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Abstract: Within the Optimal Foraging Theory framework, parasitoids constitute ideal models to elucidate combined physiological and environmental determinism of foraging behavior between current and future fitness gains. Parasitoid females need hosts to lay eggs for their reproduction (immediate gain), but also sugar food resources for their survival (future gain). According to theoretical models and previous empirical studies, fed females should favor host foraging, whereas females with lower energetic reserves should search for food. Surprisingly, the influence of mating status and food quality has not been considered, whereas they may both constitute major factors altering animals' choices between reproducing and feeding. We tested decision-making on *Aphidius rhopalosiphi* parasitoid females with different life expectancy levels (as set by recent feeding history) and mating status, using two flower species with contrasted attractiveness and nectar suitability. Interestingly, all fed and unfed females with different expected lifetime levels favored reproduction over nutrition since they are mated. This could be explained by their reproductive status that appeared to be the main determinant of their foraging decisions. For a given expected lifetime, mated females favored more reproduction whereas unmated ones favored food. Interestingly, physiological status of females (mating and lifetime expectancy) did not interact with flower species on their foraging decisions nor did it modify their preferences, as they always favored the most attractive flower, which does not have the best nectar. These results highlight the need for more empirical studies to evaluate the interactions between different intrinsic factors and to carefully consider the mating status in model assumptions, as it influences foraging behavior between immediate and future fitness gains.

Significance Statement: Parasitic wasps need hosts to lay eggs for their reproduction (immediate fitness gain) and sugar resources for their survival (future fitness gain). Empirical studies and related theoretical models about foraging decisions of parasitic wasps between current and future gains included influences of energetic and resource availability constrains. We examined assumptions used by those mathematical models by empirically testing two new factors, food qualities provided by two nectar provisioning flower species with contrasted functional traits, which had surprisingly no impact on decision-making, and mating status which we showed to play a decisive role on decision-making between food or host resources. These factors should henceforth be considered in model assumptions or in models themselves to realize accurate predictions and to provide a better understanding of foraging decisions made by female parasitic wasps.

Introduction

Life reproductive success of organisms (*i.e.*, fitness, the net contribution to the next generation) is limited by time and nutrients (de Jong and van Noordwijk 1992; Tatar and Carey 1995) resulting in a trade-off between current reproduction (*i.e.*, immediate fitness gains) and survival (*i.e.*, future fitness gains) (Stearns 1976; Roff 2002; Bernstein and Jervis 2008). Due to limited intrinsic energetic reserves (Morano et al. 2013) and to external biotic and abiotic constraints (Török et al. 2004; Killen et al. 2013; Stienen et al. 2015), organisms modulate their resource allocation between life history traits, such as fecundity and longevity. This plasticity in energy allocation occurs mainly by changes in foraging behaviors adopted by individuals (Wolf et al. 2007), either looking for resources that could increase their current reproductive success (*e.g.* breeding sites, sexual partners, offspring care, etc.) or those that could increase their expected lifespan (*e.g.* shelters decreasing predation risks, food supplies, etc.). In this context, fitness optimization for an organism depends on the elaboration of optimal foraging decisions (Pyke 1984; Tatar and Carey 1995).

The Optimal Foraging Theory (OFT) was developed to predict the optimal decision-making of animals looking for food, like predators foraging for prey, in order to maximize their fitness at low mortality risks and energetic costs (Townsend and Hildrew 1980; Lacher et al. 1982). Parasitoid insects (*i.e.* arthropods that need another living organism as host for their reproduction) have been extensively studied within the OFT framework (Bernstein & Jervis, 2008; Wajnberg, 2006). Indeed, parasitoid females need hosts (*i.e.* other arthropods) for their reproduction (Godfray, 1994), but also sugar resources for their survival as adults (Azzouz et al. 2004; Lee et al. 2006; Tena et al. 2015). Adults of many parasitoids species are unable to feed on their hosts and sugars are mainly found in the honeydew of phloem consumers (Fischbein et al. 2016) or in floral nectar (Winkler et al. 2009). When insect hosts produce honeydew, parasitoid females may find hosts and food at the same location. However, the energetic benefits of honeydew are lower than those obtained by feeding on some flower nectar (Lee et al. 2004; Tena et al. 2018), and parasitoids that experienced nectar prefer this food resource rather than honeydew (Vollhardt et al. 2010). Consequently, as oviposition and feeding sites are often separated in

space, parasitoid females need to optimize costly movements between these different discrete patches (Van Alphen and Vet, 1986; Hassell and Southwood, 1978; Jervis et al., 1993).

Within OFT conceptual framework, predictions of optimal decision-making by parasitoids between foraging for hosts or food have been improved by the use of stochastic dynamic models (Clark and Mangel 2000). Both SB (Sirot and Bernstein 1996) and TSK (Tenhumberg et al., 2006) mathematical models predict that well-fed female parasitoids should always search for hosts whereas they should search for food only when they are close to die from starvation. However, the two models differ in their assumptions. The SB model is considering that decision-making is based on the interaction between the energetic state of the female parasitoid and the resource availability. Therefore, in the SB model, females should favor food foraging when they are starving and only when food is available and abundant. By contrast, in the TSK model, food foraging by females is assumed to be independent of the probability of finding food as well as of its quantity or quality. These model predictions strictly based on the energetic status of individuals were supported by a few empirical studies prior to their development (Roitberg et al. 1992; Wäckers 1994; Jacob and Evans 2001; Siekmann et al. 2004). Additionally, the study conducted by Lucchetta et al. (2007) supported the assumption of the SB model, showing that the tendency of females of the parasitoid *Venturia canescens* to leave a reproductive patch was mediated by both metabolic reserves and food availability in the vicinity. Nevertheless, the impact of other environmental and intrinsic factors on the decision to search for hosts or food still remains to be explored.

