Different stages of the invasion process, including transport, introduction, establishment, and spread, can act as selective filters for different combinations of phenotypic traits. Theoretical and empirical studies predict that invasive populations should have suites of behaviours that improve dispersal and spread, including higher boldness, dispersal propensity, and activity levels than native populations. In this study, we tested these predictions by comparing the morphology, life history, and behaviour of an invasive population of redback spiders, *Latrodectus hasselti,* from Japan to a population of native spiders from Australia, with additional comparisons of another invasive population from New Zealand. We found that both a longer-established invasive New Zealand population and the more recently-established invasive population from Japan were more dispersive than the native population from Australia. The invasive population from Japan showed elevated levels of sibling cannibalism relative to the native population, which may increase total reproductive success of females under food limitation. Spiders from Japan were also less bold in response to a simulated predator threat compared to native spiders from Australia. In contrast to the prediction that invasive populations would show uniformly fast life history traits, the invasive population from Japan was more fecund, yet took longer to develop than the native population under laboratory conditions. Overall, our results show that invasive populations are phenotypically distinct from native populations, with some behavioural, life history, and morphological traits that would increase spread (dispersal tendency, high fecundity) and persistence (sibling cannibalism) in new habitats.

Keywords Behaviour · Dispersal · Life history · Spider · Invasion

M. A. Mowery (✉) · A. C. Mason ·
M. C. B. Andrade
Department of Biological Sciences, University of Toronto Scarborough, Toronto, ON, Canada
e-mail: monicaan@post.bgu.ac.il

Present Address:
M. A. Mowery
Mitrani Department of Desert Ecology, The Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, Israel

C. Vink
Department of Pest-Management and Conservation, Lincoln University, Canterbury, New Zealand

Introduction

Invasive species are increasingly spread around the world by human-mediated transport, but what makes a successful invader is not clear (Hulme 2009; van Kleunen et al., 2011; Wardle et al., 2011). A common approach to trying to identify indicators of invasive success is to compare closely related native and invasive species (Dunn et al., 2009), or native and invasive populations of the same species (Lamarque et al., 2015). In some cases, invasive and native populations or species do not differ significantly, perhaps because some species have preadapted traits that predispose them to invasion success, even in their native range (e.g., Elst et al., 2016; Schlaepfer et al., 2010), or because plasticity is key to invasion (Lamarque et al., 2015). However, drift may play a role in differentiation of invasive populations, since initial invasions are expected to involve founder effects (Abdelkrim et al., 2005; Barrett et al., 1996). Selection during the invasion process is also expected (Colautti et al., 2017; Colautti and Lau 2015), and may result in invasive populations that are phenotypically different from native populations (Sakai et al., 2001). The morphological, life history, and behavioural traits that aid invasive establishment and spread past the point of introduction in new environments may differ from those that are adaptive in the native range, leading to phenotypic differences from the native source population (Chapple et al., 2012; Le Gros et al., 2016).

The invasion process can be characterized by a series of stages, including transport, introduction, establishment, and spread (Blackburn et al., 2011). Selective filters at different stages of the invasion process cause phenotypic differences between native and invasive populations of the same species, and different combinations of traits may be adaptive at different stages (Sakai et al., 2001). For example, the transport stage may select for traits that increase survival, such as selection for increased tolerance to heat stress (e.g., mussels, Lenz et al., 2018), or behavioural traits related to higher activity in novel conditions (e.g., songbirds, Mueller et al., 2017). A selective filter at the introduction stage could favour tolerance to new predators, prey, or pathogens and survival in different abiotic conditions than the native habitat. For example, in invasive bunchgrass, selection for drought tolerance occurred after introduction, but

before range expansion (Marchini et al., 2018). During invasive range expansion, traits that facilitate movement, such as increased dispersal ability, may be favoured. Such selective filtering through multiple stages of the invasion process can result in invasive populations with a mix of traits adaptive at different stages (Carrete et al., 2012; Chapple et al., 2012). Apart from selection based on the invasion pathway, once a population has established and spread, the new environment is often different and may be unpredictable compared to the native environment. Thus, as invasive populations become more well-established, the signature of selection during transport and spread may become less prominent as selection increases for local adaptation or plasticity. In this study, we focus on morphology, life history, and behavioural traits that may affect invasive success at different stages.

Morphological and life history traits that increase survival in transport, establishment, and spread may differ from those in the native range. For example, compared to native populations of the same species, Asteraceae plants grow larger in the invasive range, which may facilitate movement and dispersal, and also aid in outcompeting native species (Jakobs et al., 2004). However, there is often a tradeoff between advantageous large size and development time (Gadgil and Bossert 1970; Nijhout 2015), which may depend on environmental conditions, both biotic (competitors and predators present) and abiotic (temperature and seasonality). For example, invasive individuals may be smaller if investment in high reproductive output or rapid development decreases offspring size (Thorlacius and Brodin 2018). This trade-off may be adaptive if new conditions are unfavourable, or population density is low (Brownscombe and Fox 2012). Thus, life history traits such as high fecundity and fast development time, which may be important for successful establishment and population growth after initial colonization (fish: Amundsen et al., 2012; reptiles and amphibians: Allen et al., 2017; mammals: Capellini et al., 2015) or at the invasion front (Burton et al., 2010), are linked in complex ways with body size, mediated by environmental factors.

Similarly, different sets of behaviours could be adaptive at different stages of invasion, resulting in opposing selection pressures over time. For example, exploratory behaviour and high levels of dispersal may be favoured during transport to a new habitat

(Pettit et al., 2016) and spread. The result can be shifts in allele frequencies at loci governing higher activity levels in response to novelty (Mueller et al., 2017). In addition, natal dispersal distance or propensity may determine the likelihood of colonizing new habitats, and is often positively correlated with activity level, exploratory behaviour (Korsten et al., 2013), or boldness and aggression (Rehage and Sih 2004). These correlated behaviours, called syndromes, often vary within populations, and may show patterns of spatial sorting, with individuals with the highest dispersal propensity (and highest activity levels, boldness, or exploratory behaviours) found closest to the edge of the invasion front (Atwell et al., 2012; Liebl and Martin 2012). This process accelerates invasion (Ochocki and Miller 2017) by supporting population expansion and likelihood of exploiting novel conditions. As a result, more aggressive, bolder, more exploratory individuals may be common at the invasion front, but less common in subsequent waves of individuals establishing in the new habitat, when population densities are higher and local adaptation is important (Duckworth and Badyaev 2007; Sih et al., 2012). Thus, in addition to differences between native populations and those at the early stages of invasion, long-term differentiation between established invasive populations compared to the native source population is expected (Michaelides et al., 2018). Although there may be evolutionary lags (Crooks and Soulé 1999; Pyšek and Jarošík 2005), with sufficient time, introduced populations are expected to adapt to the novel environment (Caut et al., 2008; Colautti et al., 2017), which may lead to new trade-offs relative to the native population or the early stages of invasion (Burton et al., 2010).

We assess traits leading to invasion success in the Australian redback spider, *Latrodectus hasselti*, native to Australia and now introduced and spread in New Zealand (detected in 1984 Forster 1984) and 11 years later, in Japan (detected in 1995 Ori et al., 1996). We predict that, in comparison to the native Australian population, invasive populations from Japan and New Zealand will be larger, more fecund, more exploratory, bolder, more dispersive, develop more rapidly and have higher rates of sibling cannibalism (a behaviour that may buffer against low food availability). In addition, we expect the more recently-established population (Japan) will score higher on these traits than the longer-established invasive population (New Zealand).

