FITNESS LANDSCAPES REVEAL CONTEXT-DEPENDENT BENEFITS OF OVIPOSITION CHOICE

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ABSTRACT

Resource choice behaviour has enormous fitness consequences and can drive niche expansion. However, individual behavioural choices are often mediated by past experience. Are such context-dependent behaviours adaptive? Using the red flour beetle, we demonstrate that context-dependent oviposition choice indeed reflects distinct, context-specific local fitness peaks. Manipulating female egg allocation in a habitat containing optimal and novel resource patches, we measured offspring fitness to generate fitness landscapes as a function of all possible oviposition behaviours (i.e. combinations of fecundity and resource preference). Females from different age and density contexts exhibit distinct behaviours that optimize different fitness components. With increasing age and experienced population density, they produce few but fast-developing offspring that are advantageous under high resource competition; whereas young naïve females produce many slow-developing offspring, which is beneficial under weak competition. Systematically mapping complete context-dependent fitness landscapes is thus critical to infer behavioural optimality, and offers predictive power in novel contexts.

Keywords – optimal choice, context-dependence, female oviposition, resource preference, heterogeneous habitat

INTRODUCTION

Organisms often encounter heterogeneous habitats, and their behavioural choices in such situations ultimately determine their fitness. This is perhaps best exemplified by females' reproductive decisions when faced with alternate resources. For example, females of phytophagous insects can lay eggs on different host plants, affecting offspring survival and growth and determining their reproductive success (Jaenike 1978; Craig & Itami 2008; Gripenberg *et al.* 2010; Charlery de la Masselière *et al.* 2017). Therefore, oviposition preference is predicted to face strong selection on par with other life history traits (Resetarits Jr. 1996), which may result in strong preference hierarchies across alternate resources (Gripenberg *et al.* 2010). However, oviposition choice often varies dramatically with females' prior experience, reflecting the ecological or internal context determined by their environment or life history (Anderson & Anton 2014). For instance, females of the polyphagous moth *Spodoptera littoralis* that develop on a specific host plant as larvae also prefer it for oviposition (Proffit *et al.* 2015). More generally, in many species, ecological factors such as age and resource competition change across individuals' lifespan, altering key components of oviposition behaviour such as fecundity (mammals – Sand 1996; Coulson *et al.* 2000; fish – Bobko & Berkeley 2004, Karjalainen *et al.* 2016; insects – Barnes *et al.* 2008; Berggreen *et al.* 2018; Khan *et al.* 2018) and oviposition choice (Resetarits Jr. & Wilbur 1989; Yoshioka *et al.* 2012; Raitanen *et al.* 2014). Given the potentially enormous range of contexts experienced by different individuals across generations, how do context-dependent oviposition behaviours evolve?

To address this question, we must understand what kinds of selection pressures may drive context-specific oviposition choice. Female choice may evolve under strong selection for a single globally optimal preference, with deviations reflecting either weak selection or females' inability to behave optimally in specific contexts. For instance, limited perception of resource quality (Bernays 1998, 2001) or other search-related constraints (Thompson 1988; Gripenberg *et al.* 2010; Wood *et al.* 2018) can prevent females from accessing an adaptive resource (Price 2003). Optimal behaviour may also be limited by tradeoffs between maternal and offspring fitness (e.g., Garcia-Robledo 2012), or by the

presence of competitors or predators (e.g., Resetarits Jr. & Wilbur 1989; Rieger *et al.* 2004; Binckley & Resetarits Jr. 2008; Touchon & Worley 2015). A second possibility is that context-specific female choice reflects context-specific selection to optimize distinct fitness peaks. In other words, female choice in each context may be perfectly attuned to optimality in that context (e.g. Dvorak & Gvozdik 2010). However, to our knowledge, no study has distinguished between these alternative hypotheses, by connecting past context to future fitness. In addition, it is critical to measure multiple fitness components to identify context-specific fitness optima, because multiple traits contribute to fitness and may trade off with each other (Schluter *et al.* 1991; Walsh & Blows 2009; Lailvaux & Kasumovic 2011; Taff *et al.* 2012). Finally, most studies are restricted to analysing females from a limited set of prior contexts, in which only a subset of possible behaviours are expressed. As a result, they only sample a part of the full behavioural fitness landscape, making it difficult to infer whether a specific observed behaviour is locally adaptive or globally maladaptive. Ideally, we need to generate landscapes that encompass all possible behavioural choices, including those outside the range of observed behaviours. An added advantage of such landscapes is that we gain the ability to predict female fitness in novel contexts, based only on information about their oviposition behaviour. Illuminating the entire phenotypic fitness landscape is thus critical to understand the evolution of context-dependent female oviposition behaviour.

We created such fitness landscapes for the red flour beetle *Tribolium castaneum,* a widespread generalist pest of cereal flours that has long served as a model system in ecology and evolutionary biology (Sokoloff 1972, 1974, 1977; Pointer *et al.* 2021). Prior work demonstrates significant variation in key oviposition behaviours such as fecundity and resource preference, modulated by age and population density (indicating strength of resource competition). Here, we explicitly connect prior female context, behavioural choice, and fitness, by conducting three sets of experiments focused on a choice between an optimal resource (wheat flour) and a suboptimal resource (finger millet flour) (Figure 1). To test the impact of context on behaviour, we first measured oviposition behaviour (fecundity and preference) of females from six different age and density contexts (Experiment 1). Second, we generated complete fitness landscapes as a function of the full range of observed female fecundity and

possible oviposition choices. To do this, we experimentally manipulated egg allocation in a habitat with both resource patches, and measured multiple components of offspring fitness (Experiment 2). Finally, we validated the fitness landscape by jointly measuring oviposition behaviours and consequent offspring fitness for females from three different contexts (Experiment 3). By placing oviposition behaviour in a comprehensive fitness landscape, we demonstrate that divergent, context-dependent oviposition behaviours could evolve via selection driving females towards context-specific local adaptive peaks for distinct fitness components.