Factors affecting food foraging by female parasitoids in species that do not host-feed have received little attention, with most focus on preferences among plant species bearing nectar (Russell 2015) and always as an alternative to the host foraging behavior. In contrast, several physiological parameters are known to influence host foraging behaviour. These parameters includes the expected lifespan, the number of mature eggs available or the mating status (Minkenberg et al. 1992; Heimpel and Collier 1996; Fauvergue et al. 1999; Jacob and Evans 2001). So far, only the energetic status or associated lifetime expectancy of female parasitoids has been considered on host *vs* food foraging decision-making. However, mating status is known to modify foraging behavior in several groups of organisms

(Reaney 2007; Wexler et al. 2017). For parasitoids, haplodiploidy results in females producing only males when unmated versus both sexes when mated, and therefore mating status may also constitute a determinant intrinsic factor of their foraging decisions (Fauvergue et al. 2008; Kant et al. 2012). For instance, it has been shown that mated females of *Monoctonus paulensis* (Hymenoptera; Braconidae) are more predisposed to reproduce and stay longer on host patches than unmated ones when foraging for hosts (Michaud and Mackauer 1995). Consequently, the potential influence of female parasitoid mating status on their foraging decisions within the trade-off between current or future fitness gains remains to be studied.

Additionally, host foraging behavior is also known for being mediated by extrinsic abiotic conditions such as temperature or precipitation (Fink & Völkl, 1995; Le Lann, Outreman, van Alphen, & van Baaren, 2011), as well as by biotic factors, as for instance the presence of competitors (Martinou, Milonas, & Wright, 2009; van Baaren, Outreman, & Boivin, 2005; Wang & Keller, 2005). Among these extrinsic factors, food quality and quantity are the focus of the SB and TSK models. However, the influence of both food quality and attractiveness provided by flowering plants on foraging decision, as well as potential interactions with other physiological parameters than the energetic state of females remain unknown. Better understanding of parasitoid decision-making between feeding and reproducing is thus needed to improve both model predictions and biological control programs using parasitoid insects.

The current study aimed to test the influence of intrinsic physiological factors (life expectancy as a proxy of their energetic reserves (Snart et al. 2018), and mating status), as well as extrinsic factors (nectar suitability and flower attractiveness) on the foraging decisions between food and hosts of parasitoid females *Aphidius rhopalosiphi* (Hymenoptera: Braconidae). This parasitoid species is dominant within aphid-parasitoid community of cereal crops from western part of France, and benefits from cultivated flowering plants used in agricultural landscape (Damien et al. 2017). We also examined if these physiological states influenced their flower preferences. The following hypotheses were tested: **(1)** for given flower species and mating status, female parasitoids with high life expectancy levels (*i.e.* high energetic reserves) should favor immediate fitness by choosing host patches whereas females with

intermediate and low life expectancy levels (*i.e.* lower energetic reserves) should favor future fitness by choosing food patches. **(2)** For a given flower species and a given a life expectancy status, unmated females may choose to feed whereas mated ones may choose to oviposit. **(3)** Finally, the quality of the flower nectar or the attractiveness of the flower may. Finally, the quality of the flower nectar or the attractiveness of the flower may modify female preferences for the flower species used as food patch, by interacting with the internal state of female wasps, ultimately influencing the decision-making between foraging for hosts and for food. In particular, females with low life expectancy may be expected to choose more often to feed on the most suitable flower nectar (*i.e*. increasing their longevity) or on flowers that are highly attractive (*e.g.* preferences for particular flower colors and/or odors).

Materials and methods

Flowering plants

Two different flowers species that are currently encountered in agricultural landscapes of western France were tested as nectar food resource: the buckwheat (*Fagopyrum esculentum*, var KORA, Polygonaceae) and the white mustard (*Sinapis alba*, var SIGNAL, Brassicaceae). Seeds, provided by the SA Pinault company were sown in trays (20 x 15 x 5 cm) and placed into controlled conditions (20°C, 70 ± 10% RH, 16L:8D photoperiod). After two weeks, seedlings were transplanted into individual pots (7 x 7 x 8 cm) and grown under the same conditions for two more weeks. Then, seedlings were transferred into larger pots (h = 17 cm, Ø = 7 cm) in a greenhouse until they flowered and were used in experiments. Buckwheat flowers have a highly suitable "sucrose dominant" nectar that increases fitness of several parasitoids species including *A. rhopalosiphi* (Vattala et al. 2006; Irvin et al. 2014; Damien 2018), but are considered to be poorly attractive flowers for parasitoids (Russell 2015). By contrast, white mustard flowers are highly attractive for many species (Russell, 2015), such as observed in *A. rhopalosiphi* but have a nectar of poor quality, known as "hexose dominant" nectar (Vattala et al. 2006; Tompkins et al. 2010; Damien 2018).