Methods

Latrodectus hasselti has been introduced to Japan and New Zealand, as well as India, Iran, and Papua New Guinea (Chrysanthus 1975; Hippargi et al., 2012; Shahi et al., 2011), likely through cargo ships carrying wood, steel, or produce (Vink et al., 2011). *Latrodectus* spiders and fertilized egg sacs have been intercepted in international shipments of produce and second-hand cars to Europe (Blick et al., 2004; Van Keer, 2011). Adult females build their webs in refuges in corners of wood and metal structures, so can remain undetected during transport. This iteroparous, high-fecundity species may have 1 to 3 overlapping generations per year, which may facilitate establishment. *Latrodectus hasselti* develop and hatch inside egg sacs, with clutches of up to 300. Spiderlings emerge at the 2nd instar and stay clustered on their natal web, during which time they may cannibalize siblings (Modanu et al., 2014). Invasive success of these spiders may be facilitated by sibling cannibalism, which may increase survival of cannibals when prey are scarce (Antonialli-Junior and Guimarães 2014). Spiderlings disperse after about one week by ballooning (Forster 1992) and rappelling (Forster 1995), and high dispersal propensity may increase invasive spread. Male and female widow spiders have dramatically different life histories and sizes; males, which are 1–2% of a female's mass, wander in search of females, while females are sedentary (Andrade 1996). Propensity for sibling cannibalism and dispersal both vary across family lines in *Latrodectus* spiders (Johnson et al., 2010, 2015; Modanu et al., 2014). These spiders depend on webs for prey capture and defense from predators, so after arriving in a new environment, spiders must rapidly build webs to survive. Web-construction activity may co-vary with boldness in spiders, as found in *Cyrtophora citricola*, an invasive orbweaver spider (Chuang and Riechert 2021). Like other Theridiidae, widow spiders typically rest in a protected area of the web during the day. Foraging requires movement across the web, but spiders may retreat or 'huddle' (pull in their legs and cease movement) if they detect a threat (e.g., predator vibration).

Laboratory conditions and populations

All spiders used in these experiments were reared in the lab under 12:12 L:D and at 25 °C conditions. Juvenile spiders and males were fed flies (*Drosophila*

spp.) and watered twice per week as juveniles, and female spiders were fed crickets (*Gryllodes sigillatus* or *Acheta domesticus*) once per week as adults.

Mated *L. hasselti* females (P, parental generation) were collected from North Epping, NSW, Australia (33.765°S, 151.087°E), Osaka, Japan (34.775°N, 135.490°E) and Fukuoka, Japan (33.666°N, 130.417°E) in October 2015, and from Alexandra, New Zealand (45.235°S, 169.345°E) in February 2019. Additional preserved adult females from New Zealand, used for morphological measurements, were originally collected in Bannockburn (45.085°S, 169.171°E), Cairnmuir (45.079°S, 169.1882°E), and Alexandra (45.254°S, 169.402°E). The Japan population from Osaka was near the site of the initial introduction in 1995, while the population from Fukuoka was likely established after 2000 (Nihei et al., 2003). The habitat where the New Zealand population was collected is low density and not inhabited by humans, whereas the Japanese population is high density and found near ports and cities (Forster 1984; Nihei et al., 2003; Vink et al., 2011). F1 offspring were derived from eggs produced by P females, which were reared to adulthood, then mated in the laboratory using an outbreeding protocol. Experimental individuals for measuring behaviours (boldness, exploration, and dispersal) for the Australian and Japanese populations were from the F2 and F3 (outbred) generations from P females (Supplemental Material 1). Constrained by the timing of field collecting, and the intervals needed for behavioural trials, the New Zealand juveniles tested were from the F1 generation from P females.

Across all trials described below, spiders were only assayed once across different size, life history, or behavioural assays (e.g., no individuals were reused across trials to avoid habituation or stress-related effects).

Size

Spiders were photographed using a Nikon DXM 1200 digital camera mounted on a Zeiss Stemi 2000-C dissecting microscope for later image analysis. The identification of specimens as *Latrodectus hasselti* was confirmed using morphological characters including abdominal hairs and genitalia (Vink et al., 2009). We measured body size at multiple stages of

development to assess how differences varied across sex and lifespan. We photographed a sample of five spiders from each egg sac (with each sac representing one family line) at each developmental stage. Immediately after emerging, second instar spiderlings were photographed (Australia: n = 11 family lines, Japan: n = 10 family lines, New Zealand: n = 10 family lines). We measured cephalothorax width at the second-instar stage (Modanu et al., 2014) as spiderlings were photographed alive, therefore measuring patella-tibia length was not possible. We measured cephalothorax width in fourth instar (juvenile) spiders (Australia n = 21, Japan n = 21), which were also measured alive, thus patella-tibia length measurement was not reliable. We also measured patella-tibia length of penultimate instar (the stage immediately before adulthood) males (n = 34 Australia, n = 26 Japan, n = 21 New Zealand), adult males (n = 23 Australia, n = 17 Japan, n = 17 New Zealand), and adult females (n = 48 Australia, n = 32 Japan, n = 26 New Zealand). The adult females measured from New Zealand were not laboratory reared, but were rather collected as adults, which may present a confound to this part of the analysis.

Life history

Life history traits (reproductive output, generation time) were measured from F3 spiders from Japan and Australia, and P spiders from New Zealand that had been held under laboratory conditions for at least one month. Reproductive output was assessed in two ways: egg sac production rate and fecundity per egg sac, which are positively correlated in other spider species (linyphiid spiders: Thorbek et al., 2004). Mated adult females lay egg sacs throughout their lifetimes. Fecundity (total number of eggs per egg sac) was measured for one egg sac produced by each female (n = 40 Australia, n = 40 Japan, and n = 14 New Zealand females from distinct family lines). For a subset of females, the number of egg sacs produced over a two-month period was recorded, and then averaged over that period to estimate the egg sac production rate (n = 14 Australia, n = 17 Japan, n = 14 New Zealand females). We measured juvenile development time by recording the time from emergence from the egg sac until the fourth instar (Australia n = 95, Japan n = 50). For males, we

measured development to the penultimate instar, assessed by the presence of enlarged pedipalps (Bhatnagar and Rempel 1962).

Behaviour

We measured behavioural traits predicted to be relevant to survival and persistence at multiple stages of the invasion process: sibling cannibalism, exploration, boldness, and dispersal Table 1.

Sibling cannibalism was measured in spiderlings emerged from egg sacs produced by females mated with one male in the laboratory. Cannibalism was measured from when spiderlings emerged from the egg sac to eight days after emergence (n = 15 Australian egg sacs, n = 24 Japanese egg sacs). This eight-day period was chosen as the approximate amount of time on the natal web in the field before juvenile dispersal (MAM, pers. obs.). Immediately after hatching, 30 spiderlings from each egg sac were transferred to a plastic cage (8 × 8 × 12 cm. clear plastic container, Amac Plastics, Ltd.) and observed for eight days. Food and water were withheld during this period, when spiderlings typically do not capture prey in nature. The number of spiderlings cannibalized (wrapped in silk) was counted every other day, as well as death by natural causes (legs curled and not wrapped in silk).

Exploratory behaviour (n = 49 Australian, n = 37 Japanese juveniles) and boldness behaviours (n = 49 Australian, n = 39 Japanese juveniles) were tested in fourth-instar juvenile spiderlings in the Australian and Japanese populations. Each spider was placed in a novel, empty plastic cage (5 × 5 × 7 cm. clear plastic container, Amac Plastics, Ltd.) and tested either for exploratory behaviour or boldness during three three-minute (180 s) trials. For exploratory behaviour, we recorded the time until the spider started to move and release silk to initiate web-building. Movement in a novel environment is a typical way of measuring exploration across taxa (Mead 1960). Spiders that were placed into a novel container and did not move during the trial period were categorized as non-responders. For boldness assays, spiders that had started moving and laying silk were puffed with air from an 88.7 ml air bulb from 5 cm away (Riechert and Hedrick 1993) to simulate a predator threat, after which the spider huddled and stopped moving. Boldness was measured by the time it took for the spider to start moving again after huddling. This response was considered a measure of boldness because it indicated an individual's propensity for movement under simulated risk of predation. Spiders that were puffed with air and never resumed movement over the trial periods were categorized as non-responders. We did not measure boldness or exploratory behaviour in New Zealand spiderlings at the fourth-instar for comparison because of laboratory rearing constraints.

