

Effects of reproductive state and host resource experience on mating decisions in a walnut fly

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Prior experience with conspecifics or essential resources, as well as physiological condition, can have important influences on an animal's reproductive behavior. While effects of experience and physiological state (such as reproductive condition) are generally treated separately in theoretical discussions, they often interact. No previous study has attempted to distinguish effects of experience on physiological state from other effects of experience in the context of mating behavior. In a study of a walnut-infesting tephritid fly (*Rhagoletis juglandis*), we examined the effects of host fruit experience on mating behavior. We manipulated physiological state in terms of egg load (defined as the number of mature oocytes in a female's ovaries) independently of fruit experience to distinguish the effects of these variables. We found that females with high egg loads were significantly more likely to copulate than low-egg load females; the level of fruit experience had no effect on propensity to copulate, except via effects on egg load. In contrast, females with prior exposure to fruit copulated for a significantly shorter duration than control females, while egg load had no effect on copulation duration. These results suggest that female reproductive condition and exposure to essential resources can have important, albeit diverse effects on mating behavior. We discuss how distinguishing different types of variables may provide insight into sexual conflict over mating decisions, as well as which sex controls specific aspects of behavior. *Key words*: copulation duration, egg load, mating, prior experience, resource defense, sexual conflict. [*Behav Ecol* 16:528–533 (2005)]

Reproductive decisions such as mate choice, length of copulation, egg laying, and territorial defense have important fitness consequences for both males and females. Over the last two decades, it has been increasingly recognized that such decisions are shaped by a variety of social and environmental factors. In particular, experience with conspecifics has been shown to shape mating behavior across a number of taxa. For instance, Hebets (2003) showed that among wolf spiders, juvenile exposure to a specific male phenotype created an adult mating preference for that same phenotype. Similarly, Rosenqvist and Houde (1997) showed that exposure to males with different amounts of orange coloration influenced the mating preferences of female guppies.

In resource-based mating systems, experience with an essential resource such as a host plant or territory can also influence mating behavior. Male seaweed flies, for instance, are more likely to mount females if they have had prior exposure to seaweed (Dunn et al., 2002). Prokopy et al. (1989) showed that male apple maggot flies, which guard host fruit and mate with females as they arrive, increase their territorial behavior after gaining experience with the host fruit. Similarly, Hyman et al. (2004) showed that male song sparrows that previously held territories were more likely to engage in territorial defense than those that never held territories.

Authors of these studies frequently infer or imply that learning is the basis for effects of experience on behavior (Kodric-Brown and Nicoletto, 2001; Slagsvold et al., 2002; Wagner et al., 2001; White et al., 2002; Witte and Sawka, 2003). While such behavioral changes must sometimes reflect learning or imprinting, experience can also change behavior by altering an animal's physiological (including reproductive)

state. In *Drosophila* females, for example, mating induces rapid oogenesis as well as a host of behavioral changes, including reduced receptivity (reviewed in Chapman, 2001). In Caribbean fruit flies, mating experience elevates juvenile hormone titers in males, causing them to release pheromone at higher rates, which in turn leads to greater mating success (Teal et al., 2000). In piñon jays, experience with an abundance of piñon seeds leads to increased testis growth and earlier breeding (Ligon, 1978). In these examples, learning is unlikely to play a role in mediating these physiological changes and the resulting behavioral shifts; for instance, the changes in *Drosophila* behavior are directly mediated by male accessory gland products (Chapman, 2001).

Sometimes the underlying mechanisms mediating behavioral shifts can be unclear. Landolt (1994) showed that female papaya flies increased their remating frequency in the presence of host fruit; however, it is not clear whether this shift is mediated by learning or by some direct effect on physiological state. In another study, Grieco et al. (2002) showed that blue tits shifted their egg-laying date in response to food availability in the previous year and implied that this experiential change is a result of learning. It is not clear, however, whether this shift in response to experience is in fact a learned response or a biological clock adjustment based on physiology.

