

Research



Cite this article: Merwin AC. 2019 Flight capacity increases then declines from the core to the margins of an invasive species' range.

Biol. Lett. **15**: 20190496.

<http://dx.doi.org/10.1098/rsbl.2019.0496>

Received: 3 July 2019

Accepted: 28 October 2019

Subject Areas:

ecology, evolution

Keywords:

spatial sorting, population spread, dispersal, *Megacopta cribraria*

Author for correspondence:

Andrew C. Merwin

e-mail: andrewcmerwin@gmail.com

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.4725263>.

Evolutionary biology

Flight capacity increases then declines from the core to the margins of an invasive species' range

Andrew C. Merwin

Biology and Geology, Baldwin Wallace University, Berea, OH, USA

ACM, 0000-0002-4341-097X

Individuals that disperse farther than other individuals are more likely to be on the frontlines of spreading populations and may be more likely to mate with one another as a consequence of their spatial proximity. Over generations, this process—known as spatial sorting—can produce patterns of increasing dispersal ability from a population's core towards the spreading front. By contrast, when the spread of a population is limited by the availability of suitable habitat, theory predicts that range boundaries can select against more dispersive phenotypes and produce patterns of decreasing dispersal capacity towards population margins. In a common garden study of invasive kudzu bugs (*Megacopta cribraria*)—which are limited by the availability of hostplants in their southern and western margins—I show that midrange individuals fly 49% farther than individuals in the core and 37% farther than individuals at margins. This result highlights that other processes, such as maternal effects or selection at range boundaries, may create more complicated patterns of dispersal ability across landscapes than predicted by models of spatial sorting alone.

1. Introduction

When populations spread into previously uncolonized areas, strong dispersers can populate the leading edge, where they—or their offspring—are likely to mate with one another as a consequence of their spatial proximity. This process, known as spatial sorting, can contribute to the evolution of more dispersive phenotypes at the frontlines of spreading populations [1–3]. For example, cane toads, *Rhinella marina*, at the frontline of their introduced Australian range have longer legs, higher endurance and travel further than individuals near the core [4–7].

However, we know much less about the spatial distribution of dispersal phenotypes after spreading populations reach the extent of their habitable area. In relatively homogeneous habitats, theory and some empirical observations suggest that the trend of increasing dispersal ability from the population's core to margin can attenuate, especially when other life-history traits trade-off with dispersal ability [8,9].

Conditions at habitat boundaries that are distinct from those in the core habitat may also have consequences for the distribution of dispersal phenotypes. For example, research has suggested that plastic responses of herbivorous insects to hostplant quality at range margins can change their dispersal phenotypes [10]. Additionally, hard range boundaries, like those presented by oceans for terrestrial organisms, and gradients of increasing dispersal costs are likely to select for less dispersive phenotypes, since dispersal beyond these boundaries may result in zero or reduced fitness [11,12].

As spreading populations transition to a state of relative stability, observations are needed to improve our understanding of the processes that

contribute to the spatial distribution of dispersal phenotypes. Such observations could inform our predictions for the dominant directions of gene flow within post-spread populations and, thus, our predictions for local adaptation.

Here, I report on a common garden study of the dispersal capacity of kudzu bugs, *Megacopta cribraria*, which were first discovered in North America in 2009 and are thought to have been established by a single maternal lineage [13,14]. From 2013 to 2014 their average spread rate declined dramatically—from 109 to 20 km [15] and has continued to decline. In the southern and western parts of the kudzu bug's introduced range, this reduction in spread rate is thought to be largely a consequence of limited host plants, including kudzu (*Pueraria montana*) and soya bean (*Glycine max*) [15].

In this study, I ask: (i) how do kudzu bug dispersal traits (size, speed, time spent flying and distance flown) vary from the site of their introduction to their range boundaries and (ii) are patterns of dispersal capacity consistent with spatial sorting or are other processes, such as maternal effects or selection against dispersal at range margins, potentially at play?

2. Methods

(a) Collection and rearing of kudzu bugs

From 21 to 24 July 2016, I haphazardly collected 347 kudzu bug egg masses from kudzu vine, *Pueraria montana* var. *lobata*, at 12 sites along two core-to-edge transects (figure 1; electronic supplementary material, table S1). I analysed 11 sites in total; one site was dropped from analyses because the flight capability was only successfully measured for a single adult.