Dispersal was measured with F3 spiderlings from Australia and Japan (n = 12 family lines per population, five spiderlings per egg sac tested). For the New Zealand population, spiderlings were from egg sacs produced by field-collected female after they were held in constant laboratory conditions for at least one

Table 1 Morphological, life history, and behavioural traits related to *Latrodectus hasselti* invasive potential and direction predicted in the difference between invasive and native populations

Trait	Trait measured	Predicted difference in invasive population	Predicted stage of selective filter	Evidence supports prediction?
Morphology	Size	Larger	Establishment, Spread	mixed
Life History	Fecundity	More fecund	Establishment	mixed
Life History	Development Time	Faster development	Spread	no
Behaviour	Cannibalism	More cannibalistic	Transport, Spread	yes
Behaviour	Boldness	Faster to resume movement after predator threat	Spread	no
Behaviour	Exploration	More exploratory	Transport, Introduction	no
Behaviour	Dispersal	Faster to disperse	Spread	yes

month (n = 14 family lines, five spiderlings per egg sac). Dispersal was tested seven days after hatching, with experimental spiderlings kept communally with their siblings, but food and water withheld. The dispersal arena was a plexiglass box (50 × 34 × 35 cm) laid on its long axis, with one short wall (the endpoint) replaced with a fibreglass screen and the opposite wall (the start point) including a screen-covered hole through which air from a fan blew into the arena Fig. 1. Just inside the start point wall, two wooden dowels (16 cm in length) were joined together with tape and placed upright, 11 cm from the inner surface, with the tip of the dowels centered on the screen hole. The fan created an airspeed of 1 m/s measured at the dowel, and the temperature was held at a constant at 23 °C during trials, as moderate wind speeds and temperatures are optimal for aerial spider dispersal (Simonneau et al., 2016). For each trial, a spiderling was placed inside the arena at the tip of a wooden dowel. The spiderling was allowed to settle for five minutes. The fan was then turned on and the spiderling was observed for 10 min, or until it showed dispersal behaviours (rappelling or ballooning (Forster 1995). Both dispersal behaviours began with the spider attaching a silk dragline to the top of the dowel. A ballooning spider moved into a 'tiptoe' posture with posterior end of the abdomen elevated and released additional silk which was caught by the air (Forster 1995). Rappelling occurred when the spider released a dragline of silk and using the released silk, moved from the top of the dowel to the mesh 0.29 m away. During the trial, spiderlings often rappelled for short distances (a few centimeters), but this behaviour was not counted as successful dispersal.

Dispersal was measured as a binary variable (disperse or did not disperse) and as time to dispersal for those that did disperse (time to balloon or rappel from the start of the trial).

Statistical analysis

We used the 'psych' package in R to calculate summary statistics for all of the variables by population (Revelle 2017). We investigated mean differences and population-level variability in adult size, development time, fecundity, and egg sac production rate of the native and invasive populations using one-way ANOVA tests followed by Tukey post-hoc tests for comparisons among Australia, Japanese, and New Zealand populations, and two-tailed t-tests for comparisons between Australian and Japanese populations. We used Levene's test to assess the homogeneity of variance. In web building and boldness response times, assumptions of normality were not met. To compare spiderling size among populations, we created a generalized linear mixed model with cephalothorax width as the response variable, egg sac ID as a random factor, and population as a fixed factor.

To compare cannibalism between the populations from Australia and Japan, we used a generalized linear model with the number of spiderlings cannibalized as the response variable (Poisson distribution), population by day as an interaction, and female ID as a random factor using the 'lme4' package in R (Bates et al., 2015). To compare boldness and exploratory behaviour between Australian and Japanese populations, we used chi-squared tests for each behaviour to
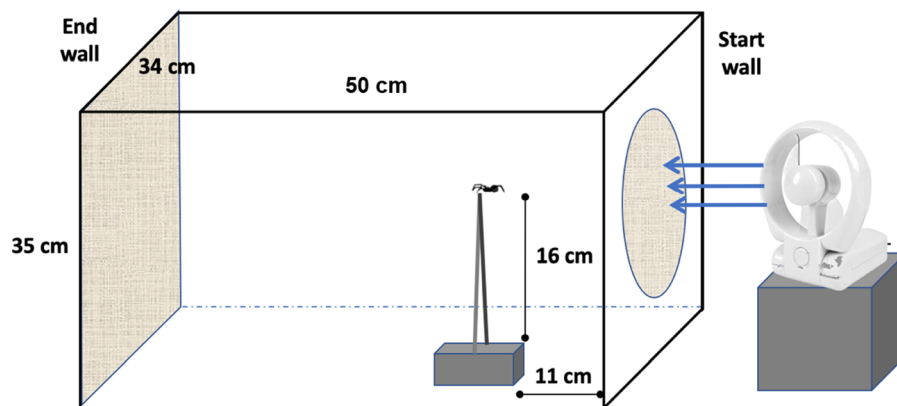

Fig. 1 Arena used for trials to measure dispersal propensity and time to disperse in *Latrodectus hasselti* spiderlings

assess differences in response rate (resumed movement or did not resume movement during any of the three-minute trials). To compare differences among those spiders that responded during the trials, we conducted Kruskal–Wallis tests. To compare dispersal of native and invasive spider populations, we first made a generalized linear model with dispersal as the (binary) response variable and population as a predictor and family line as a random factor, with a binomial link function. To test for population differences in dispersal time, we included only those spiders that dispersed within ten minutes and used an ANOVA with dispersal time as a response variable and population as a predictor. All statistical tests were conducted in R version 3.3.2.

Results

Size

Invasive second-instar spiderlings from Japan were similar in size to the native spiderlings from Australia (Fig. 2a, means $\pm$ SE, Japan: n = 120, 0.50 ± 0.01 mm, Australia: n = 139, 0.49 ± 0.01 mm; GLMM, $t = 1.612$, $p = 0.116$). However, the invasive New Zealand spiderlings were smaller than both the Australian and the Japanese populations (mean $\pm$ SE, New Zealand: n = 138, 0.38 ± 0.01 mm, GLMM, $t = -11.043$, $p < 0.001$). Fourth-instar juvenile invasive spiders from Japan were larger than native spiders from Australia (Fig. 2b, means $\pm$ SE, Australia: n = 21, 0.59 ± 0.01 mm, Japan: n = 21, 0.68 ± 0.02 mm, t-test, $t = 4.351$, $p < 0.001$). Among adult females, leg length was the largest for invasive spiders from New Zealand compared to the native Australian and invasive Japanese populations (Fig. 2c, means $\pm$ SE, Australia: $n = 48$, 5.43 ± 0.06 mm, Japan: $n = 32$, 5.55 ± 0.07 mm, New Zealand: $n = 26$, 6.23 ± 0.10 mm, ANOVA, $F = 33.91$, $p < 0.001$; Tukey HSD, New Zealand and Japan/Australia: $p < 0.001$, Australia and Japan: $p = 0.323$). Body size is affected by diet, so field caught New Zealand females could differ from lab-reared Japanese and Australian spiders for this reason. However, we note that adult field-collected (P) and lab-reared (F3) Australian females do not differ in leg length (Supplementary Fig. 1).

For males, invasive males from Japan at the penultimate instar and as adults were larger than native males from Australia, though males from New Zealand were smaller than the Australian and Japanese populations at both life stages (Fig. 2d, means $\pm$ SE, penultimate instar males: Australia: n = 34, 2.32 ± 0.04 mm, Japan: n = 26, 2.45 ± 0.05 mm, New Zealand; n = 21, 2.17 ± 0.03 mm, adult males: Australia: n = 23, 2.89 ± 0.05 mm, Japan: n = 17, 3.07 ± 0.09 mm, New Zealand: n = 17, 2.58 ± 0.05 mm, GLM, population $p = 0.006$).

Life history

The population from Japan was faster to produce egg sacs than the population from Australia (means $\pm$ SE, Australia: n = 14, 12 ± 1 days between sacs, Japan: n = 17, 9 ± 1 days between sacs, two-tailed t-test, $t = 3.0764$, $p = 0.005$). Spiders from the New Zealand population (field-caught, but held on a standard diet) produced egg sacs less frequently than spiders from the lab-reared Australian and Japanese populations (Fig. 3a, mean $\pm$ SE, New Zealand: n = 14, 18 ± 2 days between egg sacs, ANOVA, $F = 14.44$, $p < 0.001$). There were no population-level differences in number of eggs per sac (Fig. 3b, means $\pm$ SE, Australia: n = 40, 102 ± 10 eggs, Japan: n = 40, 103 ± 8 eggs, New Zealand: n = 14, 122 ± 15 eggs, ANOVA, $F = 0.742$, $p = 0.479$). However, spiders from Japan took longer to develop from emergence to fourth instar than native spiders from Australia. Invasive males from the Japan population took longer to develop from emergence to the penultimate stage of development (means $\pm$ SE, Australia: n = 95, mean $\pm$ SE, 18 ± 1 days, Japan: n = 50, 30 ± 2 days, two-tailed t-test, $t = 4.2253$, $p < 0.001$). We did not measure the development time of females to mature to adulthood.