Insects

Both parasitoids and aphids were collected between 2014 and 2015 in cereal crops in the Zone Atelier Armorique (https://osur.univ-rennes1.fr/za-armorique) near Rennes (France). The parasitoid *Aphidius rhopalosiphi* (Hymenoptera, Braconidae) was reared in the laboratory on a mixed-aged culture of the aphid *Metopolophium dirhodum* (Hemiptera, Aphididae). Parasitoid cultures were annually supplied with individuals from the field to improve genetic diversity within rearing. This parasitoid species is unable to feed on the hemolymph of its host and honeydew is expected to constitute a poorly energetic resource (Lee et al. 2004; Tena et al. 2018). Without feeding, *A. rhopalosiphi* individuals have a low life expectancy that does not exceed two or three days under controlled conditions (Le Lann 2009). Aphids were reared on organic winter wheat plants (*Triticum aestivum*, cultivar Ludwig) provided by the SA Pinault company. Both aphids and parasitoids were maintained in Plexiglas cages (50 × 50× 50 cm) under controlled conditions (20°C, 70 ± 10% RH, photoperiod de 16L:8D). To obtain standardized parasitoid individuals for experiments, mummies (dead aphids containing nymphs of parasitoids) were collected from the culture and placed individually in gelatin capsules (L = 2 cm, Ø = 0.7 cm) until adult emergence. Emergences were checked twice a day, and females that had emerged within the past twelve hours were then assigned to different feeding and mating treatments before being used in the experiments.

Mated females with three different intrinsic expected lifetimes (i.e. energetic status)

Three different levels of expected lifetime (low, intermediate and high) were tested. To obtain females with low and high life expectancy, each newly emerged female was enclosed during the first 24h of the experiment under controlled conditions (20°C, 70 ± 10% RH, photoperiod de 16L:8D) in plastic tubes (Ø = 1.4cm; L = 16cm) with *ad libitum* water access and two males for mating (Le Lann, Roux, et al., 2011; Le Lann, Wardziak, van Baaren, & van Alphen, 2011). Seventy five percent of mating occur within 30 min in *Aphidius* parasitoids and all females are assumed to be mated after being enclosed with males during 24h (Levie et al. 2005; McClure et al. 2007; Bourdais and Hance 2009). During this 24h period, females were placed either without food (low expected lifetime, close to death due to starvation, N = 25), or with droplets of honey (high expected lifetime, N = 20). To obtain females with

163 "intermediate" life expectancy (N = 25), newly emerged females were individually enclosed in
164 Eppendorf tubes with two males, *ad libitum* water access but no food, and all females were tested in the
165 next 4 hours after mating occurred. These three groups of females were tested in a choice situation
166 between one host patch (aphids) and one food patch (*see '**Experimental design for behavioral**
167 ***choices')***.

168 ***Intermediate expected lifetime females with different mating status***

169 In order to assess the effect of the mating status, as all trials are independent from each other, it was
170 assigned to the 'mated females' group (N= 25) the mated females with intermediate lifetime from
171 previous comparison of low, intermediate, and high expected lifetimes. The data was completed with
172 new trials using newly emerged females that were placed in Eppendorf tubes with one to two virgin
173 males that were less than 48h-old and observed for 30 minutes, without food access but with water *ad*
174 *libitum.* Females that did not mate during this time were assigned to the 'unmated females' group (N =
175 28). These females were unfed and tested in the next 4 hours after mating that corresponds to the
176 intermediate expected lifetime, as defined in the previous experiment. These two groups of females
177 were tested in a choice situation between one host and one food patch (*see '**Experimental design for*
178 ***behavioral choices'***).

179 An absence of mating after 30 minutes decided in the protocol may result from several drivers (like
180 physiological incompatibility, kinship or diploid males linked to the rearing conditions (Werren and
181 Loehlin 2009)), that could ultimately influence female decision-making between hosts and food. To
182 take into account the potential effect of male encountering on decision-making in the 'unmated females'
183 group, a third group (N= 15) with unmated females that never encountered males was also tested in
184 presence of mustard flower as a food patch. Given the choice between hosts or flower, decision-making
185 only significantly differed between mated and both types of unmated females (GLMM: χ^2=11.09, df=
186 2, $p < 0.01$) whereas unmated females that encountered a male or not present similar proportions in their
187 patch choice ($|z| = 0.82$, $p = 0.69$). Consequently, further trials with buckwheat flower and all analyses
188 were only conducted with mated females and the unmated ones that encountered males for 30 min but
189 did not mate.

Flower preferences of females with different physiological conditions

To establish if flower species were chosen more often by *A. rhopalosiphi* females according to their nectar value or because of their attractiveness, we investigated *A. rhopalosiphi* preferences for the two flowers (buckwheat or mustard) in a choice test. Females with different mating status and expected lifetime (*i.e.* mated or unmated with low or intermediate life expectancy, both as defined above) were offered to choose between two food patches constituted by mustard and buckwheat flowers (*see '**Experimental design for behavioral choices')*. Female from the high life expectancy group were not used in this experiment as all of them favored the host patch (*see result section*).

