Spatial contagion drives colonization and recruitment of frogflies on clutches of red-eyed treefrogs

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Spatial contagion occurs when the perceived suitability of neighbouring habitat patches is not independent. As a result, organisms may colonize less-preferred patches near preferred patches and avoid preferred patches near non-preferred ones. Spatial contagion may thus alter colonization dynamics as well as the type and frequency of post-colonization interactions. Studies have only recently documented the phenomenon of spatial contagion and begun to examine its consequences for local recruitment. Here, we test for spatial contagion in the colonization of arboreal egg clutches of red-eyed treefrogs by a frogfly and examine the consequences of contagion for fly recruitment. In laboratory choice experiments, flies oviposit almost exclusively on clusters containing dead frog eggs. In nature, however, flies often colonize intact clutches without dead eggs. Consistent with predictions of contagion-induced oviposition, we found that flies more frequently oviposit on intact clutches containing dead damaged eggs and rarely oviposit on intact clutches containing intact eggs. Moreover, contagion appears to benefit flies. Flies survived equally well and suffered less parasitism on clutches lacking dead eggs. This study demonstrates how reward contagion can influence colonization dynamics and suggests that colonization patterns caused by contagion may have important population- and community-level consequences.

Keywords: reward contagion; associational susceptibility; Megaselia; Agalychnis

1. INTRODUCTION

Habitat selection is a key process shaping patterns of abundance across available habitat patches [1]. Unlike patterns of colonization that result from random dispersal, habitat selection can allow individuals to distribute themselves among patches of varying quality in a way that maximizes fitness [2], such as an ideal free distribution [3]. In its simplest form, the ideal free distribution theory assumes that organisms accurately assess patch quality; however, several processes, operating across multiple spatial and temporal scales, may constrain an organism’s ability to make ideal choices [4,5]. For example, spatial contagion—which occurs when the perceived characteristics of a habitat patch are biased by characteristics of nearby patches—affects an organism’s ability to accurately evaluate patch quality [2]. Contagion generated by risk avoidance behaviour can cause organisms to avoid suitable patches near unsuitable ones (‘risk contagion’ [6]), whereas contagion based on attraction can cause colonization of non-preferred patches close to preferred patches (‘reward contagion’). Spatial contagion thus has the potential to modify colonization dynamics, particularly where patches differing in quality are in close proximity [2]. Few studies have investigated how the process of contagion might contribute to variation in patch selection, or examined how contagion affects recruitment success, although assessing this is clearly important for understanding how organisms select habitat in naturally patchy and fragmented environments.

Frogflies, Megaselia randi (Diptera: Phoridae), are an excellent model for investigating spatial contagion. They oviposit and larvae subsist on arboreal egg clutches of red-eyed treefrogs, Agalychnis callidryas [7], i.e. clutches represent habitat patches that flies choose among for their offspring (sensu [6]). Clutches vary in proximity from direct contact to many metres apart [7], and contain varying numbers of dead frog eggs, including eggs broken by predatory wasps [8]. Flies strongly prefer clutches containing dead eggs in laboratory choice tests (see the electronic supplementary material) but nonetheless oviposit on both damaged and intact clutches in nature [7]. To determine whether spatial contagion could explain colonization of intact clutches, we tested whether intact clutches near clutches containing dead eggs are colonized more frequently than intact clutches near other intact clutches. This design allowed us to also investigate post-colonization consequences of patch selection by flies. Specifically, we compared fly survival and parasitism by a eucoiline wasp (Hymenoptera: Figitidae; [7]) on intact and damaged clutches.

2. MATERIAL AND METHODS

We tested for spatial contagion at Occlop Pond (circumference ≈128 m, 9°6′9″ N, 79°40′57″ W; electronic supplementary material, figure S1), near Gamboa, Panama. The pond has abundant red-eyed treefrogs and frogflies [7,8]. Frog clutches were collected in the morning after oviposition, and maintained in the laboratory as in [9] to minimize uncontrolled clutch damage. Clutches were randomly assigned to control and contagion treatments at age 3 days post-oviposition (younger clutches are seldom colonized by flies; M. C. Hughey 2009, unpublished data). The control consisted of paired adjacent intact clutches (i.e. all live, normally developing embryos). The contagion treatment consisted of an intact clutch positioned adjacent to a clutch with simulated wasp damage. Wasp damage was simulated by using forceps to tear open five eggs, killing the embryos. We predicted flies would colonize intact clutches in addition to damaged clutches in the contagion treatment.

We ran two trials of the experiment: 23–25 June and 1–3 July 2010. For each trial, we brought 10 pairs of clutches per treatment to Occlop Pond, randomly assigning treatments to stations encircling the pond at ≈5 m intervals. At each station, the two clutches were placed 15 cm apart in 266 ml plastic cups affixed to a crossbar atop a 1 m bamboo...
pole. Clutches were attached to plastic cards (5 × 10 cm) stapled into cups (electronic supplementary material, figure S1). We left clutches at the pond for 2 days. Upon collection, frog embryos were induced to hatch and released into the pond. The clutch remains—jelly, dead frog eggs, and associated insects—were brought to the laboratory. Using a microscope at a magnification of 32×, we counted the number of fly eggs and larvae on clutches. Clutch remains were then placed into 266 ml plastic cups with perforated, mesh-lined lids to rear frogflies and parasitic wasps to emergence. Emerged insects were preserved in 70 per cent ethanol, identified and counted.