Behaviour

Invasive spiders from Japan were more cannibalistic of siblings than spiders from the native population. Invasive spiders from Japan cannibalized siblings at a higher rate over an eight-day period than native spiders from Australia (Fig. 4, means $\pm$ SE, n = 24 groups, Japan: 10 ± 2 individuals cannibalized out of
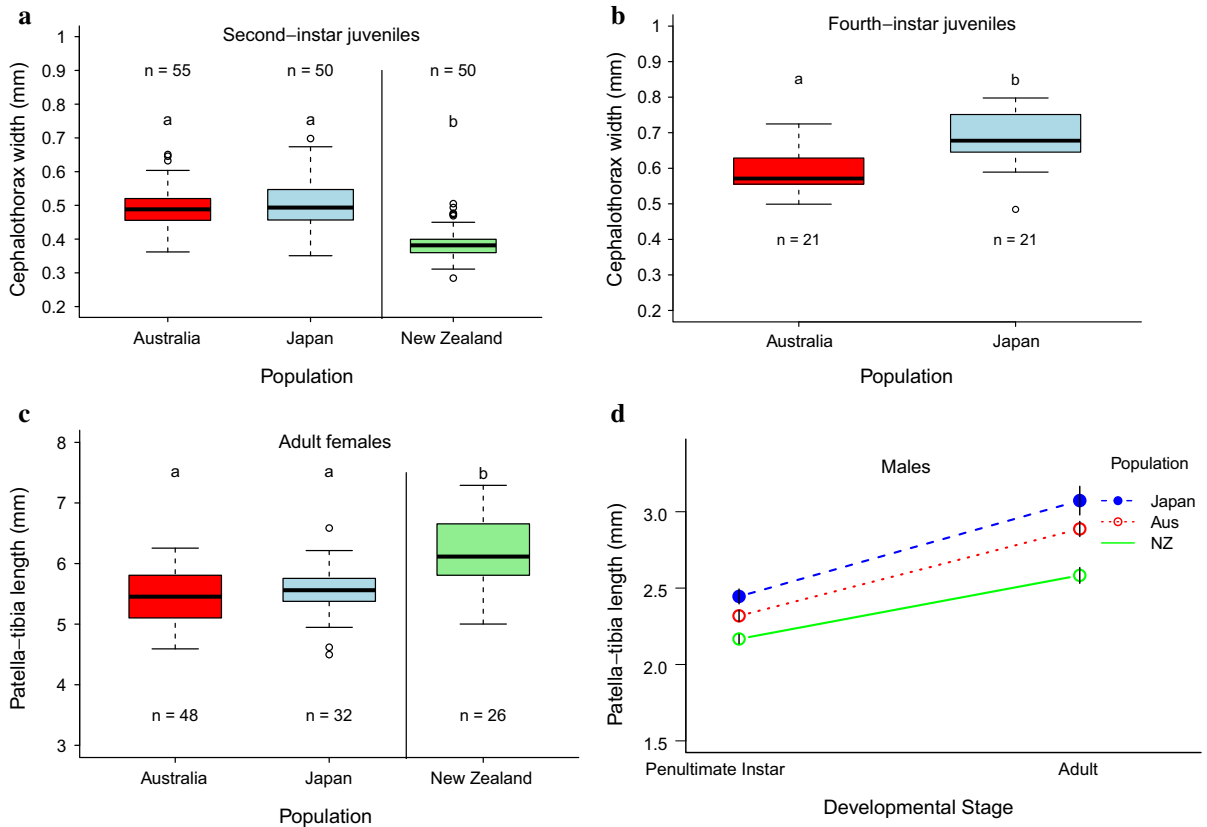
Fig. 2 Boxplots comparing the size of Australian (native), New Zealand (longer-established invasive), and Japanese (newly-established invasive) populations of *Latrodectus hasselti* as **a** second-instar newly-emerged spiderlings (cephalothorax width), **b** fourth-instar juveniles (cephalothorax width), **c** adult females (patella-tibia length), and **d** penultimate stage and adult males (patella-tibia length). Different letters above box plots indicate significant differences between locations based on Tukey HSD post-hoc tests
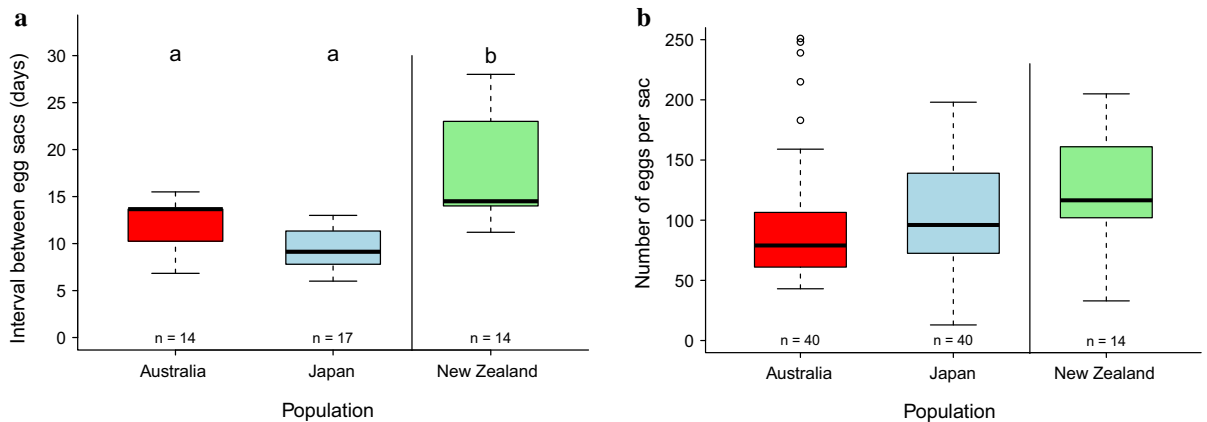
Fig. 3 Boxplots of *Latrodectus hasselti* **a** Egg sac production rate (number of egg sacs produced over two months divided by number of days) and **b** fecundity (number of eggs per sac) produced by females from native Australian, invasive New Zealand, and invasive Japanese populations. Different letters above box plots indicate significant differences between locations based on Tukey HSD post-hoc tests

30 individuals after eight days, n = 15 groups, Australia: 5 ± 1 individuals cannibalized out of 30 individuals after eight days, GLMM, population: z = 2.261, p = 0.024, day: z = 6.388, p < 0.001, population*day: z = -1.106, p = 0.269). There was no significant difference in the propensity to explore (91.9% of Australia spiders [n = 49] and 81.1% of Japan spiders [n = 37] explored during the trials, $\chi^2 = 1.328$, df = 1, p = 0.249), nor was there a difference in latency to initiate exploration between native spiders from Australia and invasive spiders from Japan of the spiders that responded during the three-minute trial (means $\pm$ SE, Australia: n = 45, 35 ± 7 s, Japan: n = 30, 45 ± 7 s, Kruskal–Wallis test, $\chi^2 = 2.325$, p = 0.127). In the boldness assay, spiders from the invasive Japan population (33.3% of 39 spiders) were more likely to stay still after a startle than were those from the Australia population (8.1% of 49 spiders) for the entire testing period of 180 s ($\chi^2 = 7.286$, df = 1, p = 0.007). Of those spiders that resumed activity within 180 s, there was no difference in the latency to resume movement (boldness) between native and invasive spiders from Japan (means $\pm$ SE, Australia: n = 45, 25 ± 7 s, Japan: n = 26, 22 ± 7 s, Kruskal–Wallis test, $\chi^2 = 0.0058$, p = 0.939). When comparing the F3 lab populations from Australia and Japan, spiders from the invasive Japan population were more likely to disperse than spiders from the native Australia population (means $\pm$ SE, Japan: n = 60, 0.83 ± 0.06, proportion dispersed out of spiderlings assayed, Australia: n = 60, 0.60 ± 0.07, GLMM, z = 2.611, p = 0.009). When

including the offspring of field-collected females from New Zealand (n = 70, mean $\pm$ SE, 0.78 ± 0.06 dispersed out of spiderlings assayed), invasive spiders from New Zealand and Japan were more likely to disperse than the native Australian population (Fig. 5a, GLMM, Japan to Australia, z = 2.488, p = 0.0128, New Zealand to Australia, z = 2.135, p = 0.033). Among those spiders that dispersed, when limiting the comparison to the Japan and Australia F3 lab populations, spiders from the Japan population tended to disperse faster than spiders from the Australia population (means $\pm$ SE, Japan: n = 50, 200 ± 18 s, Australia: n = 36, 263 ± 32 s, GLMM, t = 1.881, p = 0.060). When comparing the lab populations and offspring of field-collected females from New Zealand, those from the New Zealand population dispersed more quickly than spiders from the native Australian population, and tended to disperse more quickly than spiders from the Japanese population (Fig. 5b, means $\pm$ SE, New Zealand: n = 56, 132 ± 20 s, ANOVA, F = 7.866, p < 0.001, Tukey HSD, New Zealand and Australia: p < 0.001, Japan and Australia: p = 0.161, New Zealand and Japan: p = 0.069).