In short, the mechanisms underlying effects of prior experience on mating behavior can be difficult to distinguish, particularly in systems where experience mediates physiological change. Distinguishing between alternative mechanisms would give us a greater understanding of how different social, physiological, and environmental variables impact specific components of mating behavior, yet few studies have done this in a systematic fashion.

In a study of a walnut-infesting tephritid fly (*Rhagoletis juglandis*), we examined the effects of host fruit experience and physiological state on mating behavior. We manipulated physiological state in terms of egg load (defined as the number of mature oocytes in a female's ovaries) independently of fruit

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experience to distinguish an effect of experience on mating behavior due to egg load from other effects of experience. This system was of interest in part because exposure to host fruit is known to stimulate oogenesis and enhance egg load in females (Alonso-Pimentel et al., 1998) and because egg load was known to influence other aspects of a female's reproductive behavior (Alonso-Pimentel and Papaj, 1996a). We argue that distinguishing between these variables may be a way to gain insight into the mechanisms underlying mating decisions as well as providing insight into functional aspects such as sexual conflict over different components of mating behavior.

METHODS

Study system

Like other members of this genus, *R. juglandis* is characterized by a resource-defense mating system in which the males engage in territorial contests over walnut fruit. Females oviposit and larvae develop solely in the fruit. Females arriving at the fruit often mate during oviposition attempts (Papaj, 1994) in what sometimes appear to be "forced" copulations. Females mate with multiple males, and last male sperm precedence has been shown for this genus (Opp et al., 1990, 1996). Previous work with *R. juglandis* (Alonso-Pimentel and Papaj, 1996b) has shown that copulation duration is variable in this species, with longer matings occurring when the operational sex ratio is male biased and shorter copulations occurring when the population is female biased. Longer copulations are thought to benefit the male as a form of mate guarding. In southern Arizona, these flies exclusively use Arizona walnut, *Juglans major*, as a host plant, emerging between July and September from puparia in the soil. For this study, we used flies collected as larvae at six sites in central and southern Arizona in 2002. Pupae were maintained at 4°C prior to the study and warmed to room temperature (approximately 29°C) for approximately 5 weeks before eclosion.

Experiment 1

We separated flies by sex within 4 days of eclosion and placed them into 473-ml clear plastic cups containing water, yeast extract, and sugar cubes. Previous studies have indicated that sexual maturity of both sexes of *Rhagoletis*, and the onset of copulation, is not achieved until at least 6–8 days posteclosion; therefore, we are confident that the flies used in our study were virgins (Alonso-Pimentel and Papaj, 1996a; Boyce, 1934; Prokopy et al., 1972; Webster and Stoffolano, 1978). Flies were held in the cups for 7–8 days prior to testing. We created groups of high- and low-egg load females by exposing one group of females to a surrogate fruit (a 3.7-cm-diameter yellow plastic sphere) during the holding period. Males and control females were not exposed to fruit until the day of testing. This procedure causes experimental females to mature more oocytes faster than control females (Alonso-Pimentel et al., 1998). All holding cups were surrounded by white cardboard barriers to control for effects of extraneous visual stimuli.

On the day of testing, we isolated 10 males individually in clear plastic observation cups with a surrogate fruit suspended from the top of the cup. We randomly paired half of the males with a fruit-exposed female and half of the males with a control female for 1 h and observed (1) whether or not copulation occurred and (2) the duration of the first copulation in each cup, if a copulation occurred. At the end of each test, all the flies were frozen. We measured body size in all females because egg load in many insects, including this species, is positively correlated with body size (Alonso-

Pimentel et al., 1998). We additionally measured body size in males, reasoning that mating traits could conceivably vary with male size. Wing vein measurement was recorded for both males and females as a proxy for size as this measurement correlates well with body mass (mid-wing vein length; Alonso-Pimentel HA, unpublished data). We subsequently dissected females and counted the number of mature oocytes contained in the ovaries. Data were analyzed using JMP-IN statistical software (SAS Inc., Cary, North Carolina, USA).

