



Substrate choice by ovipositing mothers and consequent hatchling behaviour: the exploration sharing hypothesis



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Both maternal and offspring fitness would be higher if the offspring develop in a high-quality habitat than in a low-quality habitat. In animals without direct maternal care, it seems reasonable that either mothers or offspring should invest in finding the best habitat. Recent research, however, suggests extensive maternal and offspring exploration in fruit flies. We considered two hypotheses that could resolve this paradox, first that mothers do not choose oviposition sites that maximize larval success but rather sites that maximize their own fitness or egg survival, and, second, that the winged mothers make decisions over a larger spatial scale than the less mobile larvae are capable of. In a set of experiments, we found that larvae were more likely to explore when they hatched in poor patches lacking protective cavities and live yeast. Egg-laying females, however, also showed strong preferences for ovipositing in cavities with live yeast. These results provided no support for the first hypothesis. We then considered whether females are sensitive to larval travel costs between cavities and live yeast as suggested by the second hypothesis. We found no effect of the distance between the two patches on female oviposition choice, but we did find an effect of the intervening substrate. Females overwhelmingly preferred to lay in the cavity when the intervening substrate was an agar medium, but not when the intervening substrate was bare plastic that discourages larval travel. Therefore, we resolve the paradox of extensive exploration by both mothers and offspring by showing that larvae that hatch in habitats that are desirable to ovipositing females, but not to the larvae, can reasonably assume that there are better food patches within a safe travel distance. That is, there is an adaptive sharing of exploration between mothers and offspring. The exploration sharing hypothesis is pertinent for a large variety of species in which mothers oviposit in sites suboptimal for larval growth.

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There are many systems where females influence the success of their offspring through their choice of where to lay eggs (i.e. oviposition decisions), which can be considered an indirect form of maternal care (Wiklund & Persson, 1983). For example, many insect species that lay their eggs on plants prefer host species that increase offspring success (Gripenberg, Mayhew, Parnell, & Roslin, 2010; Janz, 2002; Refsnider & Janzen, 2010; Schäpers, Nylin, Carlsson, & Janz, 2016; Thompson & Pellmyr, 1991). Insects and amphibians that deposit eggs into water often prefer bodies of water that will not dry up during larval development, that contain suitable food for their offspring and that do not contain competitors, predators or parasites (Refsnider & Janzen, 2010). Similarly, the oviposition decisions of beach-nesting sea turtles can affect the

ability of hatchlings to navigate to the sea (Kamel & Mrosovsky, 2004).

Like more direct examples of parental care, which involve a reallocation of tasks from offspring to parents (e.g. foraging and antipredation tasks), oviposition decisions could be thought of in terms of how exploration or habitat selection tasks are allocated between mothers and offspring (Gamberale-Stille, Söderlind, Janz, & Nylin, 2014; Schäpers et al., 2016; Soler et al., 2012). If mothers reliably oviposit in the best locally available patch for their hatchlings, then the hatchlings should invest little in exploration even if they are in a low-quality patch. However, as in systems with direct parental care, strategies that maximize the parental success are not necessarily identical to the strategy that maximizes the success of a given offspring. Such a parent–offspring conflict could lead to oviposition sites that significantly deviate from the offspring's optimal habitat (Gamberale-Stille et al., 2014; Janz, 2002; Schäpers et al., 2016). This could select for early offspring exploration where hatchlings leave the egg site and search for a suitable feeding site

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(i.e. the exploration tasks are allocated to the offspring; Wiklund, 1984; Janz, 2002; Gamberale-Stille et al., 2014; Schäpers et al., 2016).

The above discussion suggests that the allocation of exploration effort would vary between species. While this framing is appealing, it does not explain systems where both mothers and offspring explore extensively. Such systems raise two linked questions. Why has natural selection favoured offspring that behave as though they do not trust their mothers' choices? And why has natural selection favoured extensive maternal exploration when the offspring will just leave? A starting point for understanding such a system is to determine why discriminating mothers might not reliably lay their eggs in the best available patch from the hatchling's perspective. We consider two hypotheses for why this might be.

HYPOTHESIS 1: DIVERGING PRIORITIES

While hatchling preferences should be influenced by factors that affect their growth and survival, maternal preferences might be partially or wholly influenced by other priorities. For example, females might choose oviposition sites that directly influence their own fitness (Janz, 2002; Refsnider & Janzen, 2010; Scheirs, Bruyn, & Verhagen, 2000), or pick patches that protect them from predators, provide them with food or other resources, or make it easier for them to place their eggs. Alternatively, females might prioritize oviposition sites that are suitable for eggs rather than hatchlings (Janz, 2002; Refsnider & Janzen, 2010).