Discussion

We found differences in size, life history, and behaviour between a native and an invasive population of *Latrodectus hasselti*, even after rearing under controlled laboratory conditions for two generations (see Table 1 for a comparison of results to predictions). In general, spiders from the invasive population from Japan were larger at several life stages Fig. 2, took longer to develop, were more cannibalistic Fig. 4, less bold, and more dispersive Fig. 5 than a native population from Australia. Including additional trait comparisons from a New Zealand invasive population, we found that offspring of field-collected females from an invasive New Zealand population were more likely and faster to disperse than the native Australia population Fig. 5. These phenotypic differences may aid survival in transport (e.g., larger size, sibling cannibalism) in colonization of a new environment (e.g., high fecundity) and spread through those novel environments (e.g., dispersal propensity). While many of these differences were consistent with our predictions, some were contrary to expectations Table 1. In
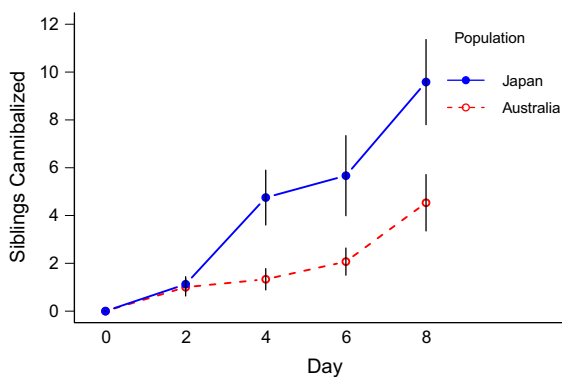

Fig. 4 Means and standards errors of sibling cannibalism in invasive Japanese and native Australian *Latrodectus hasselti* egg sacs over an eight-day period immediately after spiderling emergence
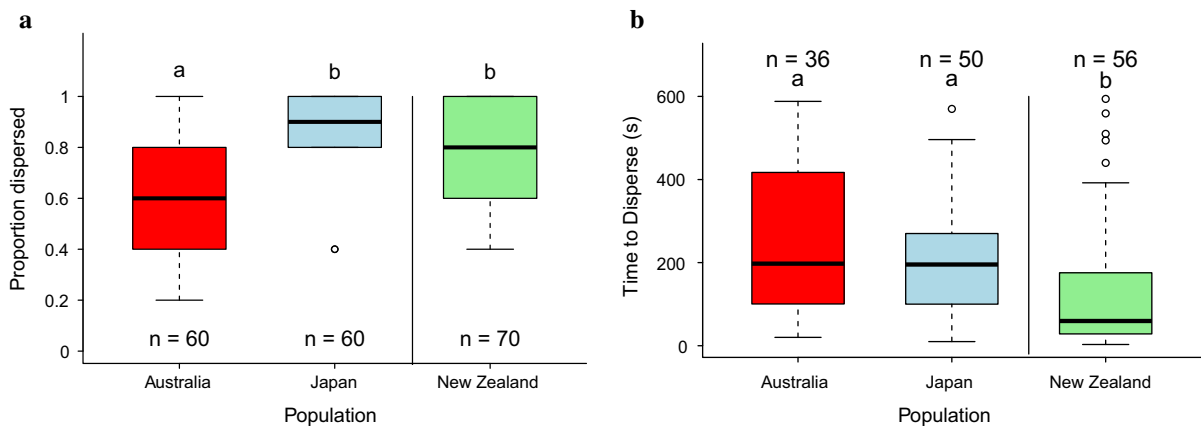
a

b

Fig. 5 Boxplots of *Latrodectus hasselti* spiderlings seven days after emergence **a** Proportion dispersed within each family line, **b** time to dispersal of those that dispersed within ten minutes) in native Australian, invasive New Zealand, and invasive Japanese populations. Different letters above box plots indicate significant differences between locations based on Tukey HSD post-hoc tests

particular, we found that Japanese and New Zealand size and fecundity differed from the native population, but these differences varied by life stage and were inconsistent. These unpredictable differences could arise from divergent selection pressures in Japan and New Zealand affecting the evolution of traits in those invasive populations. Neutral processes such as population bottlenecks and genetic drift during the invasion process could also explain these differences in phenotypic traits (Johnson et al., 2018). Some of these effects may arise because the New Zealand spiders used in this experiment were P and F1 rather than having been reared through a generation in the lab. However, we found that field-collected and F3 females from Australia were not significantly different in body size (Supplementary Fig. 1), which suggests that lab rearing for several generations does not lead to shifts in size. Overall our data suggest invasive *Latrodectus hasselti* spiders may show phenotypic shifts compared to a native population.

We found that spiders from the invasive Japanese populations were larger than native spiders at multiple life stages. Similarly, for New Zealand invasive females, adult females were larger than Australia native females. Consistent with other findings in insects and arachnids, large size may offer selective advantages to colonizing new habitats (Hemptinne et al., 2012). Moreover, for spiders, adult female body size is typically closely correlated with fecundity, which would also aid in invasive success. Interestingly, the adult females were the only life history stage

at which New Zealand spiders were larger than those from Australia (the juvenile, penultimate instar males, and adult males were smaller, Fig. 2). The longer-established New Zealand invasive population showed increased sexual size dimorphism (smaller males and larger females than the native population), similar to long-established invasive populations of cane toads (Hudson et al., 2016). In *Latrodectus*, small male size is selected for in the absence of direct competition, which may occur in low density populations (Kasumovic and Andrade 2006). Various types of environmental effects may thus underlie the results with the New Zealand population, particularly for adult females. Nevertheless, for the Japan compared to Australia populations, we compared 2nd and 3rd generation lab-reared individuals, which suggests that there has been an evolutionary shift in body size among invasive Japanese *L. hasselti*.

Surprisingly, we found that spiders from the invasive Japanese population took longer to develop at multiple life stages than native spiders. This developmental difference could reflect local adaptation to the lack of specialist predators in Japan. Slow development time results in higher risk of predation in other invertebrates (Häggström and Larsson 1995), so species with high predation pressure tradeoff faster development time for smaller body size (Dahl and Peckarsky 2003). In contrast, in Japan, there may be reduced predation pressure, allowing slower-developing *L. hasselti* higher fitness because of the overall advantages of larger body size (Honěk 1993). Slower

development time could also be caused by adaptation to cooler temperatures in the invasive habitat (Li and Jackson 1996). Though spiders from the invasive population took longer to develop, they may overcome this slower development by producing offspring more frequently as adults. We found higher fecundity among Japanese invasives relative to native spiders, in terms of the higher frequency of egg sac production. This high-fecundity phenotype is similar to that found in other invasive invertebrates (Foucaud et al., 2016; Pechenik et al., 2017), particularly in recently-established populations (Masson et al., 2016). An increase in frequency of reproduction is a bet-hedging strategy, which can increase success in unpredictable environments (Sol et al., 2012).

Spiders from the invasive Japan population were more cannibalistic and dispersive, yet less bold than native spiders. Increased rates of sibling cannibalism could be beneficial particularly in low food environments, such as during the transport stage of invasion, most likely via shipping containers (Vink et al., 2011). In contrast, there was no difference in latency to begin exploring and web building between the invasive Japan and native Australia populations. Increased exploratory behaviour may be selected for during the spread stage, but not during the transport stage, where surviving individuals are those that avoid detection (Chapple et al., 2011). Consequently, this assay in a novel environment may predominantly reflect on mobility/exploratory behaviour. The lack of differences in web building is not surprising because selection pressures on latency to initiate web building may not be different in the novel environment. Being without a web is very costly for spiders regardless of whether they are from an invasive population, since the web allows prey capture, communication, and detection of predators.

We found strong evidence for increased dispersal propensity in invasive populations. Both the Japanese and the New Zealand spiderlings were more dispersive than the native Australian spiderlings. We found similar increased dispersal propensity in the invasive Japanese population, which was reared under standard laboratory conditions for three generations like the native Australian population. This pattern in increased dispersal is consistent with predictions about selection during invasive spread past the point of introduction (Alford et al., 2009; Cote et al., 2010). Increased dispersal ability can be particularly advantageous in

changing environments (Kokko and López-Sepulcre 2006). Moreover, founder effects could quickly lead to evolutionary shifts in dispersive tendency since the invasive populations could have been initiated by chance dispersal events, whether to the habitat directly, or dispersal onto ships or other vectors (Wilson et al., 2009).