Experiment 2

We conducted a second experiment in order to manipulate egg load independently of fruit experience. In this experiment, flies were again separated by sex as above, within 4 days posteclosion. We created groups of high- and low-egg load females by treating experimental flies with the juvenile hormone analogue methoprene. In flies, rising juvenile hormone titers trigger oogenesis, and topically applied methoprene has been shown to have virtually identical effects (Duan et al., 1995). We topically applied 1 μ l of 50- μ M methoprene (technical grade, greater than 95% purity, Zoecon Corp. (Palo Alto, CA); dissolved in acetone) to the abdomen of each fly in the experimental group using a microsyringe (10 μ l syringe, Hamilton Co, Reno, Nevada, USA). Control flies were treated with 1 μ l of acetone in the same manner. Prior to methoprene or acetone-only application, all flies were exposed to gaseous carbon dioxide for 30 s in order to facilitate handling. Again, flies were held for 7–8 days prior to testing, with conditions as in experiment 1 except that no surrogate fruit was present in any of the holding cups. Mating trials were conducted as above, with a surrogate fruit present.

RESULTS

Experiment 1—effects of surrogate fruit exposure

In experiment 1, we examined the effects of fruit exposure by exposing experimental flies to surrogate fruit. We conducted trials on a total of 190 pairs of flies. Mean body size of both females and males, as measured in terms of wing mid-vein length, was not significantly different between treatments (ANOVA: for females, mean = 1.62 mm, SE = 0.01 mm for both treatments, $F = 0.193$, $p = .66$; for males, mean = 1.52 mm, SE = 0.01 mm for both treatments, $F = 0.125$, $p = .72$). Mean egg load was significantly higher for females exposed to fruit than for control females (ANOVA: control mean = 15.7, SE = 2.0, fruit-exposed mean = 35.9, SE = 2.0, $F = 49.2$, $p < .0001$). In mating trials, copulations were more frequent when females had higher egg loads (Figure 1). The results of a nominal logistic regression revealed that, although fruit exposure influenced egg load, the likelihood to copulate depended on egg load directly and was independent of fruit exposure treatment (Table 1).

Copulation duration was strongly bimodal, with all copulations in both experimental and control groups lasting 400 s or less or 600 s or more (Figure 2). We therefore analyzed copulation duration as a nominal variable, where duration was either short or long. Copulation duration also differed between treatments, with pairs containing experimental females copulating for significantly shorter durations than control females (for control, 42% of copulations were short, for fruit-exposed, 70% were short; $\chi^2 = 5.1$, $p = .02$). However, in contrast to the results for likelihood to copulate, a nominal logistic regression revealed that fruit exposure itself rather than egg load per se accounted for this difference in duration (Table 2).