METHODS

Population maintenance

We derived experimental individuals from large, outbred laboratory “stock” populations of *T. castaneum* (Ravi Kumar *et al.* 2018), maintained with ~2500-5000 adults in 750 g whole wheat flour. To propagate stocks, we introduced ~3000 adults into fresh wheat flour, removed adults after 1 day of oviposition, allowed the next generation to develop for 5-6 weeks, and used the adults to repeat the cycle. We held all populations and experimental individuals at 33±2°C in a dark incubator, except during experimental handling under white light at room temperature (never exceeding 1 hour). Flour beetles have highest fitness in wheat flour and show significantly slower development in finger millet flour (~37% slower development relative to wheat) (Ravi Kumar *et al.* 2018). Hence, we refer to wheat flour as the optimal resource, and finger millet as the suboptimal alternative resource. To remove any prior infestation, we cold-sterilized flour for at least 4 hours at -80°C before use.

Collecting females from different age and density contexts

As required for different experiments (Figure 1), we generated females from six distinct age and density contexts. Females become sexually mature within one week of eclosion and lay eggs continuously for at least 40 weeks (Good 1936; Sokoloff 1974). However, fertility begins to decline starkly ~7 weeks post eclosion (Khan *et al.* 2018). Hence, we used 'young', ‘mid-aged’ and ‘old’ females aged ~2 weeks, ~4

weeks and ~6 weeks post-eclosion respectively, corresponding to an approximately 27% decline in fertility (measured for isolated, singly-mated females; Khan *et al.* 2018). For low density ("LD") contexts we held females in isolation or with a single male (depending on their prior mating experience), whereas high density ("HD") females were taken directly from stock populations. Thus, females from each context were mated with males from the same context. For the two "aged" contexts, after the first oviposition assay (described below) we allowed young LD and young HD females to age for an additional 4 weeks in LD conditions. Further details are given in SI methods.

Measuring oviposition preference and offspring fitness

We measured the oviposition preference of each female (Figure 1, Experiment 1; regardless of her prior context) for wheat vs. finger millet flour in 2-choice assays, in identical conditions. Briefly, we released each female in the center of a 60 mm Petridish containing a patch of each resource (~1 g) on opposite ends (Figure S1; SI methods). After 45 hours (before eggs start hatching), we removed the female and counted the number of eggs in each resource patch. We used the total number of eggs in the habitat (i.e. across both resource patches) to quantify fecundity, and the percentage of eggs deposited in finger millet as a measure for oviposition preference for finger millet. In control assays (with both patches of the same resource), we confirmed that females did not exhibit any side preference (Figure S2).

To measure the fitness consequences of female oviposition behaviours (Figure 1, Experiment 3), we allowed offspring to develop in the respective resource patches undisturbed for 21 days. Larvae could move across resource patches during development. We quantified offspring fitness as the proportion of eggs that survived three weeks of development ("survival"), the proportion of offspring that had successfully pupated or eclosed ("development rate"), and the total number of live offspring of all stages ("total offspring"). All measures of fitness were evaluated for the entire habitat, i.e. including both resource patches.

Generating and validating fitness landscapes

To generate complete fitness landscapes (Figure 1, Experiment 2), we had to quantify the impact of the entire range of possible oviposition behaviours on offspring fitness. Hence, we collected females from three different contexts with distinct ranges of fecundity (young LD, young HD and old HD; see Results); but we did not allow them to express their oviposition choice. Instead, we placed each female in ~2 g wheat flour (43-45 hours in a 60 mm petri-plate), collected the eggs, and manipulated egg allocation systematically across wheat and finger millet patches in a 2-patch habitat (as in the oviposition choice assays), mimicking the range of possible oviposition preferences (n=16-20 females per allocation). By distributing females with various fecundity values across egg allocation treatments, we dissociated female fecundity from resource preference. We measured fitness for each female as described above.

Using these data, we generated fitness landscapes for each fitness component as a function of female fecundity (observed) and ‘preference’ for finger millet (manipulated egg allocation). To generate a smooth fitness landscape for each fitness component, we extrapolated fitness values using local smoothing ('loess') by estimating the value of the three fitness measures for all possible combinations of female fecundity and oviposition preference using the 'panel.2dsmoother' function (from the latticeExtra package, Sarkar 2019) in the levelplot function (lattice package, Sarkar 2008). Fitness was evaluated in an equally spaced grid of 20 by 20 points across the sampled range of fecundity and preference. Thus, we generated fitness landscapes that allowed us to estimate the fitness consequences of any given combination of fecundity and oviposition preference.

To validate fitness predictions from the fitness landscape (Figure 1, Experiment 3), we allowed females from three different contexts (young LD, young HD and old HD) to make oviposition choices; counted and returned eggs to the patch in which they were laid; and measured offspring fitness for each female. Using the median values of observed fecundity and preference for females from each context, we predicted their offspring fitness based on the fitness landscape, and compared the predicted fitness values with the median observed fitness values.

Statistical analysis

All analyses were conducted using R (R Core Team 2017) in RStudio (RStudio Team 2020). We statistically modelled the impact of age and density on female fecundity and of age, density and fecundity on oviposition preference (Experiment 1) and the impact of context, fecundity, and manipulated egg allocation on offspring fitness components (Experiment 2). We used ANOVA models for fecundity; generalised linear models with binomially distributed errors ('binomial GLM') for female oviposition preference, offspring survival and development rate; and a GLM with Poisson errors ('Poisson GLM') for the total number of offspring. In each case, we first fit the maximal model with main effects and all possible interaction terms, and then used the 'stepAIC' function from the 'MASS' package (Venables 2002) to simplify the maximal model. Further details are in the SI methods.

RESULTS

Prior context alters female oviposition behaviour

Based on earlier work, we expected that female age and experienced population density (an indicator of resource competition) would impact oviposition behaviour, i.e. female fecundity and preference for the novel finger millet resource (Figure 1, Experiment 1). As expected, female fecundity decreased with age and experience with high population density (“HD”) (Figure 2A, Table 1A). Young females at low density (“LD”) had the highest fecundity, whereas HD females of the same age laid only about half as many eggs, similar to mid-aged and older females that experienced HD throughout their adult life. This effect of age was consistent when the same set of young females were allowed to age (Figure S3); and in an independent experimental block with young LD, young HD and old HD females (Figure S4).

