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Community ecology

Social trematode parasites increase standing army size in areas of greater invasion threat

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Organisms or societies are resource limited, causing important trade-offs between reproduction and defence. Given such trade-offs, optimal allocation theory predicts that, for animal societies with a soldier caste, allocation to soldiers should reflect local external threats. Although both threat intensity and soldier allocation can vary widely in nature, we currently lack strong evidence that spatial variation in threat can drive the corresponding variation in soldier allocation. The diverse guild of trematode parasites of the California horn snail provides a useful system to address this problem. Several of these species form colonies in their hosts with a reproductive division of labour including a soldier caste. Soldiers are non-reproductive and specialized in defence, attacking and killing invading parasites. We quantified invasion threat and soldier allocation for 168 trematode colonies belonging to six species at 26 sites spread among 10 estuaries in temperate and tropical regions. Spatial variation in invasion threat was matched as predicted by the relative number of soldiers for multiple parasite species. Soldier allocation correlated with invasion threat at fine spatial scales, suggesting that allocation is at least partly inducible. These results may represent the first clear documentation of a spatial correlation between allocation to any type of caste and a biotic selective agent.

1. Introduction

Defences are costly. Therefore, to optimize fitness, organisms must trade-off allocating their finite resources between defence and reproduction [1–6]. Allocating more to reproduction should optimize fitness at low levels of biotic threats, such as predation, browsing, competition or parasitism. By contrast, when exposed to higher threat levels, allocating more to defence should be favoured. This intuitive optimal allocation theory applies to both individual organisms and to societies, particularly where the society is the functional unit of selection [1,5,7]. Some such societies are tightly organized, forming colonies with a caste division of labour involving reproductive and non-reproductive individuals specialized on defence (soldiers). Theory predicts that these colonies should invest relatively more in the soldier caste in response to increased threat [5,7,8]. Indeed, manipulative experiments show that colonial societies of a wasp, an ant and a trematode species can increase the number of soldiers in response to increased threat [9–11].

A broader prediction is that spatial variation in threat levels for colonial organisms should drive the corresponding variation in soldier allocation. Further, the scale at which such spatial covariation occurs should depend on