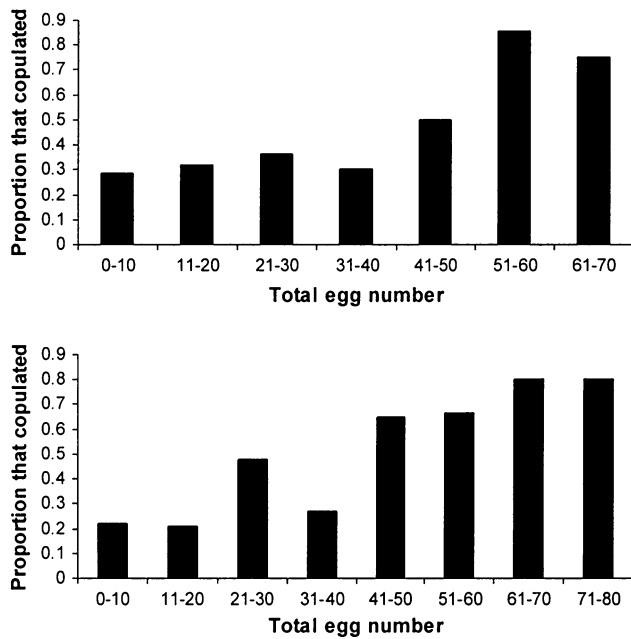


Figure 1

Propensity to copulate was higher when females had higher egg loads ($p < .01$ for experiment 1; $p < .0001$ for experiment 2; see Tables 1 and 3 for full results of the model). Results from experiment 1, fruit exposure, are shown in the top panel, while results from experiment 2, methoprene exposure, are shown in the bottom panel.

Experiment 2—effects of methoprene application

In experiment 2, we examined the effects of egg load on mating behavior independently of fruit exposure by exposing experimental flies to methoprene, a juvenile hormone analogue known to induce oogenesis. We conducted trials on a total of 150 pairs of flies. As in the first experiment, mean body size of both females and males, as measured by the length of the wing mid-vein, was not significantly different between treatments (ANOVA: for females, mean = 1.61 mm, SE = 0.01 mm for control, mean length = 1.62 mm, SE = 0.01 mm for methoprene, $F = 0.33$, $p = .56$; for males, mean = 1.52 mm, SE = 0.01 mm for both treatments, $F = 0.003$, $p = .95$). Mean egg load was significantly higher for methoprene-treated than untreated females (ANOVA: control mean = 14.4, SE = 2.2, methoprene mean = 39.3, SE = 2.2, $F = 65.2$, $p < .0001$). As in experiment 1, copulations were more frequent for females with a higher egg load (Figure 1), and again, this effect was independent of treatment (Table 3).

Copulation duration was again strongly bimodal in this experiment (Figure 2). However, in contrast to experiment 1, copulation duration did not depend on treatment; copulation duration was not significantly different between pairs with methoprene-treated versus untreated females (for control,

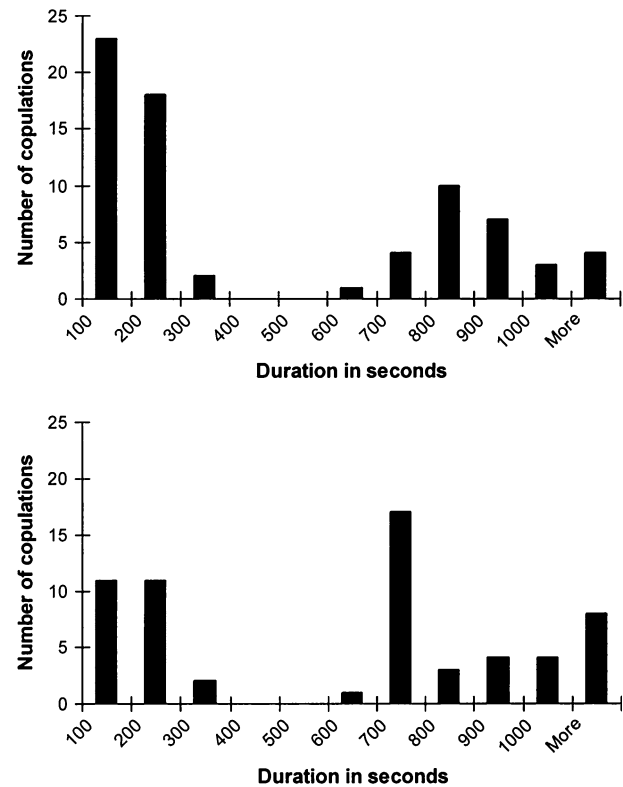


Figure 2

Copulation duration was strongly bimodal in both experiment 1 and experiment 2; thus, duration was analyzed as either short (400 s. or less) or long (600 s. or more). Results from experiment 1, fruit exposure, are shown in the top panel, while results from experiment 2, methoprene exposure, are shown in the bottom panel.