Colonies of kudzu bugs were established on eight-week-old pigeon pea (*Cajanus cajan*), a high-quality hostplant for kudzu bug development [16]. Nymphs from viable egg masses were distributed across rearing enclosures with all nymphs from one or all nymphs from two egg masses per enclosure. Placing nymphs from one or two egg masses created a continuous range of nymphal densities due to natural variation in a number of eggs per egg mass. This range of densities was created because an original, though secondary, interest of this study was to understand how nymphal density interacts with distance from the site of introduction to contribute to kudzu bug dispersal traits (e.g. [17]). However, a low number of emergences from egg masses due to parasitism (see [18]) and a low number of egg masses collected from the southern and western fronts (12 and five egg masses, respectively) precluded a robust examination of the interactions between distance from the core and nymphal density.

Nymphs from frontline populations were established with only one egg mass per enclosure due to low numbers of egg masses at these sites. This may have biased my results towards observing the increased size and flight capacity for frontline populations, though this is not what I observed (see Results).

Relatedness among individual kudzu bugs in this study is not known, but in an effort to increase genetic diversity, each site used individuals from at least four to 13 different egg masses (electronic supplementary material, table S1).

Colonies on individual hostplants were enclosed in mesh screening (1.5 × 1.7 mm) and were placed in plastic trays (a.k.a. 'flats'), where they were watered by inundating and draining trays daily. Up to three colonies, with kudzu bugs from the same collection site, were placed in a tray. After four weeks, hostplants began to outgrow their mesh enclosures. At this time, kudzu bug nymphs were censused and transferred to new hostplants. Because numbers of later-stage nymphs are likely to be a

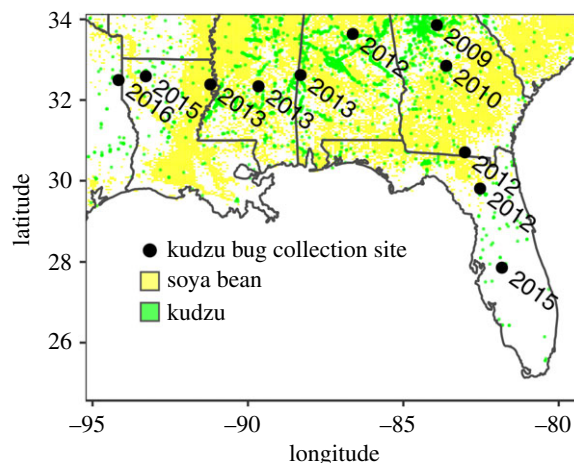


Figure 1. Map of kudzu bug egg mass collection sites and host plant distributions. Years indicate when kudzu bugs were first identified in the site's county. Soya bean and kudzu distributions were taken from CropScape and EDDMapS, respectively (accessed July 2019).

better indicator of intraspecific interaction strength than newly emerging nymphs, I used the number of nymphs during this census in analyses.

(b) Flight trials and data collection

Fourteen flight mills were constructed following Smith [19] and were placed on a level surface in a greenhouse. Duration (proportion of time spent flying), distance flown (kilometre) and average speed—total distance flown over total time spent flying—were recorded for 1 h using a flight test program provided by Smith [19] in the LabVIEW programming language (National Instruments, 2011).

Insects that did not fly or flew less than two rotations were excluded from analyses. Most, if not all, insects were capable of flight (AC Merwin 2016, personal observations), and many that did not fly on flight mills or flew less than two rotations were later found to be poorly adhered to the flight mills. Thus, excluding these individuals provided a better estimate of a population's mean flight capacity (but see electronic supplementary material, table S2 for analyses of all flights). Each individual was given 1 h to fly after their first sustained bout. Flights were recorded from 6 September 2016 to 30 October 2016 between 10.00 and 16.00 in a greenhouse where the temperature ranged from 27.9 to 33°C (30.5°C mean). Insects were weighed immediately after flying, and the width of their pronotums was later measured using callipers.

To account for differences in the body condition of adult kudzu bugs, which can arise as a result of longer feeding periods or different feeding environments, I calculated a scaled mass index [20].

In total, recordings of kudzu bug flights came from 196 insects reared in 104 different colonies distributed among 44 trays. On average 1.9 individuals were flown from each colony (range: 1–5).

(c) Statistical analyses

To investigate the factors influencing kudzu bug dispersal traits—adult size, average speed, duration of flight and distance flown—I built separate generalized linear mixed models (GLMMs). These models included the random effects of colony ID nested within the tray ID, nested within the site of collection. In preliminary analyses of distance flown, however, the random effect of colony nested within the tray was estimated as zero. In the model of distance flown, therefore, the random effect of the colony was excluded, while the effect of tray nested within the population was retained.