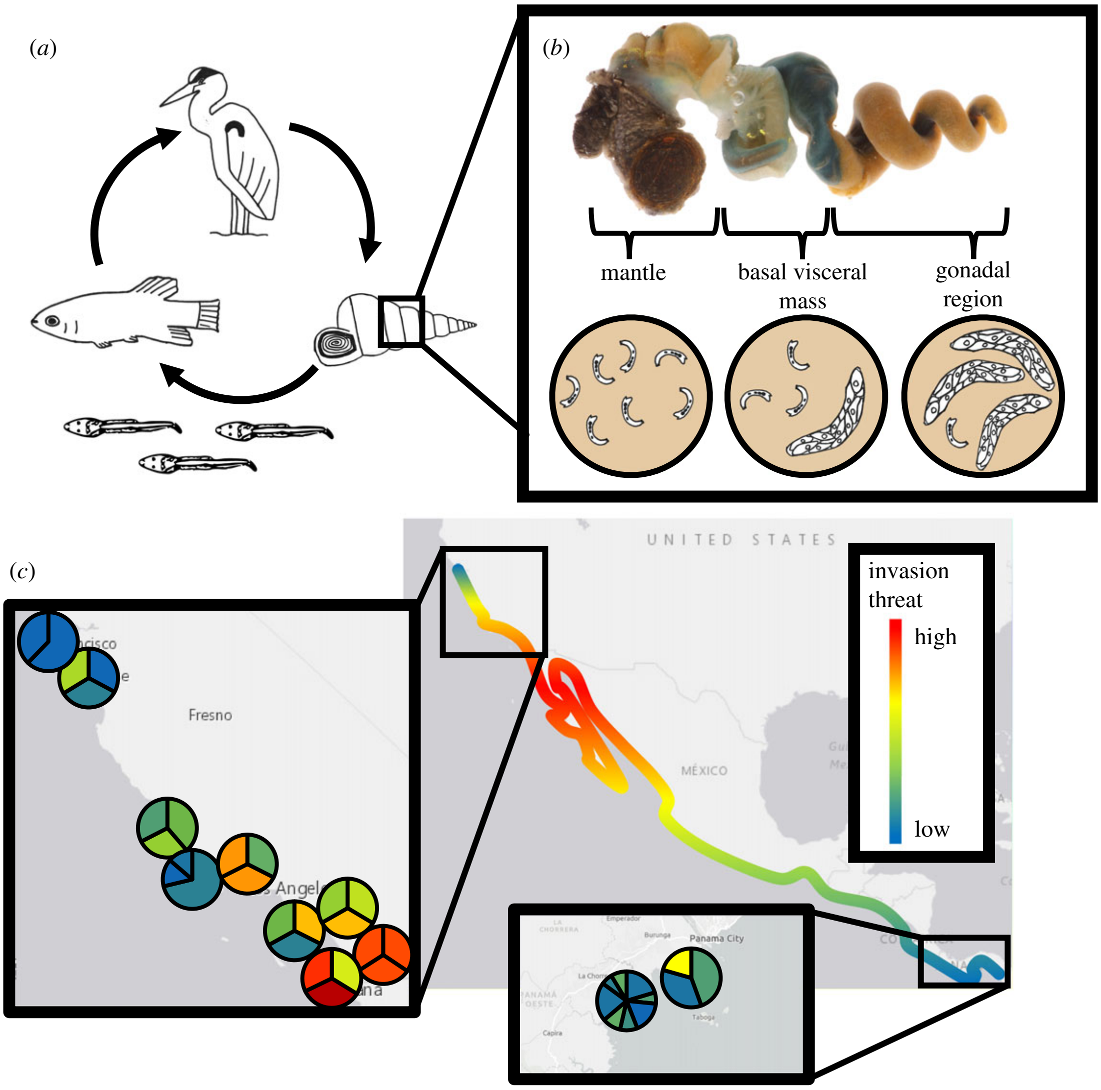

Figure 1. (*a*) Generic complex life cycle for trematode species. A single larva infects a snail and clonally produces soldier and reproductive rediae to form a colony. Dispersive larvae (cercariae) produced by reproductives leave the snail and encyst on/in second intermediate hosts, such as fish. These cysts are transmitted to wetland birds, their final hosts, via predation of the second intermediate host. In the final host, sexual trematode stages produce eggs that exit with the bird's faeces to subsequently infect and found a new colony in a new snail host. (*b*) Diagram of a dissected snail with an established trematode colony. The colony locus is in the gonadal region, where soldiers and reproductives are produced. The basal visceral mass (middle) and mantle regions are where invasion occurs, and soldiers are disproportionately represented there. Photo by Alex Wild. (*c*) Generalized invasion threat gradient from California to Panama [16]. Pies represent sampled estuaries. Pie slices represent different sites within each estuary, with slice size representing relative sample size and slice colour representing observed site-level infection prevalence.

the mechanism underlying allocation variation. If allocation to the soldier caste is plastic (inducible), soldier allocation of individual colonies should reflect variation in threat level at fine spatial scales (the immediate vicinity of a colony). By contrast, if the allocation is innate (constitutive), variation in threat levels at broader scales (where gene flow < selection) could select local populations to have different constitutive levels of soldier allocation [12]. Despite these clear predictions, we currently lack robust evidence that spatial variation in threat can drive the corresponding variation in soldier allocation at *any* spatial scale in nature.

However, there are indications that spatial variation in the threat level can drive variation in soldier allocation. For instance, studies in ants and a trematode have found geographical variation in defensive caste allocation, suggesting greater relative investment in areas with the higher threat [13–15]. However, the small number of localities in these studies preclude directly assessing the relationship between soldier allocation and invasion threat. Second, laboratory experiments using social insects and trematodes show that colonies can plastically allocate more to defence [9–11]. Despite such tantalizing evidence, we lack research with the replication required to robustly test whether spatial variability in invasion threat matches field patterns of allocation to the soldier caste.