Experimental design for behavioral choices

To assess the effects of flower species and different physiological conditions of females, as well as the potential interactions between those factors, on their foraging decision-making between hosts and food, the two flowers species were tested as food patches. The food patch was then constituted of one freshly cut inflorescence of buckwheat or mustard. The host patch was constituted of a wheat plantlet (~ 6cm high, same variety and same growing conditions as explained above), infested 30 minutes before trials with 10 second-third instars of *M. dirhodum* aphids. This aphid density is commonly encountered in the field (Dedryver 1987) and these instars are preferred by parasitoids (Outreman et al. 2005). During trials, stems of inflorescences and wheat plantlets were placed in water to avoid plant wilting.

For each treatment (different expected lifetime and mating status) and flower species (buckwheat and white mustard) described above, the foraging behavior of individual females was observed in a Plexiglas cage (28 × 15 × 16 cm) under homogeneous white light. The female was delicately released from an Eppendorf tube at the center of the cage on an introduction patch constituted of a 6 cm high plastic rod. At five centimeters on each side of the introduction patch were placed one host patch and one food patch (or two food patches with two different flowers in the last experiment). The behavioral patterns of each female were recorded by focal sampling, using the "SequenceR" plugin in the R software (Herve, 2013). Recording started when the female was deposited on the introduction patch. Recording stopped when the female stayed immobile on the last visited patch or remained outside the

last visited one for more than ten minutes. Almost 70% of the females tested met these criteria after visiting only one patch, and more than 60% of the 30% of females that performed more than one visit did it on the same patch that they chose first. Consequently, the study is focused principally on the first choice and associated behavior adopted by newly emerged females. Recorded behavioral items included: entering and leaving a patch (host or food patch), stinging a host or feeding on the flower nectar. The latency for choosing a patch, the type of patch chosen (host or food and mustard or buckwheat flowers in the respective experiments) were measured, as well as the patch time residency during each visit realized prior to meet the ten minutes criterion ending the trial. The latency for choosing a patch was defined as the duration between entering the introduction patch and entering the chosen patch. The patch residence time was defined as the total time between entering and leaving the patch for each visit.

Statistical analyses

To compare the effects of the life expectancy level or of the mating status on their choice between ovipositing and feeding, as well as on their preferences between mustard and buckwheat flowers species, three independent GLMs were performed. In each model, the response variable tested was the proportion of females choosing each patch (host or food in the two first cases, mustard or buckwheat flower in the last one), using binomial errors and logit functions. Fixed effects included physiological states ("low", "intermediate" and "high" life expectancy of mated females in a first GLM, mated and unmated females with intermediate life expectancy in the second one) and flower species (mustard and buckwheat). For the third GLM, life expectancy and mating status were tested as fixed effects on the flower preferences of parasitoid females. For each of the three situations, decision-making duration and patch time residency were also compared using Cox proportional hazards models distribution (Wajnberg, Fauvergue, & Pons, 2000). Fixed effects were the same as previously described but the chosen patch was also added as a qualitative co-variate in these models. Finally, the number of feeding occurrence and the number of attacked aphids, according to females' choices between host and food patches, were compared by performing GLMs with a Poisson distribution using log functions. Type 3 ANOVAs were performed on each model sets with all interactions between fixed effects. Models were

simplified by sequentially removing non-significant interactions, starting with the least significant highest order interaction and all fixed effects were kept in final models (Zuur et al. 2009). When singularity was observed between fixed effects, interaction terms involved were manually removed from the model until being valuable for analyses. ANOVA' assumptions were assessed prior to each test, by checking variance homogeneity and normal distribution of the residuals for LMs, or by using DHRMA package for GLMs (Hartig 2018).

Results

Effects of the expected lifetime and the flower species on the foraging behavior of mated females

There was no significant interaction between life expectancy levels and flower species on foraging decision (χ^2=2.14, df= 2, p=0.34). Decision-making of females differed according to their expected lifetime levels (chosen patch: χ^2=14.86, df= 2, p<0.001). Females with the highest life expectancy (i.e., honey-fed) always chose to reproduce whereas unfed ones with intermediate and low expected lifetime were more prone to choose the food patch, even though in proportion they also chose more often the host patch (**Fig 1-A**). Time for decision-making did not vary according to the expected lifetime of females (χ^2= 0.23, df= 2, p = 0.89) whereas time residency on the chosen patch did (χ^2= 9.31, df= 2, p<0.01). Females with the highest life expectancy level stayed longer (24.08 min ± 2.98; mean ± SE) than the ones with intermediate or lower expected lifetime (respectively 10.98 ± 1.73 and 12.50 ± 3.79). Both foraging decisions and behaviors did not change according to the flower species that constituted the food patch (patch chosen: χ^2=0.017, df= 1, p =0.9; latency before decision-making: χ^2=0.43, df= 1, p= 0.51; patch time residency: χ^2=0.81, df= 1, p= 0.37). The number of feeding behaviors for females that chose the food patch did not vary among expected lifetime (χ^2=1.69, df= 2, p =0.13), nor between flower species (χ^2=1.078 df= 2, p =0.22) and the interaction was not significant (χ^2=12.75, df= 1, p =0.062). For females that chose the host patch, there was no significant interaction between life expectancy levels and flower species fixed effects on the number of aphid attacks (χ^2=2.8, df= 1, p =0.087) nor an effect of flower type that constituted the associated food patch (χ^2=1.69, df= 2, p =0.13). However there were significantly (χ^2=9.31, df= 2, p<0.01) more aphids attacked by females with high

lifetime expectancy (19.8 ±2.48; mean ± SE) than those with intermediate ones (5.88 ± 1.1), whereas both of them did not differ from females with low expected lifetime (14.5 ± 3.54).

