



Parasitic Personalities: Consistent Individual Differences in Behavior in a Facultatively Parasitic Mite

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Abstract Host attachment is a necessary behavior in the evolution of parasitism. It is hypothesized that populations pass through a stage of facultative parasitism before the evolution of obligate parasitism. Previous research has revealed the impact of extrinsic factors on the expression of parasitic tendencies, but to our knowledge, the role of individual behavioral variation driving parasitic tendencies remains to be tested. Here, we used repeated behavioral assays to quantify attachment propensity and activity level of individual *Macrocheles muscaedomesticae*, facultatively parasitic mites of flies, from two different populations. Mites from both populations exhibited repeatability in attachment propensity and mites from one population exhibited repeatability in activity level. We did not find a relationship between an individual's activity level and attachment propensity. Our data suggest that facultative parasitism may not simply describe a phenotypically plastic strategy that responds to environmental cues, but perhaps that individual differences in parasitic tendencies may appear like facultative parasitism at the population or species level.

Keywords Activity · host attachment · *Drosophila* · *Macrocheles muscaedomesticae* · parasite behavior

Introduction

Variation in behavioral tendencies among individuals is a ubiquitous phenomenon (i.e., “animal personalities”; Sih et al. 2004; Mather and Logue 2013; Kralj-Fišer and Schuett 2014). Natural selection can operate upon this behavioral variation, but despite being thought of as an “optimizing agent,” between individual variation persists, even in the most vital behavioral traits. For example, male side-blotched lizards exhibit three different mating strategies within single populations, which are balanced by a rock-paper-scissors competition dynamic (Sinervo and Lively 1996). Individual variation in behavior can also be maintained via negative density-dependent selection, correlated selection, niche specialization, etc. (Dingemanse and Reale 2005). Furthermore, suites of correlated behavioral traits (i.e., behavioral syndromes) are often related to individuals' roles in ecological dynamics (e.g., foraging, mating, and movement Sih et al. 2012). Nevertheless, the role of individual variation in behaviors that potentially drive parasitic tendencies remains untested even though parasitic lifestyles are one of the most universal phenomena in zoology.

It is well accepted that parasites evolved from free-living ancestors (Poulin 2007). However, in most parasitic lineages, the mechanism by which this has occurred remains largely unknown (Price 1980; Poulin 2007). For ectoparasites, a commonly proposed hypothesis posits that intermediate levels of host-association (e.g., phoresy and facultative parasitism) serve as evolutionary stepping-stones to obligate parasitism (Luong and Mathot 2019). Given that processes like host-seeking

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and host-attachment are inherently behavioral, consistent between-individual differences in behavior may have played a role in pivotal steps in the evolution of parasitism.

Macrocheles muscaedomesticae (Scopoli 1772) is a predatory mite that commonly inhabits decomposing environments worldwide, feeding on small invertebrates (Wade and Rodriguez 1961; Jalil and Rodriguez 1970; Krantz 1998). Adult female mites attach to flies as a means of dispersal, causing host flies to suffer physical (Luong et al. 2015) and physiological costs, even after mite detachment (Luong et al. 2015). Although equivocal, there is evidence to suggest that *M. muscaedomesticae* occasionally feeds on fly hosts while attached (e.g. Jalil and Rodriguez 1970; Abo-Taka et al. 2014), and the congener *M. sabbadius* has been shown to feed on fly hemolymph (Polak 1996). Thus, we consider this mite to be a facultative parasite. Under laboratory conditions, some females will attach to a fly host within seconds upon exposure, while others postpone or pass on the opportunity altogether (pers. observation). Given that these individuals are raised under identical conditions with *ad libetum* resources, and given that attachment behavior is a heritable trait (Durkin and Luong 2018), the persistence of variation in attachment suggests that fundamental differences among individuals may play a role in the expression of parasitic behaviors.

Here, we quantify behaviors of individual *M. muscaedomesticae* from two lab populations generated from wild-caught mites in Alberta, Canada and Florida, USA. Specifically, we ask (1) do individual mites exhibit consistent between individual differences in host-attachment propensity? And, given that an animal's proclivity to rely on a host for dispersal may depend on its own level of motility (Bartlow et al. 2016), we ask (2) do individual mites exhibit consistent between individual differences in activity level and (3) does a mite's activity level predict its attachment behavior? Lastly, (4) we tested for evidence of population differences in activity levels and attachment behavior.