The diverse guild of trematode parasites that infect and form colonies in the California horn snail, *Cerithideopsis californica*, provides an excellent system to tackle this problem. First, the colonial stages (rediae) of several trematode species are organized into castes, with large reproductives and smaller, non-reproductive soldiers with relatively large mouthparts (figure 1*b*; [17–19]). Trematode soldiers are specialized for defence, attacking and ingesting competing trematodes [17–22], and are disproportionately deployed at 'invasion fronts'—locations of the snail body where invasions start (figure 1*b*; [17–20]). Second, colony mortality resulting from invasion by other trematodes is well-characterized in this system [21–23], where it can influence community

Table 1. Trematode species name, code, number of estuaries and sites where it was encountered, and the total number of colonies processed.

species name	code	no. estuaries	no. sites	no. colonies
Parorchis sp.	Pasp	6	10	13
Himasthla rhigedana	Hirh	6	10	21
Himasthla sp. B	Hisb	3	8	29
Acanthoparyphium spinulosum	Acsp	6	14	37
Cloacitrema michiganensis	Clmi	5	7	10
Euhaplorchis californiensis	Euca	8	18	58

structure [23] and drive adaptive resource allocation between growth and reproduction [24]. Third, invasion threat varies at multiple spatial scales, including a broad latitudinal gradient (figure 1*c*), among estuaries within a geographical region [16,25], and even among sites within an estuary [22,26]. Finally, hosts represent a relatively consistent resource and habitat, minimizing nutritional variability between colonies which can influence defence allocation [27,28] and interfere with testing relationships between invasion threat and soldier allocation.

The above attributes permitted us to perform an unprecedented test of whether spatial variation in invasion threat drives allocation to the soldier caste. We quantified invasion threat and soldier allocation for 168 colonies (single colony per snail) belonging to six trematode species at 26 replicate study sites spread among 10 temperate and tropical estuaries spanning a range of invasion threat levels. In addition to testing the general hypothesis that spatial variation in threat level leads to matching variation in soldier allocation, we also used the multiple spatial scales of our sampling to examine the general mechanism of caste allocation (inducible versus solely constitutive). We specifically predicted that fine-scale matching of soldier allocation and threat level would only occur if allocation was inducible. Additionally, we also tested the hypothesis that trematodes deploy a greater proportion of their soldiers to 'invasion fronts' under higher invasion threat, similar to what has been documented for a stingless bee and turtle ants [29,30].

2. Abridged materials and methods

(a) Target species collection

We focused on six trematode species that have a soldier caste and infect California horn snails (table 1; [17–19]). We collected over 300 snails from each of nine estuaries across California and two estuaries across Panama. We aimed to collect a minimum of 100 snails by hand during low tide from three sites per estuary. However, at one Panamanian estuary where snails were extremely patchy, we collected all snails from two sites, while at another, we opportunistically collected snails from eight sites to find our trematode species of interest. Additionally, in areas we expected to have low infection prevalence (given previous survey work), we collected more snails to get sufficient numbers of trematode colonies for dissection (electronic supplementary material, tables S3, S4). A total of 5520 snails were dissected to estimate infection prevalence, a proxy for invasion threat.

(b) Identification, colony processing and index of invasion threat

In the laboratory, snail length was measured with Vernier calliper, processed following Torchin *et al.* [16], and trematode species identified following Hechinger [31]. We assessed soldier allocation and deployment for trematodes colonies that were the only infection within a snail (i.e. no co-infection; table 1). The deshelled snails were divided into three sections, and soldiers and reproductives were counted in each section (figure 1*b*).

As a metric for invasion threat, we summed the prevalences (proportion of hosts infected) of all trematode species [32]. This metric provides the cumulative risk of invasion by any trematode species at that site. We calculated infection prevalence for each site and each estuary (pooling all snails; electronic supplementary material, tables S3, S4).

(c) Statistical analyses

After quality control, we ended up with 168 colonies across 26 sites and 10 estuaries. We examined two dependent variables for single-infection trematode colonies: total soldiers (i.e. soldier allocation) and the proportion of soldiers in the mantle (i.e. soldier deployment to invasion front; see electronic supplementary material for an additional deployment variable that provided similar results).