Effects of the mating status and the flower species on foraging behavior of female parasitoids with intermediate expected lifetime.

There was no significant interaction between mating status and flower species on foraging decisions (χ^2=2.32, df= 1, p=0.13). However, mated females chose more frequently the host patch (68 ± 9.5 %; ± SE) than the food patch (32 ± 9.5 %) whereas unmated females chose preferentially the food patch (92.9 ± 4.8 %) over the host one (7.1 ± 4.8 % ; chosen patch: χ^2=22.79, df= 1, p < 0.001; **Fig 1-B**). Foraging decisions were not affected by the flower species (χ^2=0.23, df= 1, p= 0.63). Whatever their mating status and the flower species, females who chose the host patch tended to take more time to adopt a decision than females who chose the food patch (latency before decision-making: χ^2=3.44, df= 1, p = 0.064; 5.95 ± 1.04 vs 3.49 ± 0.73 min respectively; mean ± SE). As only 2 out of 30 unmated females chose the host patch and eight out of the 25 mated females tested chose the food patch, only the time residency of unmated females on food patches (for which we had sufficient numbers) could be compared between flower species. Time residency on the food patch did not vary according to the flower species (χ^2=1.16, df= 1, p = 0.28) and there was no difference in the number of feeding events between the two flower species (χ^2=2.32, df= 1, p = 0.13).

Mating and life expectancy effects on the flower preference of parasitoids

There was no significant interaction between life expectancy levels and mating status on flower species preferred by females (flower chosen: χ^2=0.15, df= 1, p=0.7). Mustard flowers were largely preferred over buckwheat ones by females (**Fig 2**) whatever their mating status (χ^2=0.058, df=1, p= 0.81) and expected lifetime (χ^2=0.59, df=1, p=0.44). There was no difference in the time needed to make a decision and patch time residency between mating status (χ^2=0.038, df=1, p= 0.84 and χ^2=0.6, df=1, p=0.44, respectively), life expectancy levels (χ^2=2.35, df=1, p= 0.13 and χ^2=1.1, df=1, p=0.29, respectively) and chosen flower species (χ^2=0.14, df=1, p= 0.71 and χ^2=0.13, df=1, p=0.71, respectively). However, there was a significant interaction between expected lifetime levels and the

flower species chosen by parasitoids on on the number of times the wasp fed at the flower (χ^2= 4.81, df = 1, p<0.05). This results from the low number of females with an intermediate life expectancy that chose buckwheat (N=4), with only one food intake for two of them (0.50 ± 0.29 mean ± SE), but a high number of females that chose mustard flowers (N = 25) with a higher number of food acquisition events per female (1.67 ± 0.60). Additionally, parasitoids with low life expectancy had significantly higher numbers of times that they fed at buckwheat (4.86 ± 1.74) and mustard (3.96 ± 0.67) flowers than newly emerged females with intermediate life expectancy.

Discussion

Our results partly confirmed the first hypothesis as, independently of flower species constituting the food patch, mated *A. rhopalosiphi* female parasitoids with the highest life expectancy levels (*i.e.* honey-fed females with high energetic levels) favored their immediate fitness by all choosing the host patch. However, although there was an increasing proportion of females that favored the food patch and then their future fitness, as their expected lifetime decreased, more than 50% of them still favored the host patch and immediate fitness gains. The second hypothesis was validated as females with intermediate expected lifetime that were mated favored their immediate reproduction, whereas unmated ones favored in a larger proportion to feed and thus future fitness gains, still independently of the flower species. Finally, the third hypothesis was refuted as there was no interaction between their physiological status and the flower species. However, under all physiological conditions, females preferred the flower species that was the more attractive (mustard) rather than the flower species with the more suitable nectar (buckwheat).

Effects of expected lifetime on mated female parasitoids foraging decision-making

Both SB and TSK (Sirot and Bernstein 1996; Tenhumberg et al. 2006) stochastic models predict that fed female parasitoids are more prone to reproduce whereas starving ones should favor feeding. Such results are also supported empirically for several parasitoid species such as *Bathyplectes curculionis* (Hymenoptera, Ichneumonidae), *Cotesia rubecula* (Hymenoptera, Braconidae) (Wäckers 1994; Jacob and Evans 2001) and *Leptopilina heterotoma* (Hymenoptera: Figitidae) (Roitberg et al., 1992). Our

results partially confirmed this first hypothesis, as all honey-fed *A. rhopalosiphi* females tested (*i.e.* with a high expected lifetime) always choose to reproduce and favored their immediate fitness. However, only 20 to 45% of starved females (with low and intermediate life expectancies), chose to feed in our study, which contrasts with expectations based on the SB or TSK models. In their study, Siekmann et al., (2004) partially confirmed as well model predictions and demonstrated that only well-fed female favored host foraging, whereas unfed females of *Cotesia rubecula* (Hymenoptera, Braconidae) chose in similar proportions between hosts or food. The authors explained that it may partially results from consequences of food deprivation on neural network and decreased cues sensitivity of females' parasitoids, leading to a more random searching behavior. Our results are similar, by alternatively may be explained as follows. Females with intermediate and low life expectancies tested in our experiment still had upper energetic levels than the critical thresholds of remaining energy defined by mathematical models. However some of the females initially assigned to the 24h starvation treatment (*i.e.* low life expectancy) were already dead before being tested, indicating that at least part of the females were below those critical energetic levels.