(a) Statistical analyses
We used generalized linear models (GLMs), enabling us to specify error distributions (binomial, negative binomial and quasibinomial) and associated link functions for each type of data in our analyses [10]. To test for spatial contagion, we compared immature fly presence and density on intact clutches across control and contagion treatments. For fly presence, we compared the proportion of intact clutches that were colonized across treatments with a binomial GLM. For fly density, we compared counts of fly eggs plus larvae on intact clutches across treatments with a negative binomial GLM. We excluded 17 replicates where frog eggs died in an ‘intact’ clutch during the experiment, and two replicates whose stations were knocked over by animals, leaving n = 8 control and 13 contagion replicates (i.e. 16 intact control and 13 intact contagion clutches) for analysis. We accounted for non-independence of values from paired control clutches in the same replicate by including replicate as a covariate. All replicate and interaction effects were non-significant (all p > 0.05).

Colonization of non-preferred habitat may also result from density-dependent processes (e.g. spillover effects [11]). To determine whether fly density (eggs plus larvae) on damaged clutches affected colonization of nearby intact clutches, we tested for a relationship across pairs in the contagion treatment with a negative binomial GLM.

To understand the consequences of ovipositing on intact or damaged clutches, we tested for effects of clutch damage and fly density on the proportion of flies surviving (adult fly emergence/egg + larval density) with a quasibinomial GLM (dispersion parameter, δ = 12.5). We included all experimental clutches that were colonized by flies (n = 34 clutches), regardless of neighbour condition, excluding only ‘intact’ clutches in which frog eggs died. Additionally, we compared the proportion of damaged and intact clutches from which parasitoids emerged with a binomial GLM. All analyses were conducted in R v. 2.10.1 [12].

3. RESULTS
Flies colonized all damaged clutches and some intact clutches. Flies were 3.3 times more likely to colonize intact clutches if they were next to a damaged clutch (figure 1a; χ2,25 = 5.7, p = 0.017) and laid 16.2 times more eggs on intact clutches when they were next to a damaged clutch (figure 1b; χ2,25 = 12.2, p = 0.0005).

Within the damage-contagion treatment, as expected, flies laid more eggs on damaged clutches than on adjacent intact clutches (34 ± 3 versus 8 ± 3 eggs per clutch, mean ± s.e.; χ2,24 = 12, p = 0.0005). Spillover from damaged clutches did not explain increased colonization of neighbouring intact clutches. Colonization of intact clutches occurred independent of the density of fly eggs and larvae present on adjacent damaged clutches (χ2,11 = 0.1, p = 0.77). In some cases, flies did not oviposit on intact clutches despite high colonization of adjacent damaged clutches.

Fly survival to adulthood varied substantially but was unaffected by frog clutch damage or conspecific density (figure 2; damage: F1,30 = 2.1, p = 0.17; density: F1,30 = 0.001, p = 0.97; interaction: F1,30 = 0.4, p = 0.52). One factor contributing to fly mortality, parasitoid incidence, differed between damaged and intact clutches. No parasitoid emerged from any intact clutch, whereas four damaged clutches had parasitoids emerging (χ2,32 = 5.1, p = 0.024).

4. DISCUSSION
This study demonstrates that non-preferred habitat patches experience increased colonization when they occur in close proximity to preferred patches—a pattern consistent with the predictions of reward
contagion. The colonization pattern is inconsistent with density-dependent spillover. Nor can it be explained simply by increased encounter rates owing to spatial proximity, because flies failed to oviposit on intact clutches in laboratory choice tests. Our approach to testing contagion—using an ecological field experiment—admittedly limits our ability to directly address the perceptual mechanisms underlying behaviour to demonstrate misperception. Nonetheless, evidence that attractive characteristics of nearby habitat patches can increase colonization of less-preferred patches emphasizes an important ecological point: habitat patches should be studied in the context of their neighbourhoods, as their perceived characteristics may depend on the characteristics of neighbouring patches [2,6].

Surprisingly, we did not detect any direct benefits of damaged clutches for fly larvae. Overall, fly survival to eclosion was similar on damaged and intact clutches, suggesting that intact clutches represent suitable but underexploited habitat patches. Why, then, do flies show such strong patterns of preference in the field and laboratory? One possibility is that damaged clutches provide benefits in the form of colonization success (versus not finding a suitable oviposition site). Volatile cues arising from dead eggs probably make damaged egg masses easier for adult flies to detect and could bleed over to affect the perception of neighbouring patches. Despite how simple the mechanisms underlying spatial contagion may seem, the implications for populations and communities may be profound.

Spatial contagion is predicted to negatively affect populations—risk contagion by accelerating habitat loss and reward contagion by generating attractive sinks [2]. By contrast, our study highlights the possibility that contagion-induced oviposition may augment fly populations. First, contagion appears to facilitate colonization of additional suitable oviposition sites. Second, no intact clutches were colonized by parasitoids, a finding corroborated by field data demonstrating much lower levels of parasitism on clutches lacking dead eggs [7]. Pond-level data on locations of clutches, clutch condition and the fates of flies that colonize them would further elucidate whether the recruitment from intact clutches that we observed at a local scale represents a substantive contribution to fly populations.

Spatial contagion has rarely been studied as a causal process underlying patterns of colonization (but see Resetarits & Binckley [6]). However, spatial contagion may be quite common. For example, the effects of surrounding plant species on colonization dynamics of insect herbivores have long been studied under the framework of associational resistance and susceptibility [13]. Additionally, contagion could contribute to the common finding of consumer distributions that undermatch their resources [5,14]. Studies focusing on processes generating colonization patterns not only increase our understanding of the effects of the spatial distribution of habitat on patterns of colonization and species interactions, but might also increase our ability to predict how population and community dynamics will shift as habitat quality and spatial arrangement changes.

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