Concomitant with fecundity, oviposition preference for finger millet also decreased with age and density (Figure 2B, Table 1B), except for old HD females which oviposited randomly. Combining data across contexts, females with high fecundity laid more eggs in finger millet (Spearman’s rho = 0.303, $p < 0.001$; Figure 2C, Figures S5C, S5E). However, fecundity and preference were not correlated within a given

female context (except for aged LD females; see Figure S6 for additional experimental blocks), indicating more complex interactions between age, fecundity, and density (Table 1B, Figure S5). For instance, the relationship between fecundity and preference depended on competition. Under low density, preference for finger millet increased with fecundity; but females from a high-density context did not change their preference as fecundity increased (Figure S5F). Similarly, competition had opposite impacts on how young vs. old females allocate their eggs (Figure S5G). Under low density, old females became more conservative in resource use (relative to young females); whereas under high density, older females were more likely to prefer the new resource (finger millet).

The changing preference of young HD females when allowed to age under low density presents an interesting case. These females continued to show a strong preference for wheat (typical of HD females) despite experiencing LD for 4 weeks (compare young HD vs. aged, Figure 2B), and also failed to exhibit the high fecundity that is commonly observed at low density (Figure 2A). Thus, the impact of early experience with HD seemed to last for a very long time. Another interesting group is old HD females, who did not prefer wheat as predicted by the age- and density- dependent trends in other females. Hence, preference may shift non-monotonically as females experience high density for different time intervals. Nonetheless, it is clear that age and density present appropriate contexts that influence two key components of oviposition behaviour. Therefore, we proceeded with measuring the fitness consequences of these divergent context-dependent resource preference behaviours.

Fitness landscapes predict consequences of divergent oviposition behaviour

To quantify the impact of the full range of potential oviposition choices on fitness (Figure 1, Experiment 2), we allowed females to lay eggs in wheat and then manually distributed each female's eggs in wheat and finger millet patches. To include the widest possible range of fecundity (Figure 2A), we sampled females from three different contexts (young LD, young HD, and old HD females), and measured three metrics of offspring fitness (Figure S7). Across female contexts, offspring survival was largely invariable (~75% offspring survived). However, young LD females produced twice as many offspring as females

from other contexts (~20 vs. ~10 per female), although they had the slowest development (~25% offspring completed pupation in 3 weeks, vs. ~50-75% for young HD and old HD females). Thus, distinct oviposition behaviours associated with different female contexts can dramatically alter offspring fitness (see results of statistical modelling, Table 1C, Figures S8-S10). Notably, offspring development rate was strongly negatively correlated with female fecundity as well as total offspring (Figure 3A–B, Figure S8D), reflecting a well-known density-regulated tradeoff between offspring number and development in this species (Sokoloff 1974).

To visualize the impacts of oviposition behaviour on fitness, we used data for each fitness component (Figures 3C-E) to construct complete fitness landscapes as a function of the two key aspects of oviposition behaviours (female fecundity and oviposition choice; Figures 3F-H). Since the landscapes encompass the entire range of possible oviposition behaviours, they likely represent the “true” underlying landscapes for all females offered a similar choice between wheat and finger millet. Recall that females from different contexts exhibit distinct combinations of fecundity and preference (Figure 2), such that they would occupy different positions in these landscapes.

As expected, the fitness landscape for survival was relatively flat (focus on the contours, ignoring triangles; Figure 3F) – female fecundity and oviposition choice influenced offspring survival only in interaction with age and density (Table 1C, Figure S9). However, landscapes for the other two fitness components paint a more interesting dichotomy. For development rate, the landscape predicts a fitness optimum at low fecundity and low preference for finger millet; with generally rapid development at low fecundity regardless of preference (Figure 3G; fecundity and egg allocation independently alter development rate, Table 1C). In contrast, offspring production is maximized at high fecundity and strong preference for finger millet with a relatively weak impact of preference (Figure 3H, Table 1C). These contrasting predicted fitness optima for offspring development rate and total number of offspring largely reflect the underlying negative tradeoff between the two (Figure 3B, independent experimental blocks in Figure S11), primarily mediated by fecundity (Figure 3A).

Separate fitness landscapes constructed for each female context generated similar patterns, indicating that the fitness landscapes are robust (Figures S12, S13). We also confirmed that the landscapes accurately predict the fitness consequences of any combination of female fecundity and oviposition choice. In an independent experiment, we allowed females to express their oviposition preference (used to predict fitness) and measured the fitness consequences of their choice (Figure 1, Experiment 3). Observed female fitness matched predictions from the original landscape (compare the triangle colour with background colour, Figures 3G–I; Table S1, $p > 0.05$ for all three fitness parameters), even though the oviposition behaviour of old HD females in this experiment was different from what we had observed in Experiment 1 (comparison shown in Figure S4). Thus, fitness landscapes generated by scrambling the inherent association between female fecundity and preference and fitness accurately predicted the fitness consequences of diverse oviposition behaviours.

Females from different contexts use alternate adaptive oviposition strategies

The fitness landscapes generated above suggest two general oviposition strategies that each increase different fitness components – high preference for wheat with low fecundity, or high acceptance of finger millet with high fecundity. To explicitly connect prior female context with these strategies, we asked whether context-dependent behaviours are consistent with either of these predicted fitness peaks. To do this, we used the observed context-specific oviposition behaviours described in Figure 2, which represent females from diverse age and density contexts. We predicted the fitness outcomes for each context by overlaying the median values of female fecundity and preference onto the landscapes for each fitness component. As expected, females from different contexts were positioned widely across the landscape (Figures 3I-K). As noted earlier (Figure 2A, Table 1A), females that were older or experienced high density generally had low fecundity; whereas younger females or those at low density laid many more eggs. At the same time, they also had divergent oviposition choices. In light of the fitness landscapes, we can connect these contrasting patterns, now revealed as alternate adaptive strategies. For instance, young LD females were close to the peak for total offspring, whereas young HD females

produce fewer, rapidly-developing offspring. Distinct oviposition behaviours thus place females close to different locally adaptive fitness peaks.