More plausibly, these differences between the model predictions and our results imply that these expectations may not apply to all parasitoid species and/or that some other important parameters or assumptions should be considered. Firstly, it may depend on species involved in the plant-host-parasitoid system considered. Prior studies were using parasitoid species that could find both flower nectar and hosts on the same plant species under natural conditions (Wäckers 1994; Jacob and Evans 2001). Therefore, environmental cues used for decision-making by such parasitoids may derive from a strong coevolution with the host plant, making them more prone to search for hosts and food at the same time and same location. At the opposite, *A. rhopalosiphi* is a specialist of wheat aphids and consequently do not encounter flower nectar and hosts on the same plants. Consequently, *A. rhopalosiphi* females independently of their expected lifetime may have favored their immediate fitness instead of their future one because of their inability to assess flower cues without prior feeding experiences. Another explanation would be that other physiological factors such as the mating status affect the foraging decisions. Indeed, in the second experiment (see next paragraph for results on unmated females), for

the same level of expected lifetime and thus of energetic reserves, the contrast in decision-making between mated and unmated females was strong. Consequently, mating most likely drives foraging decisions either by modifying life expectancy perception, or by being a predominant factor on the elaboration of their foraging strategy. The high predisposition of females of different expected lifetime to reproduce may be the result of interacting intrinsic factors. Nevertheless, hierarchy in physiological constraints acting on foraging decisions is not documented for any organisms. Further investigations are thus needed to confirm how these physiological factors may interact and modified foraging decisions in a broader range of organisms.

Mating status effects on the foraging behavior of starved parasitoids

There was a clear difference in foraging decisions between mated females who favored their reproduction whereas unmated ones favored the food acquisition by choosing the flowering plant. In the few studies focusing on the effect of the mating status on host foraging, mated females showed higher reproductive predisposition than unmated ones (Michaud and Mackauer 1995; Kugimiya et al. 2010). This can be explained by the haplo-diploid sex determination of Hymenopteran species. Unmated females lay non-fertilized eggs developing in males whereas mated females produce both genders in their offspring. Thus, under the context of the local mate competition theory (Hamilton 1967), there is an evolutionary advantage for mated parasitoid females to favor their immediate fitness and for unmated ones to favor their future fitness, by feeding until finding a mate to be able to produce both genders. Among studies that have been focusing on the effect of mating status on host foraging behavior, increased reproductive predisposition after mating has already been observed (Kugimiya et al. 2010). For instance, under field conditions, Fauvergue et al. (2008) found that mated females of *Lysiphlebus testaceipes* (Hymenoptera : Braconidae) increased their host patch exploitation (*i.e.*, number of host attacks) according to the increase of host density contrary to unmated ones, whereas patch residency times were similar for both mated and unmated individuals. In our study, we could not compare host patch exploitation between females with different mating status, as they had highly contrasted patch choices (host *vs* food for mated and unmated respectively), which resulted into multicollinearity among predictor variables and did not allow to properly performing statistical analysis.

However, results showed that patch decisions were taken more quickly for females that chose the food patches (majority of unmated females) compared to the ones that favored host patches (majority of mated females), which would be consistent with a higher predisposition for unmated females to favor their future fitness by feeding contrary to the mated ones.

Flower species effects on female parasitoids foraging behavior

Environmental factors play a major role on the foraging decisions between breeding and feeding in many animal species such as mammals (Bronikowski and Altmann 1996; Murray et al. 2006; Corlatti et al. 2013) and birds (Hennicke and Culik 2005; Harding et al. 2011) but remain poorly studied for insects (Rasa 1998). Surprisingly, it has been understudied in parasitoids and our study is the first one to test the impact of flower species on their foraging decisions between feeding and ovipositing. Contrary to our third hypothesis, flowering plant species did not interact with physiological conditions of *A. rhopalosiphi* females on their foraging decisions. Indeed, independently of the flower species, decision-making between host and food patches was only affected by physiological factors and was similar between flower species that composed the food patch. As mustard and buckwheat flowers have opposite nectar suitability and attractiveness, these flower characteristics may have concomitantly influenced the choice of *A. rhopalosiphi* females (*i.e.* attractiveness for mustard, nectar suitability for buckwheat), resulting in similar foraging choices for both flower species.

Although the flower species did not influence *A. rhopalosiphi* females foraging decisions between reproducing and feeding, our last experiment showed that they preferred mustard flower over buckwheat one, the latter having the most suitable nectar but being the least attractive, under all physiological conditions. Usually, flower attractiveness is assumed to be the most determinant factor of the foraging decisions of female parasitoids. Foti et al., (2017) suggested that female parasitoids might use volatile organic compounds of floral plants to localize food sources and assess their suitability. However, their capacity to evaluate nectar quality may depend on a direct contact as it is the case for the evaluation of the host quality (Godfray, 1994; van Baaren et al., 2009). Thus, preferences of *A. rhopalosiphi* for mustard flowers is most likely resulting from innate preference for yellow colors (Lucchetta, Bernstein, Théry et al., 2008; Wäckers, 1994), and/or for specific floral odors (Belz et al.