48% of copulations were short, for methoprene, 44% were short; $\chi^2 = 0.075$, $p = .78$). The egg load also had no effect on copulation duration.

DISCUSSION

In behavioral ecology studies of foraging, it has been known for some time that the effects of experience and physiological state can be confounded. Rosenheim and Rosen (1991), for instance, teased apart the effects of egg load and prior host experience on host-acceptance behavior in a parasitoid wasp (see also Henneman et al., 1995). Given a growing number of studies indicating that a female's prior experience as well as her physiological state influence mating behavior (see Introduction), it is important to address this issue in the context of mating dynamics.

The present study found evidence that both physiological state, in terms of egg load, and host experience independent

Table 1

Results of the nominal logistic regression model for propensity to copulate in experiment 1, fruit exposure

	Estimate	SE	χ^2	p Value
Intercept	1.180	0.305	14.93	.0001
Fruit exposure	0.238	0.190	1.57	.21
Egg load	-0.027	0.009	8.32	.0039
Fruit exposure \times egg load	0.013	0.009	2.19	.14

Table 2

Results of the nominal logistic regression model for copulation duration in experiment 1, fruit exposure

	Estimate	SE	χ^2	p Value
Intercept	0.47	0.519	0.83	.36
Fruit exposure	-0.708	0.333	4.53	.03
Egg load	-0.007	0.015	0.28	.59
Fruit exposure \times egg load	0.002	0.015	0.01	.90

Table 3
Results of the nominal logistic regression model for propensity to copulate in experiment 2, methoprene

	Estimate	SE	χ^2	<i>p</i> Value
Intercept	1.745	0.386	20.39	<.0001
Fruit exposure	-0.037	0.234	2.48	.11
Egg load	-0.051	0.012	19.18	<.0001
Fruit exposure \times egg load	-0.007	0.011	0.35	.55

of egg load, affect mating behavior. Moreover, different components of mating behavior responded to resource experience and physiological state in different ways. Whether or not a pair copulates was dependent on egg load, with greater propensity to copulate occurring among females with higher egg loads, and on whether high egg load was induced via methoprene or fruit experience. A female's experience with host fruit did not affect propensity to copulate except as it enhanced egg load (i.e., an indirect route of experiential effects indicated by the bold arrows in Figure 3A). In contrast, the length of a copulation depended on a female's experience with host fruit. This effect was not mediated via effects on egg load as egg load per se had no effect on copulation duration. Evidently, some other mechanism related to host experience, possibly learning, was at play (i.e., a potentially direct route of experiential effects indicated by the bold arrow in Figure 3B).

The results of experiment 2 support the inferences from experiment 1 that a female's experience with fruit rather than egg load per se accounts for differences in copulation duration, whereas egg load and not host experience per se accounts for differences in the propensity to mate. The consistency of results across experiments is critical to the strength of our inferences. In particular, inferences based on statistical patterns in experiment 1 potentially lack robustness as they are contingent on the validity of assumptions about sources of error. For example, the fact that egg load explains a significant amount of variation in the likelihood of copulation, whereas fruit exposure independent of egg load does not, may reflect a biological difference, as we infer and as is supported by experiment 2. However, the same pattern might also be obtained if, for instance, egg load was measured with less error than fruit exposure treatment was "measured." We feel that this difference in measurement error is unlikely; if anything, errors in measuring egg load are more likely, not less likely, than errors in measuring treatment, particularly as we isolated the effects of fruit exposure by using blinds around all cups in both experiments.

The fact that physiological state and prior experience can influence different aspects of behavior in different ways underscores the importance of distinguishing these variables. In addition to providing potential insights about mechanism, the type of variable impacting a specific component of behavior holds implications for the functional significance of that behavior; in particular, examining each variable separately may reveal patterns of sexual conflict over mating. While we can only offer speculation on the functional significance of the patterns in this study at this point, even speculation illustrates the importance of understanding the route by which experience exerts effects on behavior.