Why don't all females maximize the same component of fitness? We suggest that this is partly explained by the tradeoff between offspring number and development rate, mediated by resource availability. At high population density, offspring face strong resource competition (Sokoloff 1974), likely imposing selection for females to produce faster-developing offspring. In contrast, under conditions of resource plenty (e.g. low population density), females can afford to lay many more eggs that develop slowly. Hence, females that have experienced high density lay fewer eggs and preferentially place them in wheat, where offspring develop much faster than in finger millet. In contrast, females that have only experienced low density can increase fecundity at the cost of offspring development rate, and can hence better utilize the suboptimal finger millet patch. However, fecundity is constrained by age (older females cannot lay more eggs), further altering females' placement on the fitness landscape (Figure 3I-K). Thus, age and density contexts primarily alter female fecundity, and females accordingly modulate their oviposition resource choice to optimize either total offspring or offspring development rate.

Although the fitness landscapes were generated using females from only three contexts, we could also use them to predict fitness for other contexts (mid-aged, aged LD and aged young HD), using only their oviposition behaviours. Strikingly, females from the two "aged" contexts also present divergent outcomes, though both (young HD and young LD females) were aged for 4 weeks under identical LD conditions. Their distinct positions in the fitness landscapes are driven primarily by their distinct fecundity, indicating a long-lasting impact of early experience with high density. Aged young HD females show a dramatic reduction in offspring production (Figure 3K), but their increased preference for wheat increases offspring development rate (Figure 3J). Hence, context-specific behaviours may show context-specific maximization of distinct fitness components, some of which may tradeoff with each other. In summary, the complete fitness landscapes reveal that maternal context alters distinct fitness components by differentially influencing two key aspects of oviposition behaviour.

DISCUSSION

Here, we present the first comprehensive analysis of the linkages between females' prior context, their oviposition behaviour, and offspring fitness. By governing female behaviour, the contexts determine females' placement on the fitness landscapes, in turn defining their fitness. Thus, a context-specific interpretation of fitness is critical to infer optimality of specific behaviours. Importantly, to identify distinct local fitness peaks we need separate landscapes for each fitness component that explains maximum variation in context-dependent oviposition behaviours. For instance, if we only measured offspring development rate, we would incorrectly conclude that young LD females behave maladaptively. However, with our approach, we used the ecological selection faced by females in their prior context (here, high vs. low competition) to assess the adaptive consequences of their behaviour. Hence, we infer that under conditions of resource plenty (when their offspring are unlikely to face stiff competition), females can effectively maximize the total number of offspring even if they are slower-developing. Such context-dependent optimization of different fitness components may also explain prior cases of apparent maladaptive resource use. For instance, flour beetles exhibit seemingly maladaptive density-dependent niche contraction in a heterogeneous habitat containing wheat and corn (a poor resource) (Parent *et al.* 2014). Based on our current results, we suggest that the observed preference for wheat at higher densities may reflect optimization of offspring development rate or survival; whereas at low density, females maximized total offspring production. Importantly, by explicitly considering female context, we gain the ability to predict fitness outcomes relevant to the range of conditions experienced within an individual's lifespan. Thus, our results demonstrate the lack of a single global fitness peak for oviposition behaviour, and show that a change in context can shift female behaviour towards alternative fitness peaks.

How generalisable is this suggested coupling between context-specific behaviour and fitness? Here, we considered two very broadly applicable contexts – age and experienced population density (competition)

– that differ both across individuals in a population and across an individuals' lifespan in many species. In *Tribolium*, transitions across contexts are expected to occur in association with population growth and dispersal events (Ziegler 1976, 1977; Gurdasani *et al.* 2018, 2019). Based on our findings, we suggest that species that experience such within-lifetime changes in context may also evolve context-specific oviposition behaviours that result in optimization of distinct fitness components. Indeed, ageing is universal and change in competition is likely a common feature of the life history of many organisms; both factors can impact oviposition. Mechanistically, any change in context that alters female body condition could influence resource allocation towards competing aspects of fitness (reflecting tradeoffs), ultimately determining oviposition behaviour (Papaj 2000; Jervis *et al.* 2005; Berger *et al.* 2008). Hence, we can broadly frame our results to make generalized predictions about the context-dependent optimization of fitness in light of widespread natural phenomena such as ageing and density changes (Figure 4). Of course, the exact fitness components that face selection or trade off across contexts will likely vary across species or environments. Even so, we suggest that the core axes that determine the impact of context on behaviour – age and density – should be widely applicable.

Our results show that females in different contexts can optimize different fitness components that trade off with each other. How does preference evolve, given that female behaviour is pulled in opposing directions across their lifetime? Broadly, frequent changes in selective context during the evolutionary history of a species could lead to the observed strong, specific associations between female context and expressed oviposition behaviour. We speculate that in *T. castaneum,* instead of selection acting independently on both fitness components, only offspring development rate evolves under strong selection. This is generally expected for species with a high intrinsic growth rate, such as pests and invasives (Sakai *et al.* 2001; Lagos *et al.* 2017). We further suggest that at different times during their life, females experience either intensified or relaxed selection to produce fast-developing offspring. For instance, prior work shows that larval development time in *Tribolium* increases under high larval or adult density (Park *et al.* 1939; Janus 1989). Thus, one way to increase offspring development rate under high resource competition is to decrease fecundity, and *T. castaneum* females may employ this strategy

(Halliday *et al.* 2019). Such selection on development rate may additionally drive high preference for optimal resources (here, wheat) under high competition, even within a narrow range of fecundity. However, how do we explain the random preference of old HD females in this framework? One possibility is that old females – especially after prolonged exposure to high density – are unable to make effective choices, and therefore allocate eggs randomly. Alternatively, the surprising niche expansion by old females may reflect a switch in the relative benefit of rapid offspring development in wheat, vs. the cost of increased resource competition when all females in the population make a similar choice. We speculate that the extended exposure of old HD females to high density crosses a threshold beyond which it becomes beneficial for females to accept the suboptimal but relatively unused finger millet patch. In contrast, under low competition (e.g. young LD females), selection on offspring development rate should be weak, allowing females to randomly allocate their eggs across habitats. Thus, distinct mechanisms may explain the convergent random preference behaviour of young LD and old HD females; this hypothesis needs to be explicitly tested. Nonetheless, our data suggest that both age and density have immediate impacts on fecundity, in turn altering female choice. Hence, fecundity and oviposition choice are inextricable; though most prior work on female context has focused on fecundity alone (Awmack & Leather 2002; Berger *et al.* 2008; Halliday *et al.* 2019). We suggest that for dispersing species that often encounter heterogeneous habitats, joint measurement of fecundity and resource choice is essential to fully understand oviposition behaviour. This is particularly important if changes in either behaviour influences different fitness components in different contexts, as observed here.