HYPOTHESIS 2: SPATIAL SCALE FACTORS

Recently hatched individuals make exploration decisions at a local spatial scale, and therefore, may need to decide whether or not to explore based solely on the conditions surrounding the hatching site. In most species, ovipositing females could consider a much larger spatial scale when choosing where to lay their eggs. More generally, any system where ovipositing females attend to a larger spatial scale than their recently hatched young might lead to different observed preferences that could potentially favour early exploration. Note that such spatial scale factors might interact with Hypothesis 1; females might prefer a specific oviposition site that is consistent with maternal or egg priorities, but only if that site is relatively close to a site that would maximize hatchling success (Refsnider & Janzen, 2010; Soler et al., 2012). For example, butterfly species that lay eggs that will overwinter seem to be inclined to find the larval host plant and then lay the eggs some distance from the host in a location that might be better suited for egg survival (Wiklund, 1984).

One system that may involve extensive maternal and offspring exploration is the fruit fly *Drosophila melanogaster*. Recent published research and personal observations within our laboratory suggest extensive maternal and larval exploration. In particular, Yang, Belawat, Hafen, Jan, and Jan (2008) suggested that females extensively sample a potential egg-laying substrate before laying each egg, and a number of studies have shown that females are discriminating in where they lay their eggs (Durisko, Anderson, & Dukas, 2014; Golden & Dukas, 2014; Mery & Kawecki, 2002; Miller et al., 2011; Rodrigues et al., 2015; Sarin & Dukas, 2009; Schwartz, Zhong, Bellemer, & Tracey, 2012; Yang et al., 2008). Similarly, several studies have shown that larvae are quite mobile and are inclined to seek out better substrates (Durisko & Dukas, 2013; Rodrigues et al., 2015; Schwartz et al., 2012; Schwarz, Durisko, & Dukas, 2014). Finally, our preliminary observations indicated that newly hatched larvae engage in extensive exploration even when they are on high-quality media.

Our strategy was to first determine whether recently hatched *D. melanogaster* larvae do explore when they hatch in patches of different qualities. We then tested the hypotheses proposed above for why the newly hatched larvae might act as though they do not trust their mothers. We started by testing a prediction derived from Hypothesis 1: egg-laying females and recently hatched larvae will show different patch preferences when presented with choices at a similar spatial scale.

EXPERIMENT 1: EXPLORATION IN RECENTLY HATCHED LARVAE

Methods

Our exploration arenas were 35 mm petri dishes, each filled with 5 ml of medium containing agar (22 g/litre), cornmeal (83 g/litre) and orange juice concentrate (204 g/litre) and containing a central patch 5 mm in diameter. We used a 2 × 2 factorial design to vary two patch features attractive to fruit fly larvae, live yeast and a cavity (Fig. 1a). Hence the four patch treatments were yeasted cavity, yeast, cavity and plain. The yeasted cavity patches involved a 2.5 µl drop of live yeast suspension (0.6% weight/volume active dry baker's yeast in warm water plus one drop of red food colouring per ml solution) in a 5 × 5 mm depression (created by removing an inverted pyramid-shaped piece of the medium with a spatula). The yeast patches were created with the yeast solution without the cavity. The cavity patches consisted of a cavity and a 2.5 µl drop of red food colouring solution (one drop of food colouring per ml of warm water). The plain patches contained only a 2.5 µl drop of red food colouring solution.

Subjects for this and all subsequent experiments were from a Canton-S population that has been maintained under standard conditions in our laboratory for 7 years (Sarin & Dukas, 2009). Our flies are kept at low density in large Plexiglas cages at an ideal temperature (25 °C) and high humidity (60%), and provided regularly with fresh food optimized for larval growth and adult survival and reproduction. We transferred a single recently laid egg to the centre of each patch of the exploration arenas and kept them in chambers at 25 °C and high humidity (>90% RH). The following day, we monitored the arenas over the period of peak larval hatching. While we wished to observe the movement decisions of hatchlings based only on their hatching environment, our preliminary experiments suggested that the hatchlings responded to our presence. We thus designed a protocol that minimized observer interference. We scanned for hatched eggs in full darkness using a 10x magnifying glass and a flashlight equipped with a filter transmitting red light above 600 nm (Rosco Roscolux no. 27, medium red), which is beyond the visible spectrum of the larvae (Keene & Sprecher, 2012). Following hatching, we moved the dishes and covered them with tinfoil muffin cups, where the larvae remained undisturbed in full darkness for 30 min. We then placed the dishes on ice to arrest larval movement and later transferred them into a –20 °C freezer. After a minimum of 24 h in the freezer, we thawed the exploration arenas and determined whether larvae were within the central patch (residents) or away from the patch (explorers). The central patch was not always visible in the plain arenas, so for consistency, in all conditions, we defined patch residency in terms of distance of the larvae from the egg casing such that larvae that were <5 mm from the egg casings were classified as residents and larvae that were ≥5 mm were classified as explorers. We preserved the exploration arenas of 111 hatchlings, but our final sample size included only 96 arenas because we failed to locate the larvae in 15 arenas (see Results). We analysed

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