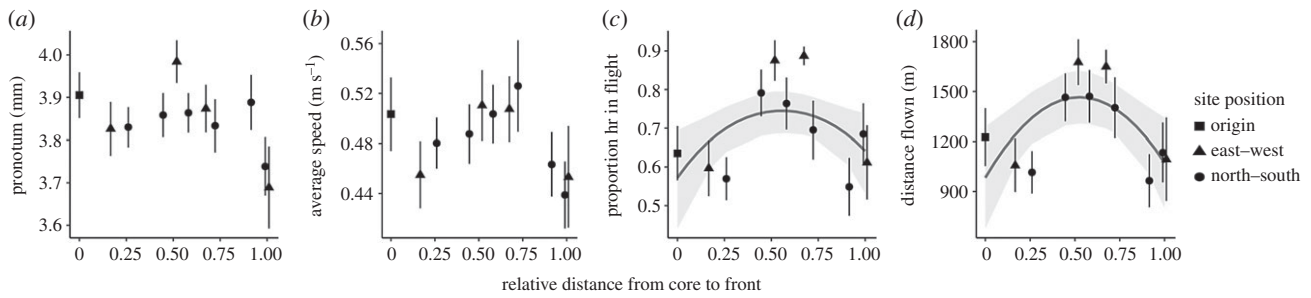


Figure 2. Mean dispersal-related traits of kudzu bugs with distance from the site of introduction: pronotal width (a), average flight speed (b), duration of flight (c) and total distance flown (d). Error bars show s.e. and shaded areas represent the 95% confidence intervals of models in which distance squared was significant.

Models included the density of nymphs and linear and quadratic terms for the distances between the site of introduction and the site of collection. In addition, models of average speed, duration of flight and distance flown included size (pronotal width) and condition (scaled mass index) as covariates. Sex was included in the model of adult size, but not in models of speed, duration, nor distance flown because preliminary analyses of these data and previous research have demonstrated that these dispersal traits are not influenced by sex once one accounts for size [21]. Flight duration, as a proportion from 0 to 1, was modelled using a beta distribution and a logit link function, while other dispersal traits were modelled using Gaussian distributions. GLMMs were built in the package *glmmTMB* [22] and significance was determined using Wald χ^2 -tests (package 'car'). All analyses were conducted in R v. 3.5.1 [23].

3. Results

Size, as measured by pronotal width, did not vary significantly with a population's distance from the core of the introduced range (figure 2a, $p=0.101$, table 1). Rather, variation in size was explained by sex and nymphal density. Males were 30% smaller than females ($p<0.001$, table 1) and adults were smaller when reared on plants with more conspecifics ($p=0.004$, table 1; electronic supplementary material, figure S1).

Average flight speed also did not vary significantly with distance from the site of introduction ($p=0.777$, figure 2b), but was positively correlated with size and condition ($p<0.001$ for both size and condition, table 1), and negatively correlated with nymphal density ($p=0.003$, table 1; electronic supplementary material, figure S2).

The proportion of time insects spent in flight exhibited a concave down relationship with their population's distance from the site of introduction regardless of the inclusion of other factors in the model. Insects from intermediate distances were predicted to fly 7% and 15% longer than core and frontline populations, respectively (distance²: $p=0.018$, figure 2c). Larger insects and those with a greater relative mass also spent more time flying ($p=0.008$ and $p=0.003$ for size and condition, respectively), but flight duration did not depend on nymphal density ($p=0.597$).

The total distance flown was largely determined by the time an insect spent flying (linear regression of distance versus flight time: $r^2=0.83$). Therefore, the total distance an insect flew also exhibited a concave downward trend with distance from the site of introduction (distance²: $p=0.005$, figure 2d). Insects from intermediate distances were predicted to fly 395 and 216 m further in an hour on average than insects at the origin or frontlines, respectively.

4. Discussion

Theoretical and empirical research have shown that spatial sorting can contribute to the evolution of increased dispersal capacity from the core to the frontlines of spreading populations [1,2,4,24,25]. By contrast, reduced habitat quality and selection against dispersal at certain range boundary types may lead to patterns of reduced dispersal capacity from the core to margin for populations that have reached the extent of their suitable area [11,12]. How these forces shape distributions of dispersal phenotypes—once a species reaches the extent of the habitable area—remains an open empirical question. Using flight mills in a common garden experiment, I show that flight capacity (duration and distance flown in an hour) of an invasive insect, *M. cribraria*, increases and then declines along two transects from the core of its range to the southern and western margins—a pattern that is consistent with predictions of an early role for spatial sorting followed by selection against dispersal at the range margin.

These results are surprising because the kudzu bugs' potential for evolution was limited by both their time since the introduction and their introduced genetic diversity. Kudzu bugs are thought to have two generations a year [26]. Thus, they had only passed through approximately 16 generations between the time of their discovery in North America and when eggs were collected. Further, they are believed to have been introduced by a single maternal lineage [27]. Their populations, however, have swelled to tremendous densities [28], raising the possibility that dispersal-related mutations may have arisen. In addition, selection pressure on phenotypes—though not necessarily genotypes—at the front line may have contributed to the observed hump-shaped pattern of flight capacity.