As mentioned above, our results indicate context-specific, adaptive female oviposition choices corresponding to local fitness peaks. However, we observe a surprising exception. Aged young HD females – despite a 4-week exposure to low density – continued to produce fast-developing offspring (which is optimal at high density) instead of increasing fecundity to maximize total offspring (which is optimal at low density). This suggests a long-lasting impact of prior context on behaviour, resulting in a significant reduction in lifetime reproductive success (producing ~15 fewer offspring than expected under low density). The failure to increase fecundity in response to a relaxation in adult competition is

surprising (Sonleitner 1961), because flour beetles routinely experience changes in population density that drive their population dynamics (Costantino & Desharnais 2012) and dispersal (Ziegler 1976, 1977; Gurdasani *et al.* 2018). As a result, we expect flour beetles to experience strong selection to rapidly respond to changes in competition and alter oviposition behaviours. Hence, the behaviour of aged young HD females appears to be maladaptive. We speculate that early physiological changes due to high density (Forchhammer *et al.* 2001; Stewart *et al.* 2005; Ramsay *et al.* 2006; Assie *et al.* 2008; Reading & Clark 2010) may be irreversible, preventing females from optimizing their oviposition behaviours even under favourable conditions. Such “carry-over effects” are widespread in the animal kingdom (Boonstra *et al.* 1998; Van Allen & Rudolf 2013; Burgess & Marshall 2014) and can impact the choice of the colonized habitat. Alternatively, the suboptimal suppression of fecundity may persist in the population due to weak selection, e.g. if old isolated (i.e., recently dispersed) females are rare in the normal life cycle of *T. castaneum* (Ziegler 1976). Further work is needed to understand this interesting phenomenon and distinguish between the various hypotheses.

Our results demonstrating context-dependent oviposition behaviour also have longer-term implications for species’ evolution. For instance, reduced female preference for the ancestral or optimal resource could initiate the process of niche expansion by exposing offspring to selection in a new habitat, or by influencing the resource preference and performance of subsequent generations. We showed previously that in flour beetles, larval experience with novel resources increases later use of the same resources (Ravi Kumar *et al.* 2018); a pattern that is also observed in many other insects (Jermy *et al.* 1968; Bernays & Weiss 1996; del Campo *et al.* 2001; Henniges-Janssen *et al.* 2011; Soler *et al.* 2012; Gretes *et al.* 2016). Hence, initial female acceptance of a new resource can increase its use by offspring, exposing offspring to selection and potentially improving their performance over time. Therefore, preference can lead and performance may follow when species colonize new habitats (Dethier 1954; Butlin 1987; Bernays 2001; Feder & Forbes 2008). More generally, random or no-preference behaviours have been suggested to drive the evolution of generalist species (Tabashnik *et al.* 1981; Singer 1983; Agosta 2006). Our work indicates that such effects may occur only when females from specific contexts

colonize new habitats (in our case, old HD and young LD females). Hence, the prior experience and history of colonizing females may be important determinants of successful niche expansion.

In conclusion, we suggest that it is important to quantify the linkages between female experience, body condition, oviposition behaviour, and offspring fitness to enable context-informed interpretations of optimality. Although a large body of prior work has partially addressed these links, we have lacked predictive power in new environmental or individual contexts. Understanding these links is also important to successfully use oviposition behaviours for pest management, such as in the push-pull strategy (Alkema *et al.* 2019). Here, we show an effective and reliable way to generate broad predictions about the fitness consequences of female oviposition behaviours. By dissociating females' preference from their fecundity, one can systematically cover the entire range of phenotype values that comprise the fitness landscape, including combinations of fecundity and preference that may not be directly or easily observed. One can then predict the fitness consequences of female behaviour in new contexts, without the need to measure fitness and preference in each scenario. Studies documenting evolutionary traps already highlight the power of explicitly considering longer-term historical context to understand behaviour (Hale & Swearer 2016; Singer & Parmesan 2018). We suggest that considering short-term female context is similarly important for understanding female behaviours as drivers of ecological and evolutionary niche expansion.

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AUTHOR CONTRIBUTIONS

VRK and DA conceived the work; VRK, DA and GA and designed experiments; VRK and GA conducted experiments; VRK and DA analysed data and wrote the manuscript; DA acquired funding.

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TABLES

Table 1. Summary of the minimal adequate models for factors explaining (A) female fecundity, (B) oviposition preference (shown in Figure 2) and (C) fitness components (shown in Figure 3). In (B), "preference" refers to observed female oviposition choice for finger millet; but in (C), the explanatory variable "preference" refers to manipulated egg allocation to finger millet. Significant retained terms are in bold.

(A) Female fecundity				
Starting maximal model	**Model type**	**Explanatory terms**	**F**	**p**
Fecundity ~ age*density	ANOVA	**age**	43.39	<0.0001
		density	102	<0.0001
(B) Observed female oviposition preference				
Starting maximal model	**Model type**	**Explanatory terms**	**Model estimate**	**p**
Preference ~ age*density*fecundity	Binomial GLM	**fecundity**	0.025	<0.0001
		age	-1.900	<0.0001
		density	0.380	0.87
		fecundity*age	0.033	<0.0001
		fecundity* density	-0.050	0.03
		age* density	1.920	<0.0001
(C) Fitness components				
Starting maximal model	**Model type**	**Explanatory terms**	**Model estimate**	**p**
		age	1.196	<0.001