Materials and Methods

The Albertan *M. muscaedomesticae* culture was established from roughly 100 adult female mites attached to *Drosophila* spp. flies collected from compost in Edmonton, Alberta, Canada in Autumn 2013. The Alberta mite population was maintained in Edmonton, AB until February 2019, when it was moved to

Gainesville, FL. The Florida population was established from roughly 10 mites attached to *Drosophila* spp. flies collected from compost in Gainesville, Florida USA in Spring 2019. Mites were maintained in ventilated 4 L plastic containers with wheat bran and wood chips moistened with distilled water and inoculated with wild-caught Rhabditid nematodes from M. Polak at the University of Cincinnati (OH, USA) for food. Fresh ingredients were added weekly. For the duration of these experiments, both mite cultures were maintained at ambient lab conditions (23 °C, 33% RH) in Gainesville, FL. Host fly (*D. hydei*) cultures were established from flies collected from the same compost in Florida. Flies were maintained at ambient lab conditions (23 °C, 33% RH) on BDSC cornmeal food (<https://bdsc.indiana.edu/information/recipes/bloomfood.html>).

All assays were measured from age-structured virgin female mites. We controlled for age and reproductive status by isolating female *M. muscaedomesticae* deutonymphs into 29.5 mL plastic cups containing roughly 10 mL of culture medium containing nematodes. *M. muscaedomesticae* are deutonymphs for approximately 24 h and mate immediately upon adult eclosion (Wade and Rodriguez 1961). By isolating deutonymphs, females were the same age (within ~24 h) and virgin. Deutonymphs remained in their plastic cup for three days to allow for complete adult development before behavioral measurements. We measured the activity level of each mite three times, 24 h apart. Subsequent to activity measures, we measured the attachment behavior of each mite three times, 24 h apart. After each behavioral measurement, mites were placed into a new labeled 29.5 mL plastic cup filled with 10 mL of new nematode culture medium.

Bioassays were performed in Gainesville, FL at ambient lab conditions (23 °C, 33% RH) between 09:00 and 16:00 h. Activity level was measured as the mean number of lines crossed in a 9 cm petri-dish atop a 1 cm² grid during a five-minute period. Each mite was placed into a petri-dish lined with a piece of damp filter paper and given a 15-min acclimation period before we began recording the number of lines the mite crossed for a further five minutes. Attachment behavior was measured as the number of mite attachments out of three host exposure assays (0/3, 1/3, 2/3, or 3/3 times). Each mite was placed into an exposure chamber, constructed from a 200 µL pipette tip reduced to half its length (~1.5 cm) and stoppered with cotton. To reduce heterogeneity in host resistance behavior, the cotton was pushed far enough into the chamber to limit fly

mobility while still allowing the mites free movement. Mites were exposed to the fly for 60 min and then scored as “attached” or “unattached” at the end of the 60 min. The fly was then killed by crushing the thorax with fine forceps, taking care to not injure an attached mite. Attached mites were gently brushed off the deceased fly using a small paintbrush and transferred to a new labeled cup. Unattached mites were simply transferred from the exposure chamber to a new labeled cup using a paintbrush.

All data were analyzed with R 3.5.2 (R Core Team 2018). We used the “rptR” package (Stoffel et al. 2017) to test for repeatability (i.e., interclass correlation; Nakagawa and Schielzeth 2010) in our two behavioral measures, employing 1000 parametric bootstraps. We adjusted for trial order, for each experiment, and we used a binary error structure when testing for repeatability in attachment and a Poisson error structure when testing for repeatability in activity.

We examined whether an individual’s mean activity score across all trials was correlated with its attachment propensity (number of attachments / number of host exposures) using a Pearson product-moment correlation. Lastly, we explored whether the *M. muscaedomesticae*

populations were significantly different in each of our two personality measures. We compared mean activity level between the two populations using a t-test after verifying that the distributions of mean activity were normal (Shapiro-Wilk test; Alberta population: $p = 0.760$; Florida population: $p = 0.243$). Values of attachment propensity were not normally distributed (Shapiro-Wilk test, both $p < 0.001$), so we used the “coin” package (Hothorn et al. 2006) to conduct a Mann-Whitney U test that accounted for the presence of ties to explore whether the populations differed in attachment levels.

Results

Activity level was weakly repeatable in the Alberta *M. muscaedomesticae* (original scale $R \pm SE = 0.146 \pm 0.074$; $p = 0.014$; 95% CI = 0.003 to 0.294; Fig. 1a). In contrast, there was no significant repeatability in the activity of Florida mites (original scale $R \pm SE = 0.035 \pm 0.069$; $p = 0.367$; 95% CI = 0 to 0.231; Fig. 1b). Attachment was highly repeatable for the Alberta mites (original scale $R \pm SE = 0.622 \pm 1.524$; $p < 0.001$; 95%