New Zealand spiderlings were lab-produced offspring of field-collected females held on a constant diet, and their behaviour may have been influenced by maternal effects. In spiders, field and lab-reared individuals can differ in prey capture, activity level, and mating behaviour (Carducci and Jakob 2000; Wiggins et al., 2018). The laboratory can act as a selective environment after several generations in captivity, as was the case of the Australia and Japan populations, and can affect morphology, life history, and behaviour. For example, mosquitos (*Culex tarsalis*) that were field-collected dispersed further than lab-reared flies (Nelson and Milby 1980), so the finding of lower dispersal in the Australia population compared to the New Zealand population could be influenced by laboratory rearing. In addition, lab conditions of a constant diet and unvaried environment conditions may also affect development time, size, and fecundity.

In contrast to dispersal, we found that invasive spiders from Japan were less bold than native spiders from Australia when presented with a simulated predator threat. Under high predation risk, this decrease in boldness would be adaptive. Although habitats in Japan and New Zealand are less likely to have specialist predators such as parasitoid wasps, spiders in Japan are more likely to live in areas with a high human footprint (Mowery, Luo, & Andrade, unpublished) than in Australia. Behaviourally, invasive redback spiders from Japan are more cannibalistic and dispersive, yet less bold, than native Australia spiders, which suggests that there are no underlying constraints that link boldness, cannibalism, and dispersal in this species, in contrast to other studies that found population-level behavioural correlations in boldness and dispersal (Duckworth and Badyaev 2007). Differences between two invasive populations could also be explained by differences in biotic or abiotic conditions. In addition, adaptation to climatic conditions in Japan and New Zealand could explain the size and fecundity differences. The range of mean minimum and maximum temperatures in Osaka, Japan

is 1.4 °C to 32.4 °C, and the range of mean minimum and maximum monthly temperatures in Alexandra, New Zealand is −0.8 °C to 23.1 °C. Both climates are cooler than Sydney, Australia, where the mean monthly minimum is 7.1 °C and the mean monthly maximum is 26.3 °C (Fick and Hijmans 2017).

Future work will investigate whether these traits are common across invasive arthropods, or whether they are specific to species and transport method. The mechanisms of transport, establishment, and spread of invasive spiders (Hänggi and Straub 2016; Nentwig 2015; Nentwig et al., 2017) could be examined along with species and population-level studies of traits leading to invasion success (Houser et al., 2014; Krehenwinkel and Tautz 2013). By investigating how behavioural shifts influence patterns of establishment and spread in spiders, we can better understand what factors make a successful invader. In this study, we made predictions based on how sequential stages of the invasion process may act as selective filters, resulting in invasive populations with different morphology, life history, and behaviour from the native population of origin. We found substantial phenotypic differences between an invasive and native spider population, even after rearing in common conditions for several generations. These phenotypic differences suggest an integrated invasive phenotype shaped by the invasion process may include traits favoured at different stages of invasion and establishment, which lead to differences in colonization success and spread through the new habitat.

Declaration

Conflicts of interest No conflicts of interest to declare.

References

Abdelkrim J, Pascal M, Samadi S (2005) Island colonization and founder effects: the invasion of the Guadeloupe islands by ship rats (*Rattus rattus*). Mol Ecol 14(10):2923–2931. https://doi.org/10.1111/j.1365-294X.2005.02604.x

Alford RA, Brown GP, Schwarzkopf L, Phillips BL, Shine R (2009) Comparisons through time and space suggest rapid evolution of dispersal behaviour in an invasive species. Wildl Res 36(1):23–28. https://doi.org/10.1071/WR08021

Allen WL, Street SE, Capellini I (2017) Fast life history traits promote invasion success in amphibians and reptiles. Ecol Lett 20(2):222–230. https://doi.org/10.1111/ele.12728

Amundsen P-A, Salonen E, Niva T, Gjelland KØ, Præbel K, Sandlund OT, Knudsen R, Bøhn T (2012) Invader population speeds up life history during colonization. Biol Invasions 14(7):1501–1513. https://doi.org/10.1007/s10530-012-0175-3

Andrade MCB (1996) Sexual selection for male sacrifice in the Australian redback spider. Science 271(5245):70–72. https://doi.org/10.1126/science.271.5245.70

Antonialli-Junior WF, Guimarães I (2014) Aggregation behavior in spiderlings: a strategy for increasing life expectancy in *Latrodectus geometricus* (Araneae: Theridiidae). Sociobiology 59(2):463–475. https://doi.org/10.13102/sociobiology.v59i2.611

Atwell JW, Cardoso GC, Whittaker DJ, Campbell-Nelson S, Robertson KW, Ketterson ED (2012) Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. Behav Ecol 23(5):960–969. https://doi.org/10.1093/beheco/ars059

Barrett SCB, Emerson B, Mallet JW, Clarke BC, Grant PR (1996) The reproductive biology and genetics of island plants. Phil Trans R Soc Lond Series b: Biol Sci 351(1341):725–733. https://doi.org/10.1098/rstb.1996.0067

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Sof 67(1):1–48. https://doi.org/10.18637/jss.v067.i01

Bhatnagar RDS, Rempel JG (1962) The structure, function, and postembryonic development of the male and female copulatory organs of the black widow spider *Latrodectus curacaviensis* (Müller). Can J Zool 40(3):465–510. https://doi.org/10.1139/z62-043

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends Ecol Evol 26(7):333–339. https://doi.org/10.1016/j.tree.2011.03.023

Blick T, Bosmans R, Buchar J, Gajdoš P, Hänggi A, van Helsdingen P, Růžička V, Staręga W, Thaler K (2004) Checkliste der Spinnen Mitteleuropas. Checklist of the spiders of Central Europe. (Arachnida: Araneae). Version 1.

Dezember 2004. http://www.Arages.de/Files/Checklist2004_araneae.Pdf

Brownscombe JW, Fox MG (2012) Range expansion dynamics of the invasive round goby (*Neogobius melanostomus*) in a river system. Aquat Ecol 46(2):175–189. https://doi.org/10.1007/s10452-012-9390-3

Burton OJ, Phillips BL, Travis JMJ (2010) Trade-offs and the evolution of life-histories during range expansion. Ecol Lett 13(10):1210–1220. https://doi.org/10.1111/j.1461-0248.2010.01505.x

Capellini I, Baker J, Allen WL, Street SE, Venditti C (2015) The role of life history traits in mammalian invasion success. Ecol Lett 18(10):1099–1107. https://doi.org/10.1111/ele.12493

Carducci JP, Jakob EM (2000) Rearing environment affects behaviour of jumping spiders. Anim Behav 59(1):39–46. https://doi.org/10.1006/anbe.1999.1282

Carrete M, Edelaar P, Blas J, Serrano D, Potti J, Dingemanse NJ, Tella JL (2012) Don't neglect pre-establishment individual selection in deliberate introductions. Trends Ecol Evol 27(2):67–68. https://doi.org/10.1016/j.tree.2011.11.011

Caut S, Angulo E, Courchamp F (2008) Dietary shift of an invasive predator: rats, seabirds and sea turtles. J Appl Ecol 45(2):428–437. https://doi.org/10.1111/j.1365-2664.2007.01438.x

Chapple DG, Simmonds SM, Wong BBM (2011) Know when to run, know when to hide: can behavioral differences explain the divergent invasion success of two sympatric lizards? Ecol Evol 1(3):278–289. https://doi.org/10.1002/ece3.22

Chapple DG, Simmonds SM, Wong BBM (2012) Can behavioral and personality traits influence the success of unintentional species introductions? Trends Ecol Evol 27(1):57–64. https://doi.org/10.1016/j.tree.2011.09.010

Chrysanthus F (1975) Further notes on the Spiders of new Guinea II (Araneae, Tetragnathidae, Theridiidae). Zool Verh 140(1):1–50

Chuang A, Riechert SE (2021) Personality shifts are inconsistent across two rapid range expansions of a non-native spider. Anim Behav 173:67–79. https://doi.org/10.1016/j.anbehav.2020.12.018