Survival ~ age*density*fecundity*preference	Binomial GLM	**density**	-2.022	<0.001
		preference	-0.003	0.61
		fecundity	-0.01	0.4
		density*preference	0.033	<0.001
		age*fecundity	-0.071	<0.001
		density*fecundity	0.106	<0.001
		density*preference*fecundity	-0.002	<0.0001
Development rate ~ age*density*fecundity*preference	Binomial GLM	**age**	-0.968	0.003
		density	0.545	<0.0001
		preference	-0.006	<0.0001
		fecundity	-0.092	<0.0001
		age*fecundity	0.060	0.001
Total offspring ~ age*density*fecundity*preference	Poisson GLM	age	2.3980	0.08
		density	-1.4200	<0.001
		preference	-0.0500	0.98
		fecundity	0.4490	<0.001
		age*preference	-0.1740	0.04
		density*preference	0.1766	0.04
		age*fecundity	-0.5196	0.09
		density*fecundity	0.9879	<0.001
		preference*fecundity	0.0080	0.91
		age*preference*fecundity	0.1445	0.03
		density*preference*fecundity	-0.1454	0.02

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FIGURES

Figure 1. Experimental design. (A) Overview of key experiments (B) Details for experiment 2, used to generate fitness landscapes as a function of female fecundity and egg allocation across resource patches (W = wheat flour, FM = finger millet flour).

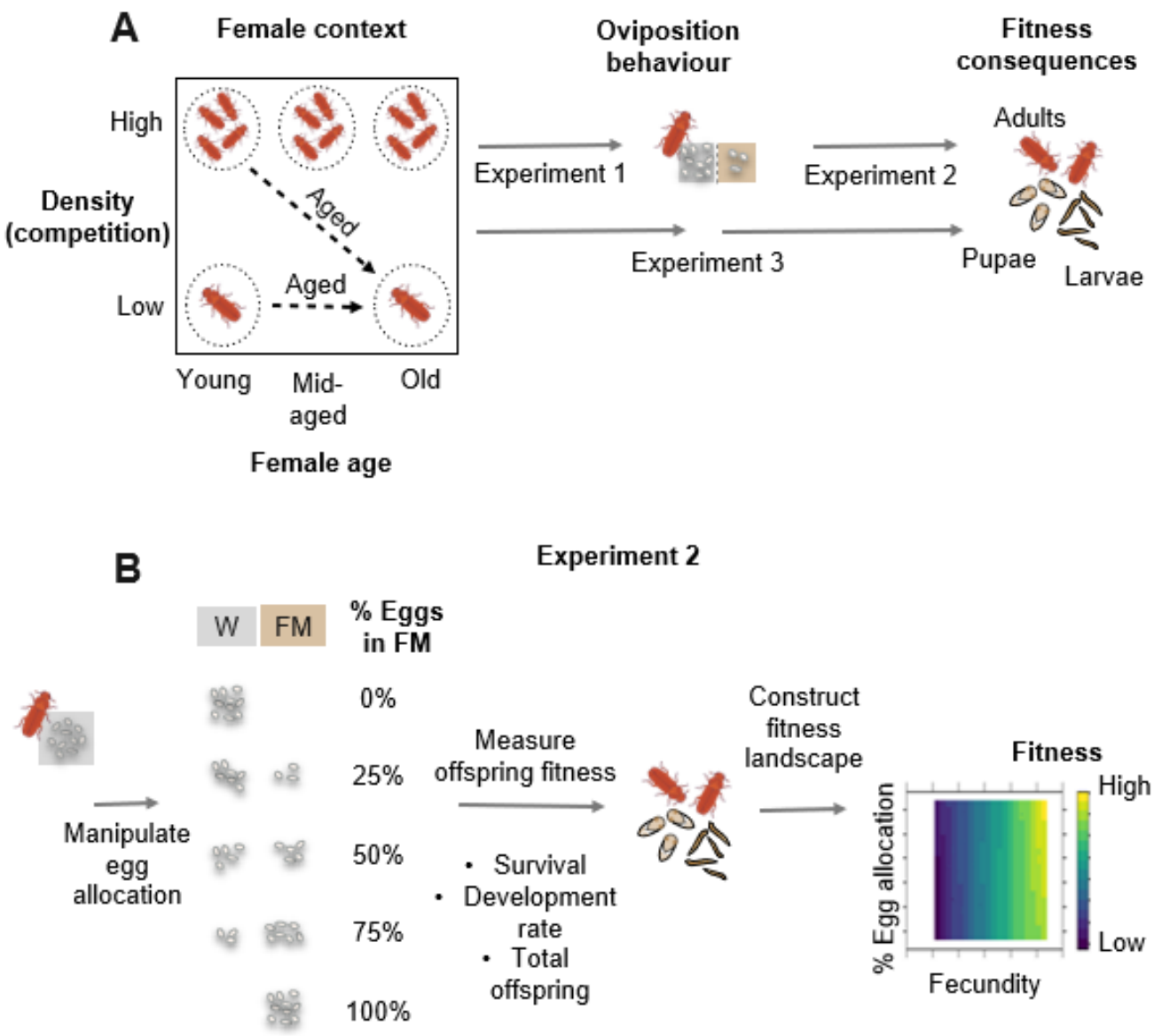

Figure 2. Oviposition behaviours of females from different prior contexts (Experiment 1). (A) Total fecundity and (B) % Eggs laid in finger millet (FM) in a two-patch habitat ("LD": low density, "HD": high density). Boxplots are coloured by female context; darker shades of a given colour represent the same set of females after ageing. Boxplots connected by the same letter are not significantly different, as estimated by a binomial generalized linear model. (C) Correlation between total fecundity and preference for finger millet for females from each context (for aged LD females, Spearman's rho = 0.315; ns = correlation not significant); lines indicate best-fit linear regressions for each context. Each point represents data for a single female; large filled circles indicate the median fecundity and preference for females from a given context; points and lines are coloured by context, as in panels A and B.