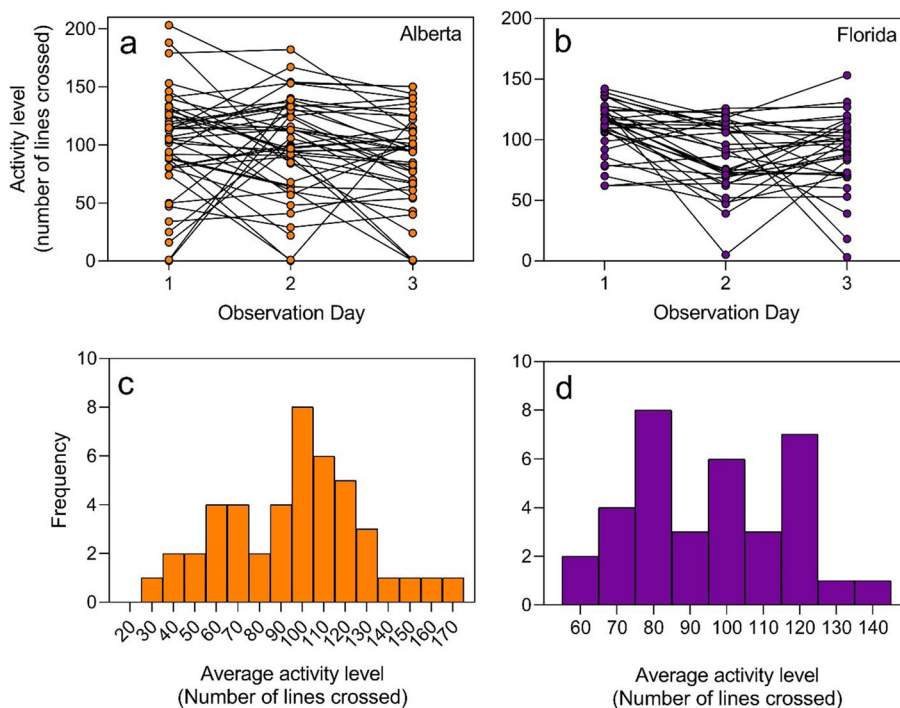


Fig. 1 Activity level (measured as the number of lines crossed after 5 min of movement in a gridded petri dish) of individual mites from an Alberta, Canada population (a) and a Florida, USA population (b). Activity was assayed 3 times, 24 h apart for each

individual mite. Figures a and b illustrate the activity measures for each mite on days 1, 2 and 3 of observation. Figures c and d illustrate the frequency distribution of mean activity level for each mite in the Alberta (c) and Florida (d) populations

CI = 0.590 to 0.809) and moderately repeatable for the Florida mites (original scale $R \pm SE = 0.334 \pm 2.013$; $p = 0.007$; 95% CI = 0.004 to 1.174; Fig. 1b). Individual activity and attachment propensity were not correlated in the Alberta mite population ($r = 0.07$; $p = 0.69$). We did not test for this correlation in mites from Florida, given their lack of repeatability in activity level. Although the Florida (mean = 95.2 ± 29 lines crossed) and Alberta (mean = 95.9 ± 42 lines crossed) populations had similar measures of activity ($t = 0.20$; $p = 0.84$; $df = 83.116$), the Florida population exhibited significantly higher mean attachment propensity (Mean = 0.69 ± 0.35 SD) compared to the Albertan population (Mean = 0.17 ± 0.29 ; $Z = 5.353$; $p < 0.001$; Fig. 2).

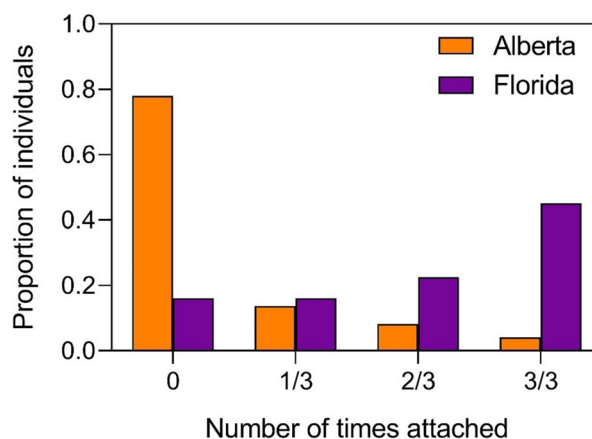
Discussion

Consistent between-individual differences in host-attachment behavior may have important implications for the ecology and evolution of ectoparasitism. We found that mites from both populations exhibited repeatability in host-attachment behavior. This highlights the potential for facultatively parasitic mites to exhibit multiple strategies (free-living and parasitic) consistently rather than in response to the environment alone. Other studies have focused on facultative parasitism at the population level, linking the propensity for parasitic behavior with external factors like temperature, habitat quality, and population density (Stasiuk et al. 2012; Durkin and Luong 2018, 2019). Here, we provide the first examination of differences in intrinsic parasitic strategies at the individual level.