Functional aspects: physiological state

With respect to physiological state, in this case egg load, both female and male perspectives would seem to dictate that females of relatively higher egg load will copulate relatively more readily, as we found. This effect could reflect increased

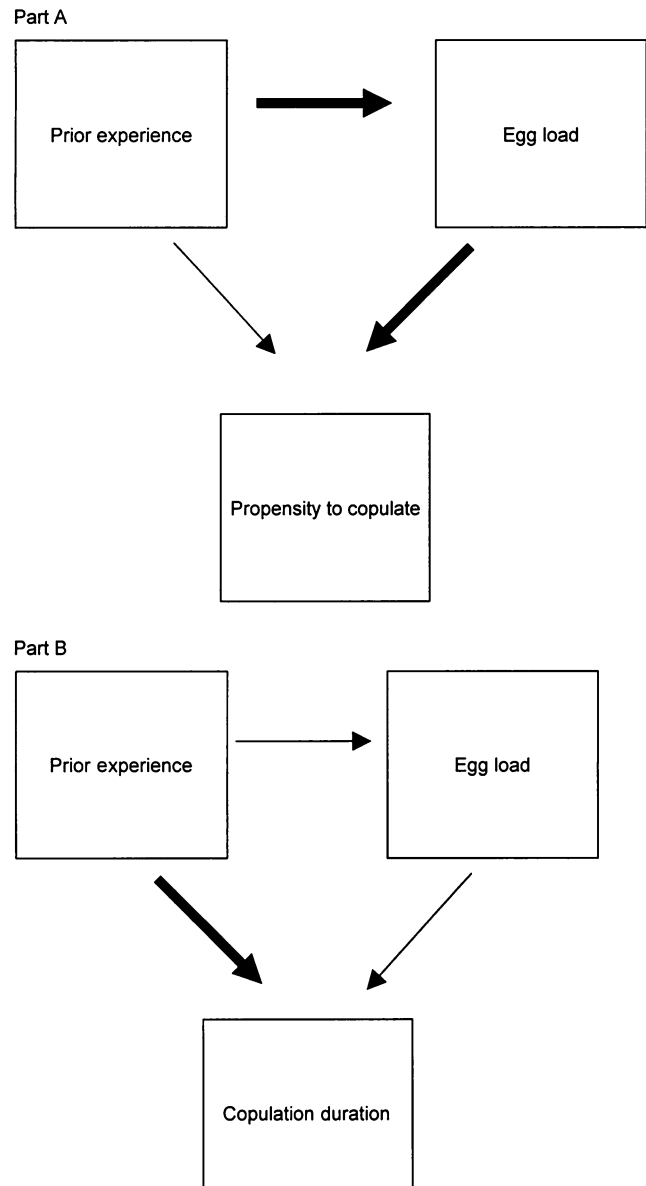


Figure 3

Egg load and prior experience have different effects on different components of mating behavior. Part A: Egg load directly determined propensity to copulate, whether high egg load was induced via fruit exposure or methoprene. Prior experience had no direct effect on propensity to copulate but had an indirect effect by increasing egg load in experiment 1. Part B: Prior experience had a direct effect on copulation duration, but egg load had no effect.

mating effort by the male, the female, or both sexes. Because oviposition facilitates oogenesis (reviewed in Papaj, 2000), females with high egg loads and available sperm can rapidly lay eggs and go on to develop multiple clutches, resulting in high fecundity. Females that maintain high egg load without possibility to lay fertile eggs, therefore, may pay a fitness cost in terms of reduced lifetime fecundity. From a virgin female perspective, this scenario would favor an increased propensity to copulate, perhaps even at the expense of mating with a low-quality male. Although we used virgins in our study, these results could also apply to already-mated females as they could also potentially benefit from copulating more readily when many eggs are mature (direct benefits, genetic diversity, and

genetic compatibility, to name three; see Vahed, 1998; Jennions and Petrie, 2000).