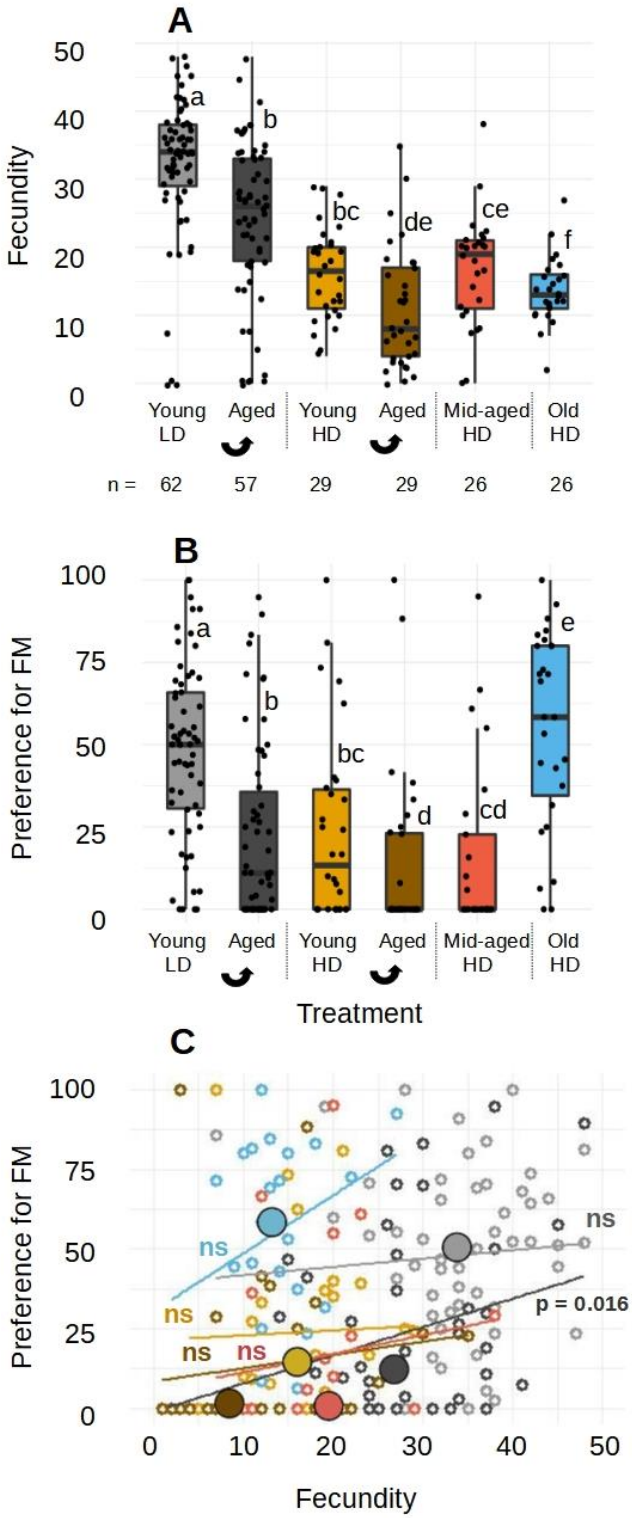
A
Fecundity
50
40
30
20
10
0
a
b
bc
de
ce
f
Young LD
Aged
Young HD
Aged
Mid-aged HD
Old HD
n = 62 57 29 29 26 26
B
Preference for FM
100
75
50
25
0
a
b
bc
d
cd
e
Young LD
Aged
Young HD
Aged
Mid-aged HD
Old HD
Treatment
C
Preference for FM
100
75
50
25
0
ns
ns
ns
ns
ns
p = 0.016
0
10
20
30
40
50
Fecundity

Figure 3. Complete fitness landscapes predict the fitness consequences of female oviposition behaviour in diverse contexts. Linear relationship between offspring development rate and (A) maternal fecundity and (B) total offspring (colour scheme as in Figure 2; n = 96 for young LD; n = 92 for young HD; n = 80 for old HD). Each point indicates data for a single female. (C-E) Measured fitness values (indicated by the z-axis color bar on the right) for individual females for each egg allocation treatment (Experiment 2; n = 16-20 per egg allocation) spanning their natural fecundity range. Points are slightly jittered along the y axis for clear visualization. (F–H) Fitness landscapes generated for each fitness component using loess smoothing on data shown in (C-E). For validation, landscapes are overlaid with data from an independent experiment (Experiment 3) where we measured both oviposition preference (which determines the position of each triangle in the landscape) and offspring fitness (which determines the colour used to fill each triangle). A close match in the colour of the triangle and its background indicates high predictability of fitness consequences (also see Table S1). (I–K) The same fitness landscapes overlaid with median observed oviposition behaviours for females from different contexts (obtained from Experiment 1, Figure 2), indicated by black filled circles. Lines connect cases where the same set of females were aged (indicated by “A”). The position of each circle thus indicates

the predicted fitness values for females from a given context.