2013). For instance, the closely related parasitoid *Aphidius ervi*, is stimulated by both innate visual cues (Battaglia et al. 1995) and innate odor recognition (Budenberg 1990) during host foraging.

As flower species did not affect decisions of *A. rhopalosiphi* females in any of the trials, it may be confidently assumed that it did not interact with their physiological internal state. Our results support the assumption that tested females were not able to assess nectar quality from a distance to make an optimal choice, and that they had to make decisions based on their innate preferences and their physiological state. Interestingly choosing buckwheat flowers, with the more suitable nectar, would have been more beneficial for females that had favored future fitness gains by choosing nutritional patches. As relationships between parasitoids and many potential nutritive flower species do not result from a long-term adaptive coevolution such as with their hosts, variation in flower quality may mislead parasitoids in their foraging decisions. When encountering flowers with opposite attractiveness and profitability, inexperienced female parasitoids may face ecological traps by being attracted toward plants with low energetic nectar rewards. Associative learning for odors (Takasu and Lewis 1996) and visual cues (Lucchetta et al., 2008) relative to food was demonstrated for parasitoids species. Therefore, feeding experiences of adult females (Lucchetta et al. 2008; Giunti et al. 2015) may help them to optimize their foraging decisions (Siekmann et al. 2004), notably through the decrease of environmental uncertainty as predicted by the information primacy hypothesis (Woodworth 1958; Inglis et al. 2001). Indeed, it is interesting to note that food foraging behavior of parasitoid insects has never been extent to this conceptual framework whereas it was done for birds (Giles et al. 2002) or bees (Katz and Naug 2015). This theoretical context would most likely bring complementary insights to the OFT approach on parasitoids foraging behavior.

Conclusion

The tradeoff between immediate and future fitness gains is a key determinant in foraging decisions taken by organisms. The complexity of such decisional processes has led to the use of dynamic modeling to disentangle how intrinsic and extrinsic factors of individuals may modify their optimal foraging strategies. However, our study showed that there is a need to test theory with empirical studies, to clarify assumptions made by modelers that may result in divergent output from theoretical

predictions. According to our results for instance, reproductive status, such as the mating condition, has been understudied and needs to be considered in future empirical and theoretical studies. Moreover, the potential hierarchy between intrinsic factors and their interactions with environmental parameters should be investigated to improve our understanding of foraging strategies adopted by these organisms. Finally, results of this study highlight that new interactions between parasitoid insects and flowering plants may constitute a challenge for developing environmental methods using plant diversity to promote diversity and trophic system stability of pest natural enemies, such as parasitoids in biological control programs.

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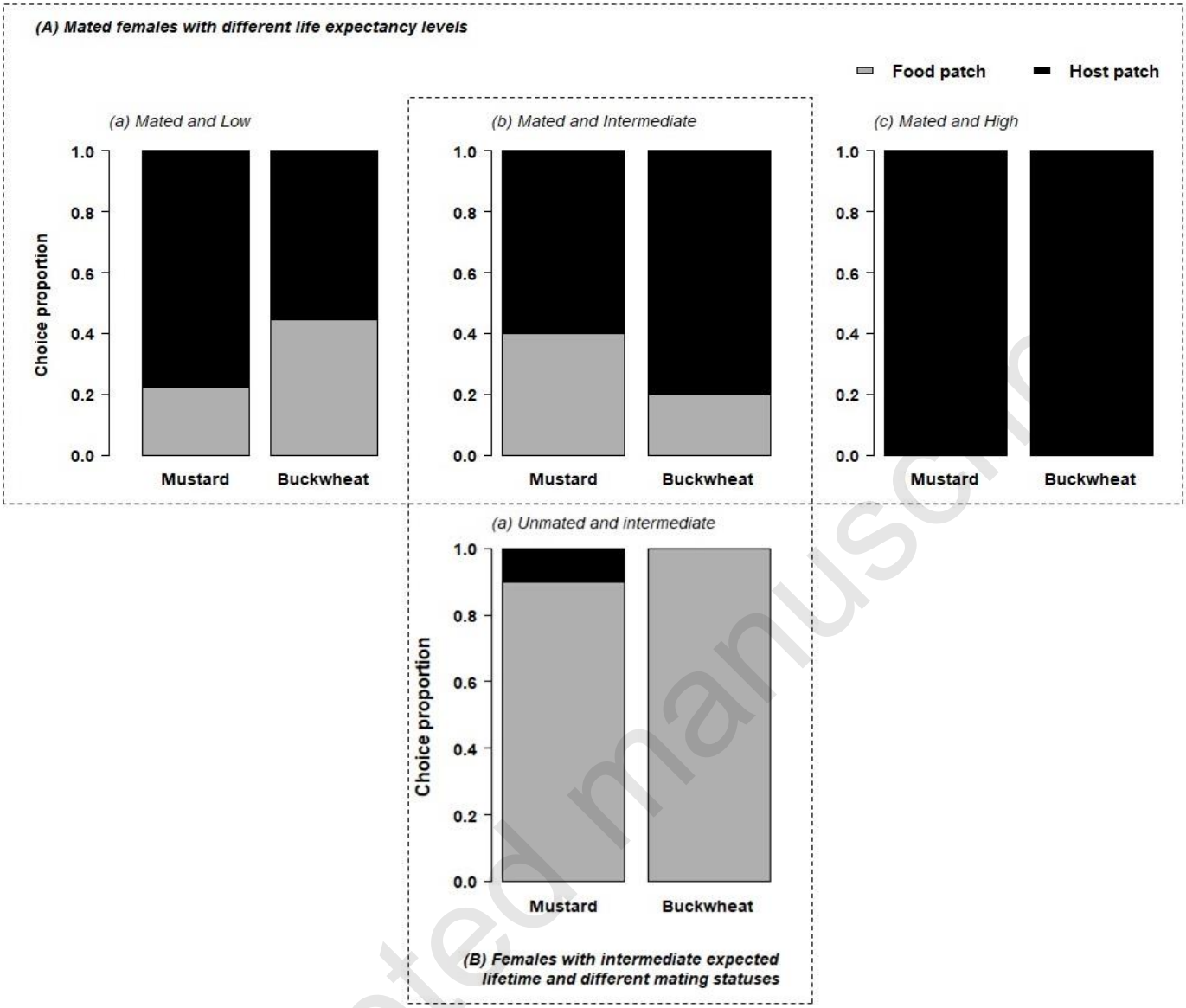
Figure legends