While many studies have documented a pattern of increasing dispersal capacity toward range margins or no pattern at all [29], to my knowledge, this is the first study to document a pattern of decreasing flight capacity toward the margin of an invasive population's range, despite theoretical predictions that this pattern can arise as a consequence of particular types of range margins selecting against dispersal traits [11,12,30]. The limited diet breadth of kudzu bugs may help to account for this observation. Many other studies of dispersal traits at range margins track changes of opportunistic predators and omnivores (e.g. crickets, [31]; cane toads, [4]; damselflies, [32]; ladybird beetles, [33]). Kudzu bugs, by contrast, depend on a spatially limited resource: a restricted suite of plants in the family Fabaceae [34]. Because their two main hosts, soya bean and kudzu, are uncommon at and beyond the frontline

Table 1. GLMM estimates of factors influencing kudzu bug dispersal-related traits. Italic values are considered significant.

	β	s.e.	χ^2	<i>p</i> -value
size (pronotum in millimetres)				
sex	−0.306	0.028	139.331	<0.001
Julian day	0.002	0.026	0.020	0.886
nymphal density	−0.040	0.014	8.008	0.005
distance from core	−0.031	0.019	2.661	0.103
distance from core ²	0.002	0.017	0.017	0.896
speed (metres per second)				
size (pronotum in millimetres)	0.068	0.008	73.397	<0.001
condition (scaled mass index)	0.043	0.008	29.671	<0.001
nymphal density	−0.020	0.007	8.639	0.003
distance from core	0.002	0.008	0.092	0.761
distance from core ²	−0.007	0.007	1.068	0.301
proportion of hours in flight				
size (pronotum in millimetres)	0.299	0.100	9.017	0.003
condition (scaled mass index)	0.257	0.097	6.971	0.008
nymphal density	−0.036	0.083	0.191	0.662
distance from core	0.083	0.095	0.777	0.378
distance from core ²	−0.204	0.085	5.583	0.018
distance flown (metres)				
size (pronotum in millimetres)	324.80	52.53	38.226	<0.001
condition (scaled mass index)	240.83	51.94	21.498	<0.001
nymphal density	−53.82	45.10	1.424	0.210
distance from core	44.64	48.51	0.847	0.350
distance from core ²	−122.55	44.10	7.723	0.005

areas sampled (figure 1, Liang *et al.* [15]), there may be strong selection against dispersal at their range margins.

Maternal effects may also account for the observed patterns of flight capacity. I reared insects from eggs in a common environment, but I did not rear insects through subsequent generations and, thus, cannot rule out the possible influence of non-genetic inheritance. For example, the nutritional quality of kudzu plants may decline towards the margin of their range. To account for the possibility of maternal effects, offspring body size and condition were included in my models. These factors did not influence the significance of the observed hump-shaped pattern of distance flown with distance from the site of introduction. Further, climatic factors experienced by the parental generation—mean temperature and precipitation from two months prior to collection—were not significant in models of dispersal traits (electronic supplementary material, table S3), nor was the distance between a collection site and the nearest soya bean field (electronic supplementary material, table S4). Nevertheless, variance in the duration of flight and distance flown may have a maternal component for which my observations did not account. For example, genetic variation in vertically transmitted endosymbionts, which have been shown to influence the movement of nymphs [35], may also contribute to changes in adult flight capacity.

This study carries important implications for future research on the drivers of dispersal along invasion gradients.

While studies of cane toads have shown that traits may have curvilinear responses with distance along an invasion gradient [36–38], here, I provide a clear demonstration across two transects that the trait of dispersal capacity itself can have a nonlinear relationship with distance from the core and, thus, its characterization requires more than two observations (e.g. core versus frontline). Further, because flight distance was driven by a propensity to continue flying, not an observed morphological trait, this study, like others before it, argues that documenting morphological traits alone may be insufficient to observe changes in realized dispersal distances [7,33]. Finally, the observed reduction in dispersal capacity towards the range margin suggests that maternal effects, perhaps associated with kudzu plant quality at the site of collection, or selection against dispersal may create more complex spatial patterns of dispersal ability than those predicted by spatial sorting alone.

Data accessibility. Data are available from the Dryad Digital Repository: <https://dx.doi.org/10.5061/dryad.pk0p2nghq> [39].

Competing interests. I declare I have no competing interests.

Funding. I received no funding for this study.

Acknowledgements. I thank S. Biscoe, Z. Lankist and T. Jepsen for assistance with flight mills and colonies, and C. Brassil, M. Cenzler, M. Steck, members of the Underwood and Inouye Labs (FSU), and three anonymous reviewers for useful comments on earlier versions of this manuscript.

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