Colautti RI, Lau JA (2015) Contemporary evolution during invasion: evidence for differentiation, natural selection, and local adaptation. Mol Ecol 24(9):1999–2017. https://doi.org/10.1111/mec.13162

Colautti RI, Alexander JM, Dlugosch KM, Keller SR, Sultan SE (2017) Invasions and extinctions through the looking glass of evolutionary ecology. Phil Trans r Soc B 372(1712):20160031. https://doi.org/10.1098/rstb.2016.0031

Cote J, Fogarty S, Weinersmith K, Brodin T, Sih A (2010) Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). Proc R Soc B-Biol Sci 277(1687):1571–1579. https://doi.org/10.1098/rspb.2009.2128

Crooks JA, Soulé ME (1999) Lag times in population explosions of invasive species: causes and implications. Invasive Species and Biodiversity Management. Based on Papers Presented at the Norway/United Nations (UN) Conference on Alien Species, 2nd Trondheim Conference on Biodiversity, Trondheim, Norway, 1–5, 103–125

Dahl J, Peckarsky BL (2003) Developmental responses to predation risk in morphologically defended mayflies. Oecologia 137(2):188–194. https://doi.org/10.1007/s00442-003-1326-0

Duckworth RA, Badyaev AV (2007) Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. Proc Natl Acad Sci USA 104(38):15017–15022

Dunn JC, McClymont HE, Christmas M, Dunn AM (2009) Competition and parasitism in the native White Clawed Crayfish *Austropotamobius pallipes* and the invasive Signal Crayfish *Pacifastacus leniusculus* in the UK. Biol Invasions 11(2):315–324. https://doi.org/10.1007/s10530-008-9249-7

Elst EM, Acharya KP, Dar PA, Reshi ZA, Tufto J, Nijs I, Graae BJ (2016) Pre-adaptation or genetic shift after introduction in the invasive species *Impatiens glandulifera*? Acta Oecologica 70:60–66. https://doi.org/10.1016/j.actao.2015.12.002

Fick SE, Hijmans RJ (2017) WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. Int J Climatol 37(12):4302–4315. https://doi.org/10.1002/joc.5086

Forster LM (1984) The Australian redback spider (*Latrodectus hasselti*): its introduction and potential for establishment and distribution in New Zealand. Commerce and the Spread of Pests and Disease Vectors. 273–289

Forster LM (1992) The stereotyped behavior of sexual cannibalism in *Latrodectus hasselti* Thorell (Araneae, Theridiidae), the Australian redback spider. Aust J Zool 40(1):1–11. https://doi.org/10.1071/zo9920001

Forster LM (1995) The behavioural ecology of *Latrodectus hasselti* (Thorell), the Australian redback spider (Araneae: Theridiidae): a review. Rec West Aust Mus Suppl 52:13–24

Foucaud J, Moreno C, Pascual M, Rezende EL, Castañeda LE, Gibert P, Mery F (2016) Introduced *Drosophila subobscura* populations perform better than native populations during an oviposition choice task due to increased fecundity but similar learning ability. Ecol Evol 6(6):1725–1736. https://doi.org/10.1002/ece3.2015

Gadgil M, Bossert WH (1970) Life historical consequences of natural selection. Am Nat 104(935):1–24. https://doi.org/10.1086/282637

Häggström H, Larsson S (1995) Slow larval growth on a suboptimal willow results in high predation mortality in the leaf beetle *Galerucella lineola*. Oecologia 104(3):308–315. https://doi.org/10.1007/BF00328366

Hänggi A, Straub S (2016) Storage buildings and greenhouses as stepping stones for non-native, potentially invasive spiders (Araneae) – a baseline study in Basel, Switzerland. Arachnologische Mitteilungen 51:1–8. https://doi.org/10.5431/aramit5101

Hemptinne J-L, Magro A, Evans EW, Dixon A (2012) Body size and the rate of spread of invasive ladybird beetles in North America. Biol Invasions 14:595–605. https://doi.org/10.1007/s10530-011-0101-0

Hippargi RV, Bolde PM, Manthen SV, Shaikh AR (2012) Ecology of venomous spider *Latrodectus hasselti* Thorell, 1870 (Araneae: Theridiidae) from Solapur and

Osmanabad District, Maharashtra. Indian J Arachnol 1(1):169–174

Honěk A (1993) Intraspecific variation in body size and fecundity in insects: a general relationship. Oikos 66(3):483–492. https://doi.org/10.2307/3544943

Houser JD, Ginsberg H, Jakob EM (2014) Competition between introduced and native spiders (Araneae: Linyphiidae). Biol Invasions 16(11):2479–2488. https://doi.org/10.1007/s10530-014-0679-0

Hudson CM, Brown GP, Shine R (2016) It is lonely at the front: Contrasting evolutionary trajectories in male and female invaders. Royal Soc Open Sci 3(12):160687. https://doi.org/10.1098/rsos.160687

Hulme PE (2009) Trade, transport and trouble: Managing invasive species pathways in an era of globalization. J Appl Ecol 46(1):10–18. https://doi.org/10.1111/j.1365-2664.2008.01600.x

Jakobs G, Weber E, Edwards PJ (2004) Introduced plants of the invasive Solidago gigantea (Asteraceae) are larger and grow denser than conspecifics in the native range. Divers Distrib 10(1):11–19. https://doi.org/10.1111/j.1472-4642.2004.00052.x

Johnson JC, Kitchen K, Andrade MCB (2010) Family affects sibling cannibalism in the black widow spider. Latrodectus Hesperus Ethology 116(8):770–777. https://doi.org/10.1111/j.1439-0310.2010.01792.x

Johnson JC, Halpin R, Stevens D, Vannan A, Lam J, Bratsch K (2015) Individual variation in ballooning dispersal by black widow spiderlings: the effects of family and social rearing. Current Zool 61(3):520–528. https://doi.org/10.1093/czoolo/61.3.520

Johnson MT, Prashad CM, Lavoignat M, Saini HS (2018) Contrasting the effects of natural selection, genetic drift and gene flow on urban evolution in white clover (Trifolium repens). Proc R Soc B: Biol Sci 285(1883):20181019. https://doi.org/10.1098/rspb.2018.1019

Kasumovic MM, Andrade MCB (2006) Male development tracks rapidly shifting sexual versus natural selection pressures. Curr Biol 16(7):R242–R243. https://doi.org/10.1016/j.cub.2006.03.017

Kokko H, López-Sepulcre A (2006) From individual dispersal to species ranges: perspectives for a changing world. Science 313(5788):789–791. https://doi.org/10.1126/science.1128566

Korsten P, Van Overveld T, Adriaensen F, Matthysen E (2013) Genetic integration of local dispersal and exploratory behaviour in a wild bird. Nat Commun Lond 4(1):2362. https://doi.org/10.1038/ncomms3362

Krehenwinkel H, Tautz D (2013) Northern range expansion of European populations of the wasp spider Argiope bruennichi is associated with global warming–correlated genetic admixture and population-specific temperature adaptations. Mol Ecol 22(8):2232–2248. https://doi.org/10.1111/mec.12223

Lamarque LJ, Lortie CJ, Porté AJ, Delzon S (2015) Genetic differentiation and phenotypic plasticity in life-history traits between native and introduced populations of invasive maple trees. Biol Invasions 17(4):1109–1122. https://doi.org/10.1007/s10530-014-0781-3

Le Gros A, Clergeau P, Zuccon D, Cornette R, Mathys B, Samadi S (2016) Invasion history and demographic processes associated with rapid morphological changes in the Red-whiskered bulbul established on tropical islands. Mol Ecol 25(21):5359–5376. https://doi.org/10.1111/mec.13853

Lenz M, Ahmed Y, Canning-Clode J, Díaz E, Eichhorn S, Fabritzek AG, da Gama BAP, Garcia M, von Juterzenka K, Kraufvelin P, Machura S, Oberschelp L, Paiva F, Penna MA, Ribeiro FV, Thiel M, Wohlgemuth D, Zamani NP, Wahl M (2018) Heat challenges can enhance population tolerance to thermal stress in mussels: a potential mechanism by which ship transport can increase species invasiveness. Biol Invasions 20(11):3107–3122. https://doi.org/10.1007/s10530-018-1762-8

Li D, Jackson RR (1996) How temperature affects development and reproduction in spiders: a review. J Therm Biol 21(4):245–274. https://doi.org/10.1016/0306-4565(96)00009-5