We first describe the models for total soldiers and then detail differences for deployment models. For total soldiers, we used generalized linear mixed models (GLMMs) with a Poisson distribution, a log-link function, and included site nested within estuary as a random variable to control for potential non-independence of trematode colonies. We also included individual snail as an observation-level random effect to account for overdispersion [33]. Our global model included snail size, total reproductives, species ID, total reproductive × species ID, site-level prevalence, estuary-level prevalence and latitude. Although snail size (a proxy for total available resources) and total reproductives can vary positively with total soldiers [17], all continuous variables had low variance inflation factor scores (less than 5) permitting the inclusion of both variables [34]. Total reproductives is an index of colony size, and including it permits us to express soldier allocation per unit reproductive, providing relative allocation to soldiers (∼caste ratios). Using total soldiers as our response variable also permitted us to directly model exponential changes in relative soldier allocation with total reproductives (as documented in [17]) without suffering from contaminating the response variable with a predictor variable [35,36], which would occur if we directly modelled caste ratio. The total reproductives × species ID term permits species to differ in how their relative allocation changes with colony size. Latitude, total reproductives and snail size were z-score transformed to improve model convergence because variables were on very different scales [37].

First, we determined which spatial scale (site-level prevalence, estuary-level prevalence or latitude) best explained

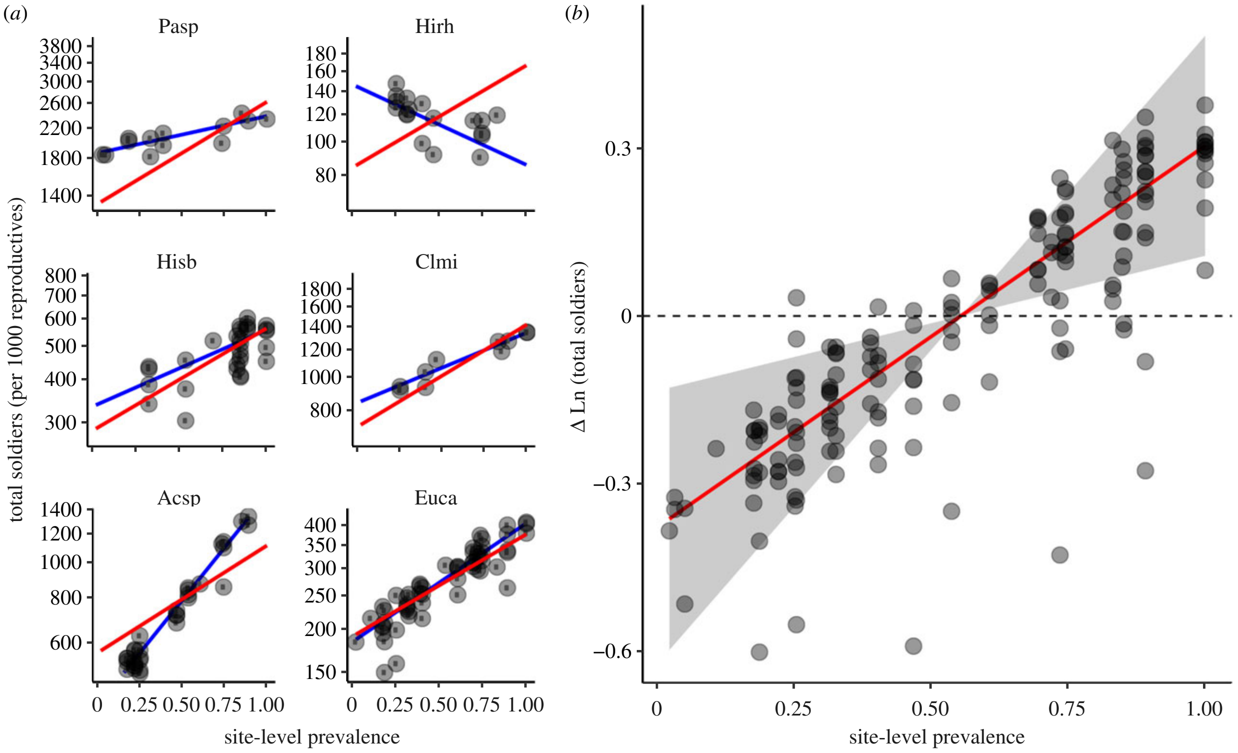

Figure 2. Trematode colonies allocate more to soldiers at sites with increased invasion threat. (*a*) The number of soldiers in a colony versus site-level infection prevalence (proxy for invasion threat) for six species, statistically holding constant the number of reproductives to 1000 and snail size to its median (26.78 mm). The data are conditioned on the third-ranked model (electronic supplementary material, table S1) to visualize best fit slopes for each species (blue lines). However, the top model indicates that all species share the same slope (red lines). (*b*) Contrast plot based on the top model, showing how variation in site-level prevalence alters the expected allocation to soldiers, along with confidence intervals, holding a number of reproductives to 1000 and all other parameters to their median values.

total soldiers by comparing models with only one scale metric (but all other variables) to each other using AICc differences (ΔAICc; [38]). Due to issues of model overfitting, only after picking one prevalence variable did we add the prevalence × species ID term. A significant prevalence × species ID interaction would indicate that species vary in the degree (slope) to which they alter soldier investment in response to invasion threat. Then we used that model to examine simpler models and evaluated all models using ΔAICc [38].