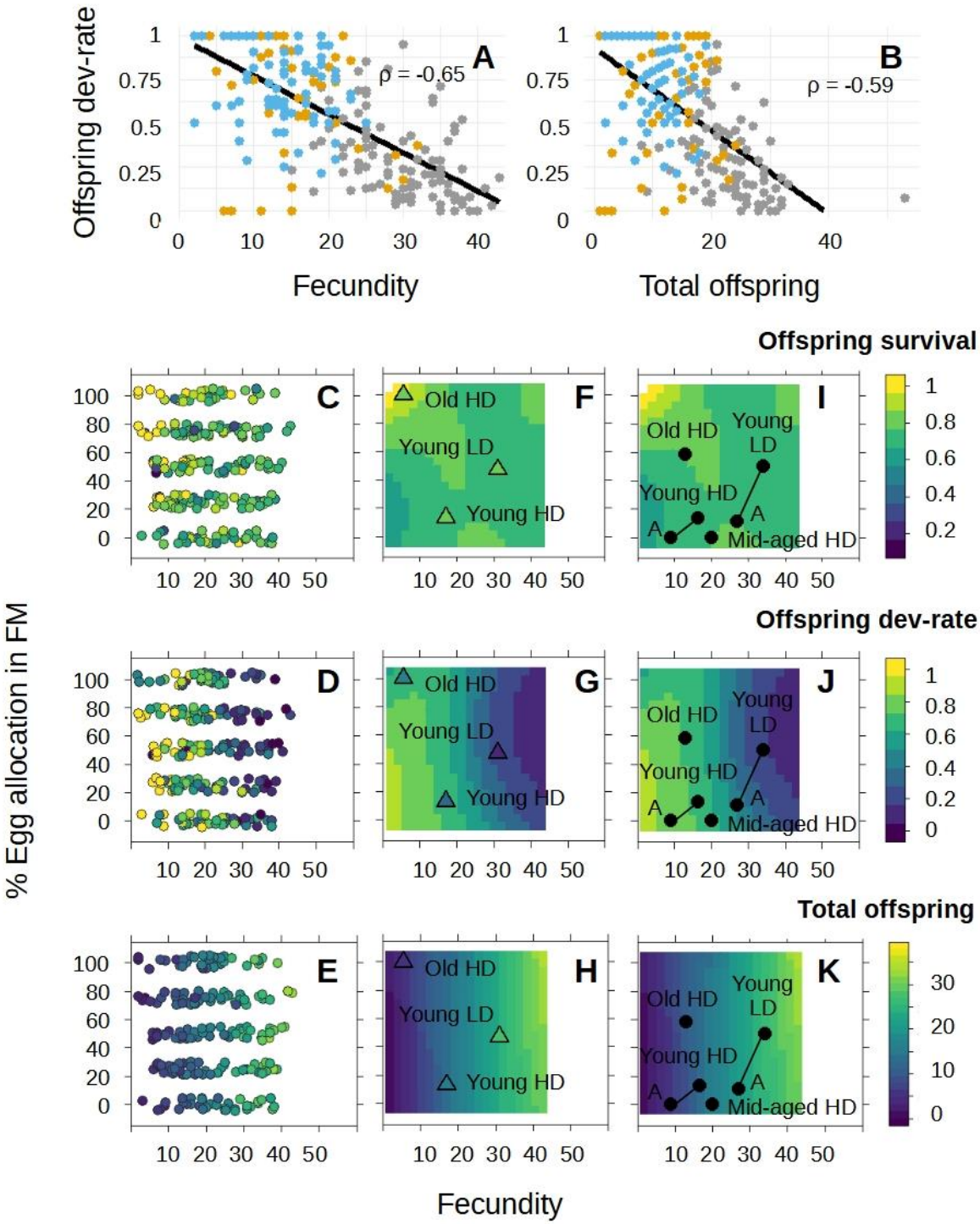
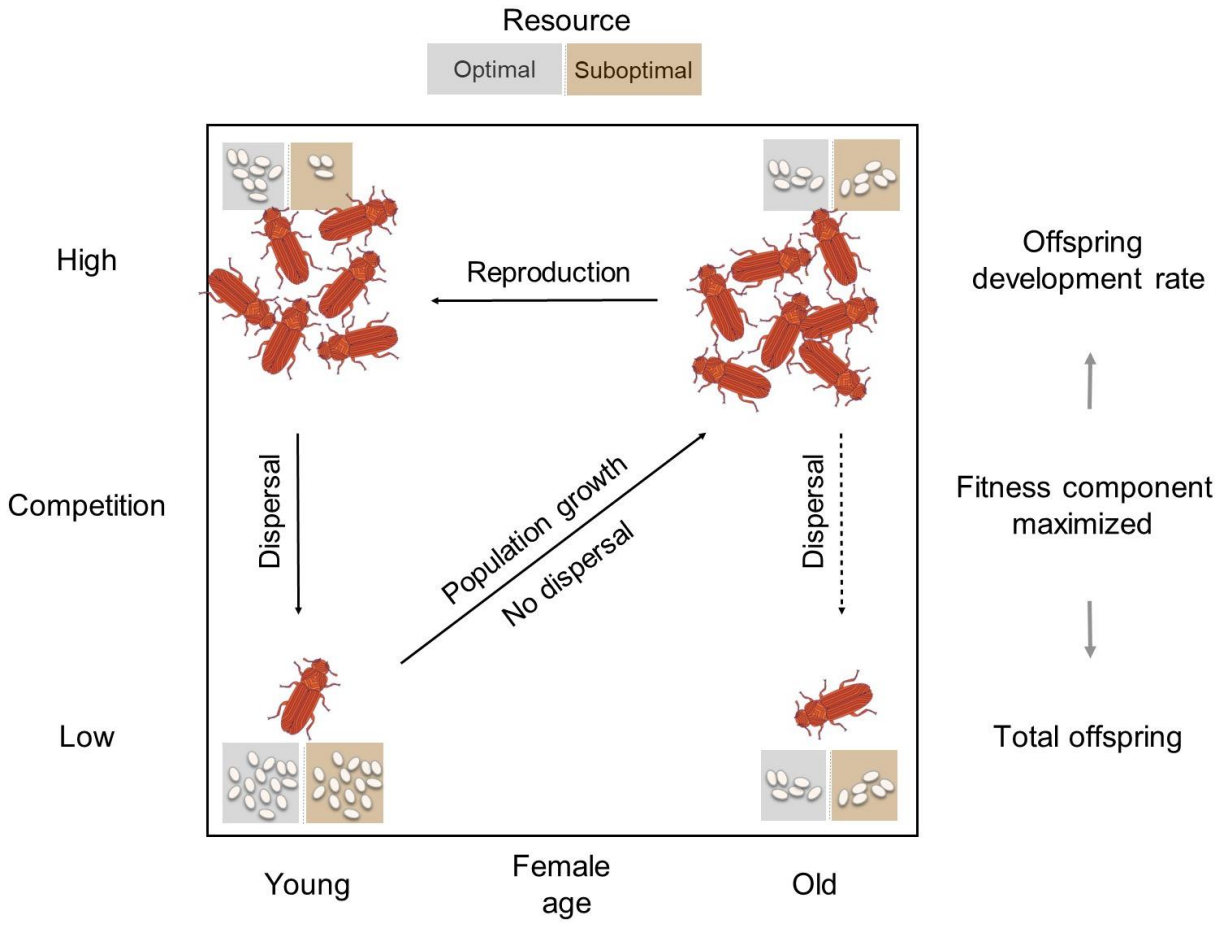
Figure 4. Schematic showing the proposed general linkages between female context, oviposition behaviour and its fitness consequences. Young females that experience low density (bottom left) may reproduce and establish a population as they age, increasing population density (top right). Reproduction will give rise to young females that also experience high density (top left), which may then show density-dependent dispersal, returning to a low-density condition where they can colonize a new habitat (bottom left). Old females may also disperse away from high density conditions (bottom right), though we do not have data on this aspect (indicated by dashed line).