Fig1-(A) Proportion of mated females with **(a)** low (N =18), **(b)** intermediate (N = 25) and **(c)** high (N = 25) expected lifetimes, choosing between the host patch (black bars) and the food patch (*i.e.* mustard or buckwheat flowers) (grey bars). **1–(B)** Proportion of **(a)** mated (N = 25) and **(b)** unmated (N = 28) parasitoid females with intermediate expected lifetime, choosing between the host patch (black bars) and the food patch (*i.e.* mustard or buckwheat flowers) (grey bars).

Fig2 Proportion of (**a)** mated parasitoid females with intermediate (N = 13) and low (N = 16) life expectancy levels and **(b)** unmated ones with intermediate (N = 15) and low (N = 16) life expectancy levels, choosing between the mustard (*Sinapsis alba*) and the buckwheat (*Fagopyrum escalutum*) flowers.



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699 **Fig1-A** Proportion of mated females with **(a)** low (N =18), **(b)** intermediate (N = 25) and **(c)** high (N
700 = 25) expected lifetimes, choosing between the host patch (black bars) and the food patch (*i.e.* mustard
701 or buckwheat flowers) (grey bars). **1-B** Proportion of **(a)** mated (N = 25) and **(b)** unmated (N = 28)
702 parasitoid females with intermediate expected lifetime, choosing between the host patch (black bars)
703 and the food patch (*i.e.* mustard or buckwheat flowers) (grey bars).

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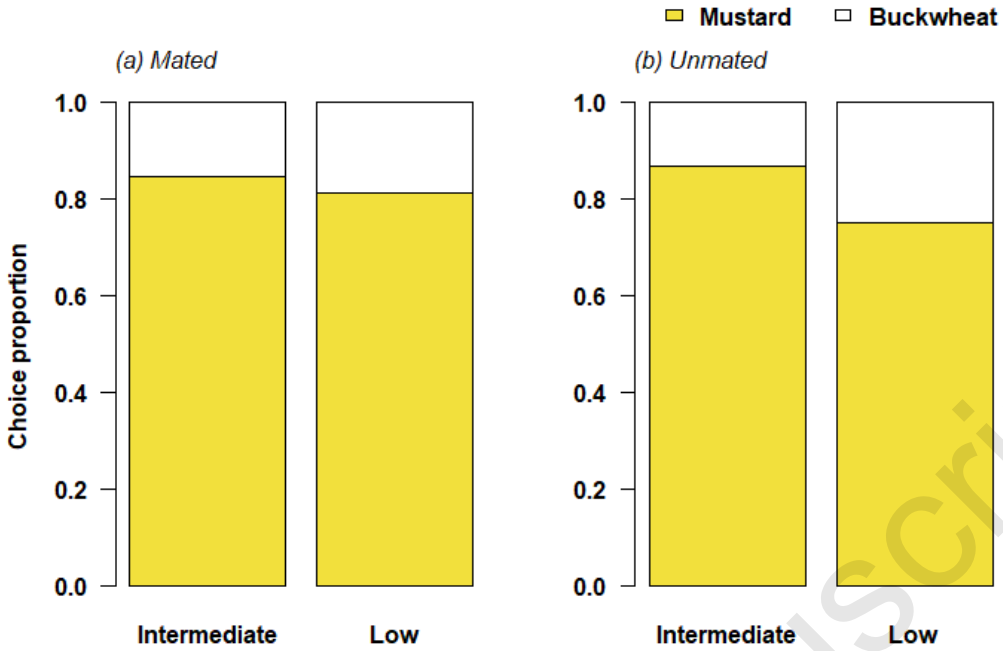

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707 **Fig2** Proportion of (**a)** mated parasitoid females with intermediate (N = 13) and low (N = 16) life
708 expectancy levels and **(b)** unmated ones with intermediate (N = 15) and low (N = 16) life expectancy
709 levels, choosing between the mustard (*Sinapsis alba*) and the buckwheat (*Fagopyrum escalutum*) flowers.