Liebl AL, Martin LB (2012) Exploratory behaviour and stressor hyper-responsiveness facilitate range expansion of an introduced songbird. Proc R Soc B 279(1746):4375–4381. https://doi.org/10.1098/rspb.2012.1606

Marchini GL, Arredondo TM, Cruzan MB (2018) Selective differentiation during the colonization and establishment of a newly invasive species. J Evol Biol 31(11):1689–1703. https://doi.org/10.1111/jeb.13369

Masson L, Brownscombe JW, Fox MG (2016) Fine scale spatio-temporal life history shifts in an invasive species at its expansion front. Biol Invasions 18(3):775–792. https://doi.org/10.1007/s10530-015-1047-4

Mead AP (1960) A quantitative method for the analysis of exploratory behaviour in the rat. Anim Behav 8(1):19–31. https://doi.org/10.1016/0003-3472(60)90005-1

Michaelides SN, Goodman RM, Crombie RI, Kolbe JJ (2018) Independent introductions and sequential founder events shape genetic differentiation and diversity of the invasive green anole (Anolis carolinensis) on Pacific Islands. Divers Distrib 24(5):666–679. https://doi.org/10.1111/ddi.12704

Modanu M, Li LDX, Said H, Rathitharan N, Andrade MCB (2014) Sibling cannibalism in a web-building spider: effects of density and shared environment. Behav Proc 106:12–16. https://doi.org/10.1016/j.beproc.2014.03.011

Mueller JC, Edelaar P, Baños-Villalba A, Carrete M, Potti J, Blas J, Tella JL, Kempenaers B (2017) Selection on a behaviour-related gene during the first stages of the biological invasion pathway. Mol Ecol 26(21):6110–6121. https://doi.org/10.1111/mec.14353

Nelson RL, Milby MM (1980) Dispersal and survival of field and laboratory strains of Culex tarsalis (Diptera: Culicidae). J Med Entomol 17(2):146–150. https://doi.org/10.1093/jmedent/17.2.146

Nentwig W (2015) Introduction, establishment rate, pathways and impact of spiders alien to Europe. Biol Invasions 17(9):2757–2778. https://doi.org/10.1007/s10530-015-0912-5

Nentwig W, Pantini P, Vetter RS (2017) Distribution and medical aspects of Loxosceles rufescens, one of the most invasive spiders of the world (Araneae: Sicariidae). Toxicon 132:19–28. https://doi.org/10.1016/j.toxicon.2017.04.007

Nihei N, Yoshida M, Kobayashi M, Kaneta H, Shimamura R, Agui N (2003) Geographic information systems (GIS) analysis of the distribution of the redback spider *Latrodectus hasseltii* (Araneae: Theridiadae) in Osaka Japan. Med Entomol Zool 54(2):177–186. https://doi.org/10.7601/mez.54.177

Nijhout HF (2015) Big or fast: two strategies in the developmental control of body size. BMC Biol 13(1):57. https://doi.org/10.1186/s12915-015-0173-x

Ochocki BM, Miller TEX (2017) Rapid evolution of dispersal ability makes biological invasions faster and more variable. Nat Commun 8:14315. https://doi.org/10.1038/ncomms14315

Ori M, Shinkai E, Ikeda H (1996) Introduction of widow spiders into Japan. Med Entomol Zool 47(2):111–119

Pechenik JA, Diederich CM, Browman HI, Jelmert A (2017) Fecundity of the invasive marine gastropod *Crepidula fornicata* near the current northern extreme of its range. Invertebr Biol 136(4):394–402. https://doi.org/10.1111/ivb.12194

Pettit LJ, Greenlees MJ, Shine R (2016) The behavioural consequences of translocation: How do invasive cane toads (*Rhinella marina*) respond to transport and release to novel environments? Behav Ecol Sociobiol 71(1):15. https://doi.org/10.1007/s00265-016-2245-5

Pyšek P, Jarošík V (2005) Residence time determines the distribution of alien plants. In: Inderjit (ed) Invasive plants: ecological and agricultural aspects. Birkhäuser-Verlag, pp 77–96. https://doi.org/10.1007/3-7643-7380-6_5

Rehage JS, Sih A (2004) Dispersal behavior, boldness, and the link to invasiveness: a comparison of four *Gambusia* species. Biol Invasions 6(3):379–391. https://doi.org/10.1023/B:BINV.0000034618.93140.a5

Revelle WR (2017) psych: procedures for personality and psychological research. https://www.scholars.northwestern.edu/en/publications/psych-procedures-for-personality-and-psychological-research

Riechert SE, Hedrick AV (1993) A test for correlations among fitness-linked behavioural traits in the spider *Agelenopsis aperta* (Araneae, Agelenidae). Anim Behav 46(4):669–675. https://doi.org/10.1006/anbe.1993.1243

Sakai A, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. Annu Rev Ecol Syst 32(1):305–332. https://doi.org/10.1146/annurev.ecolsys.32.081501.114037

Schlaepfer DR, Glättli M, Fischer M, van Kleunen M (2010) A multi-species experiment in their native range indicates pre-adaptation of invasive alien plant species. New Phytol 185(4):1087–1099. https://doi.org/10.1111/j.1469-8137.2009.03114.x

Shahi M, Hosseini A, Shemshad K, Rafinejad J (2011) The occurrence of red-back spider *Latrodectus hasselti* (Araneae: Theridiidae) in Bandar Abbas, southern part of Iran. Iranian J Arthropod-Borne Dis 5(1):63–68

Sih A, Cote J, Evans M, Fogarty S, Pruitt J (2012) Ecological implications of behavioural syndromes. Ecol Lett 15(3):278–289. https://doi.org/10.1111/j.1461-0248.2011.01731.x

Simonneau M, Courtial C, Pétillon J (2016) Phenological and meteorological determinants of spider ballooning in an agricultural landscape. CR Biol 339(9):408–416. https://doi.org/10.1016/j.crvi.2016.06.007

Sol D, Maspons J, Vall-llosera M, Bartomeus I, García-Peña GE, Piñol J, Freckleton RP (2012) Unraveling the life history of successful invaders. Science 337(6094):580–583. https://doi.org/10.1126/science.1221523

Thorbek P, Sunderland KD, Topping CJ (2004) Reproductive biology of agrobiont linyphiid spiders in relation to habitat, season and biocontrol potential. Biol Control 30(2):193–202. https://doi.org/10.1016/j.biocontrol.2003.10.004

Thorlacius M, Brodin T (2018) Investigating large-scale invasion patterns using-small scale invasion successions—Phenotypic differentiation of the invasive round goby (*Neogobius melanostomus*) at invasion fronts. Limnol Oceanogr 63(2):702–713. https://doi.org/10.1002/lno.10661

Van Keer K (2011) Exotische spinnen in België. Een stand van zaken en recente trends. Natuur Focus 10(3):96–103

van Kleunen M, Schlaepfer DR, Glaettli M, Fischer M (2011) Preadapted for invasiveness: Do species traits or their plastic response to shading differ between invasive and non-invasive plant species in their native range?: shade plasticity and invasiveness. J Biogeogr 38(7):1294–1304. https://doi.org/10.1111/j.1365-2699.2011.02495.x

Vink CJ, Sirvid PJ, Malumbres-Olarte J, Griffiths JW, Paquin P, Paterson AM (2009) Species status and conservation issues of New Zealand's endemic *Latrodectus* spider species (Araneae: Theridiidae). Invertebr Syst 22(6):589–604. https://doi.org/10.1071/IS08027

Vink CJ, Derraik JGB, Phillips CB, Sirvid PJ (2011) The invasive Australian redback spider, *Latrodectus hasseltii* Thorell 1870 (Araneae: Theridiidae): current and potential distributions, and likely impacts. Biol Invasions 13(4):1003–1019. https://doi.org/10.1007/s10530-010-9885-6

Wardle DA, Bardgett RD, Callaway RM, der Putten WHV (2011) Terrestrial ecosystem responses to species gains and losses. Science 332(6035):1273–1277. https://doi.org/10.1126/science.1197479

Wiggins WD, Bounds S, Wilder SM (2018) Laboratory-reared and field-collected predators respond differently to same experimental treatments. Behav Ecol Sociobiol 72(2):19. https://doi.org/10.1007/s00265-017-2437-7

Wilson JRU, Dormontt EE, Prentis PJ, Lowe AJ, Richardson DM (2009) Something in the way you move: dispersal pathways affect invasion success. Trends Ecol Evol 24(3):136–144. https://doi.org/10.1016/j.tree.2008.10.007

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