For soldier deployment, we used GLMMs with a binomial error distribution and a logit link, but with a similar structure for predictor variables as those used for soldier allocation. However, we removed total reproductives × species ID due to convergence issues and did not need to include individual snail as an observation-level random effect.

For our best fit models, we examined parameter estimates and their 95% confidence limits to evaluate the importance and strength of predictor variables [38]. We also provide Wald's χ^2-tests of predictor effects for readers accustomed to *p*-values [39].

3. Results

Soldier allocation substantially increased with infection prevalence (invasion threat) across sites and estuaries ($\chi^2 = 9.19$, d.f. = 1, $p\text{-value} < 0.01$). The top model substantially favoured site-level prevalence over estuary-level prevalence or latitude (ΔAICc = 2.8 and 4.5, respectively; figure 2*b*; table 2). The positive allocation versus site-level prevalence pattern for five of the six species was so similar that adding the species × prevalence interaction was strongly disfavoured (ΔAICc = 4.3; figure 2*a*; electronic supplementary material, table S1). Hence, the top model indicates that the different species share a similar response, doubling their soldier allocation moving from lowest to highest invasion threat level (slope: $e^{0.68} = 1.97\times$; 95% CI: 1.27×, 3.06×).

The best fit model for soldier deployment included species ID, snail size and site-level prevalence, suggesting that colonies deployed a smaller proportion of their standing army towards the invasion front in larger snails under higher site-level prevalence. However, removing site-level prevalence did not substantially reduce model fit (ΔAICc = 0.3), the parameter estimates 95% CI overlapped zero, and the *p*-value was 0.11, all suggesting that this negative effect is weak or non-existent. Further, in our alternative metric of soldier deployment (see electronic supplementary material), the site-level prevalence was not in any of the top models.

4. Discussion

Our results reveal the first clear spatial relationship between a society's soldier allocation and invasion threat, supporting a wide body of optimal allocation theory [1,5,6,28]. There was a remarkable consistency among trematode species concerning soldier allocation patterns. Only one species (Hirh) appeared to differ, but its deviation from the typical positive relationship was not statistically favoured (it is also worth noting that Hirh has the weakest physical caste structure of the studied species; [18]). Hence, most of these species allocate approximately twice as much to the soldier caste in highest threat areas compared to lowest threat areas.

We also found that soldier allocation within a colony was better explained by site-level invasion threat than estuary-level threat or latitude. The relatively poor explanatory value of latitude provides additional support that soldier

Table 2. Parameter estimates and Wald χ^2 significance values for the best fit models for soldier allocation (total soldiers) and deployment (prop soldiers in mantle). Parameter estimates and 95% CIs are in original model space. Species codes denote species-specific intercepts and species-specific slopes with the total number of reproductives. Parentheses denote the reference dummy species variable.