The increase in propensity to copulate when females carry a high egg load is consistent with the male perspective, as well. Studies have shown that males prefer to mate with females in better overall condition (Danielson-Francois et al., 2002) or advanced reproductive state (Kelso and Verrell, 2002). In particular, several studies with insects have shown that males prefer females with relatively larger abdomens, presumably a cue that she carries a higher egg load (reviewed in Bonduriansky, 2001). In walnut flies, males may also improve their chances of siring offspring by mating with high-egg load females as such females are likely to lay large clutches relatively quickly and prior to remating. This advantage is particularly meaningful given the form and intensity of sperm competition in this species: mating in the genus *Rhagoletis* and in other tephritid flies has been uniformly shown to be last male precedence (Opp et al., 1990, 1996; Saul and McCombs, 1993; Yamagishi et al., 1992), and female *R. juglandis* remate frequently in nature (Papaj, personal observation).

While the perspectives of both sexes appear to be congruent in terms of propensity to copulate with respect to egg load, the perspectives of the two sexes over copulation duration with respect to egg load appear to diverge. From a male perspective, a female with a high egg load may be a more valuable reproductive resource. Therefore, a male might engage in long copulations with high-egg load females for at least three reasons: (1) to preclude other males from mating with the high-quality female through contact mate guarding; (2) to ensure sufficient sperm transfer to fertilize all eggs, which may prevent a female from remating due to sperm depletion; or (3) to transfer sufficient sperm to flood out previously deposited sperm from rivals (Simmons, 2001). In contrast, from a female perspective, a female with a high egg load should copulate for a shorter duration, as long copulations could be costly in terms of reducing time available for laying eggs (Sherman, 1983). When females mate with multiple males, optimal mating strategies, including copulation duration, may differ between the sexes, and thus sexual conflict over reproductive decisions may arise (Stutt and Siva-Jothy, 2001). The observed absence of an association between copulation length and egg load in our study may be the net result of such conflict (cf. Simmons, 2001).

Functional aspects: prior experience

With respect to effects of prior experience independent of egg load (for instance, effects reflective of learning), a female perspective would seem to favor an increased propensity to copulate and shorter copulation duration for fruit-exposed females. One effect of fruit experience could be to provide information to the female about the quality and availability of host fruit. A fruit-exposed female has learned that high quality fruit are consistently available, and thus she would benefit from obtaining sperm quickly and allocating more time to laying eggs.

In contrast, males in experiment 1 were uniformly held without fruit prior to testing. Because male experience was not manipulated, the male perspective for propensity to copulate and for copulation duration should be neutral with respect to female experience. As such, our results with respect to prior experience reflect a congruence with the male perspective in terms of propensity to copulate (fruit experience did not determine propensity, consistent with the neutral perspective) and with a female perspective in terms of copulation duration (copulations were shorter for fruit-exposed females). This pattern implies that, in relation to effects of experience, copulation duration was under female

control, but the decision to copulate in the first place was under male control. Evaluating these inferences will require some independent means for assessing gender control over mating traits.

GENERAL IMPLICATIONS

As illustrated in the sections above, the perspective of an individual from the standpoint of changes in physiological state is not necessarily congruent with its decision from the standpoint of an experiential process such as learning. Thus, understanding whether behavioral plasticity stems from changes in physiological state per se or an experience-related change such as learning can be important in understanding the function of behavioral traits. While teasing apart these potentially confounding effects could hold implications for many kinds of behavior, mating provides a particularly interesting focus, as the fitness consequences for mating decisions can differ between genders. We argue that this approach may be an effective way to gain insight into which sex is in control of a specific aspect of mating behavior.

In closing, we note that a long tradition in experimental psychology has wrestled with the issue of interactions between experience and physiological state, the latter commonly referred to as "motivation." A clearer understanding by behavioral ecologists of the fitness consequences of behavioral change with experience is sure to benefit from the approaches developed in that discipline.

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