Fig. 2 Attachment propensity (measured as the number of fly attachments after 3 host exposures) was repeatable at the individual level in female *Macrocheles muscaedomesticae* from Alberta, Canada (a), and from Florida, USA (b). Florida mites exhibited higher attachment propensity compared to the Alberta population

Activity level was significantly repeatable in Alberta mites but not Florida mites. Although all of our assays were conducted under identical laboratory conditions, our Alberta population had spent 6 years (~300 generations) under laboratory conditions whereas our Florida population had only spent two months in laboratory conditions. A meta-analysis by (Bell et al. 2009) found that behavioral measures are more repeatable under field conditions compared to laboratory conditions, where greater environmental variance in the field might allow the expression of more behavioral variation among individuals (Bengston et al. 2014); but see (Witsenburg et al. 2010) which demonstrates greater behavioral repeatability for individuals taken from laboratory populations compared to individuals in the field. Because these two populations differed in a variety of ways (e.g., time spent in lab, environmental characteristics, founding population size), we are unable to identify the underlying mechanism driving this difference in attachment behavior. However, our primary goal was not to compare these populations, but rather to verify that consistent individual differences arise in multiple populations. More studies are needed to identify whether laboratory conditions erode or amplify behavioral consistency in these facultatively parasitic animals, such as monitoring the behavior of populations every several generations in the lab.

There was no relationship between activity level and attachment propensity in individual mites from the Alberta population. There are a couple of potential explanations for the apparent lack of behavioral correlation between activity and host attachment in these mites. First, our experimental methods may have prevented us from detecting this relationship. For example, we measured



behavior in a single environment, but behavioral correlations can be context specific (Coleman and Wilson 1998). It is possible that future studies, in which behaviors are assayed in multiple environments, could reveal a correlation. Furthermore, our activity and attachment assays were not paired. We measured activity level the first 3 experimental days and attachment on days 4,5 and 6. Adult females live 11 ± 5.23 days (Durkin et al. 2019). Thus, our experiments lasted approximately half of the mite's lifetime, and senescence could affect their behavior. Future studies that alternate between activity and attachment assays would control for the effects of senescence. Second, activity and attachment behaviors may not be coupled in these mites for biological reasons. For example, *M. muscaedomesticae* is a predator and may rely heavily on its mobility. Thus, we may expect natural selection to decouple these behaviors. Perhaps activity and attachment behavior are regulated by independent mechanisms (genetics, physiology, etc.) and are therefore unlikely to be coupled (Sih et al. 2004). Behaviors associated with host-seeking (potentially exploration or aggressive behavior) might be expected to exhibit a stronger correlation with attachment than activity.

Attachment propensity was much higher in the Florida *M. muscaedomesticae* population compared to the Alberta population. There may be some question as to whether repeatability in unattachment is biologically meaningful. Lack of attachment could result from physical inability or weakness due to senescence. We tried to control for these confounding variables as best we could by first limiting host mobility to allow mite attachment and second eliminating data from mites that died during 3-day period of attachment assays. There are a few potential reasons for the differences in attachment prevalence between the two populations. Although we generated both mite populations from mites attached to wild-caught *Drosophila*, the Alberta population has been maintained in the lab without host-exposure for six years and attachment behavior in this species has previously been demonstrated to be heritable ($h = 0.17$; Durkin and Luong 2018). Thus, in the absence of host exposure, and any selective pressures favoring attachment behavior, the Alberta mite population has likely lost some of its attachment propensity over time. However, it may also be that differences between Florida's and Alberta's environmental characteristics, like temperature and food availability, also influence attachment propensity at the population level. Future personality studies on allopatric *M. muscaedomesticae* populations

collected at a similar time could provide clarification on this issue. We would also like to note that all behavioral assays were performed on virgin females. Although this choice controlled for differences in mating status, it too may have influenced attachment propensity. For example, in a closely related mite species, mated females were found to be more likely to attach to flies compared to virgins (Luong et al. 2017). In nature, it is more likely that females would be mated than unmated. Thus, behavioral studies on mated *M. muscaedomesticae* may provide clearer insight to natural behaviors.

Classically, facultative parasitism has been thought of as a strategy driven by phenotypic plasticity, where individuals may be more or less likely to parasitize hosts based on extrinsic factors. Our data suggest that facultative parasitism may not simply describe a strategy in response to the environment, but rather that individual differences in parasitic tendencies (i.e., some individuals are parasitic while others are free-living) may appear like facultative parasitism at the population or species level.

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