variable	parameter estimate	95% CI	χ^2	d.f.	*p*-value	groups	*n*	s.d.
GLMM(total soldiers ∼ species ID + total reproductives + snail size + total reproductives × species ID + site-level prevalence + (1|estuary/site) + (1|colony ID), family = 'poisson')								
	fixed effects					random effects		
snail size	0.17	[0.05, 0.29]	7.24	1	<0.01	site:estuary	26	0.09
site-level prevalence	0.68	[0.23, 1.13]	9.19	1	<0.01	estuary	10	0.16
total repro (Pasp)	3.27	[−2.19, 8.72]	1.38	1	0.24	colony ID	168	0.54
total repro : species ID			15.29	5	<0.01			
Hirh	3.49	[−2.96, 9.93]						
Hisb	3.32	[−2.98, 9.60]						
Clmi	1.37	[−5.78, 8.53]						
Acsp	3.36	[−2.11, 8.82]						
Euca	0.33	[−5.12, 5.77]						
species ID			36.98	5	<0.0001			
Pasp	8.96	[5.39, 12.53]						
Hirh	6.32	[2.18, 10.46]						
Hisb	7.45	[3.47, 11.43]						
Clmi	7.33	[2.88, 11.78]						
Acsp	8.15	[4.62, 11.68]						
Euca	5.45	[1.90, 9.00]						
GLMM(proportion soldiers in mantle ∼ species ID + snail size + site-level prevalence + (1|estuary/site), family = 'binomial')								
	fixed effects					random effects		
snail size	−0.32	[−0.34, −0.30]	533.86	1	<0.0001	site:estuary	26	0.42
site-level prevalence	−0.71	[−1.59, 0.17]	2.55	1	0.11	estuary	10	0.32
species ID			1879.28	5	<0.0001			
Pasp	−2.01	[−2.52, −1.50]						
Hirh	0.18	[0.06, 0.30]						
Hisb	−1.54	[−1.62, −1.46]						
Clmi	−1.39	[−1.49, −1.29]						
Acsp	−1.9	[−1.98, −1.82]						
Euca	−1.42	[−1.50, −1.34]						

investment is a response to invasion threat, rather than some unknown factor that varies with latitude. Although microgeographic adaptation can occur at fine spatial scales [12,40], we do not believe that local adaptation explains the strong association at the site level, because this scale is miniscule (approx. 100 m^2) compared to the scale of trematode dispersal and recruitment via bird final hosts (i.e. gene flow > selection; [41–43]). Hence, although the broader-scale patterns of allocation to soldiers may partly result from local adaptation in constitutive defence, our results combined with previous laboratory work [11] provide evidence that adaptive phenotypic plasticity plays a role in dictating spatial patterns in standing army size (i.e. soldier number) in the field.

Lagrue *et al.*'s [11] laboratory work on a New Zealand trematode reveals that trematode colonies can plastically increase soldier investment at high threat levels, but only when actively contending with a heterospecific invader (i.e. during co-infection; [11]). By contrast, we studied single-species colonies lacking detectable co-infection, and they still exhibited higher levels of soldier allocation in areas of greater threat. This indicates that these trematodes can perceive local risk (perhaps by previous failed invasion attempts) and respond by having larger standing armies to better prepare for subsequent invasion.

Contrary to one of our predictions, soldier deployment to the invasion front was not greater in areas with increased invasion threat. However, soldier deployment should be a faster process than changing soldier allocation (generating new soldiers), and colonies may only alter soldier deployment while actively contending with a new invasion, similar to how soldiers of a turtle ant and a stingless bee move to the colony's nest entrance only when directly confronted with a heterospecific threat [29,30]. Because we focused on snails with a single parasite colony, we would not have seen such a transient state. Hence, it appears that trematode colonies respond to invasion threat not by deploying a greater proportion of their standing army to invasion fronts, but by simply having a larger standing army.

Ethics. All fieldwork occurred with permission of Panama (SE/APO-3-17) and California (SC-7273).

Data accessibility. The datasets and R code supporting this article have been uploaded to the Dryad Digital Repository: https://doi.org/10.5061/dryad.dfn2z34wx [44].

Authors' contributions. E.J.R. co-conceived and co-designed the study, collected specimens, analysed data, initially drafted manuscript and constructed figures. M.E.T. and R.F.H. contributed to project conception, study design, data analysis, figure design and writing. All authors agree to be held accountable for the content therein and approve the final version of the manuscript.

Competing interests. We declare we have no competing interests.

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