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The male mate search: An optimal foraging issue?

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Abstract

Male insects must find and mate females to have some descendants; male fitness therefore depends on the number of females they inseminate. Males are for this reason expected to optimize the behaviors related to mate location, orientation and copulation. Although optimization of the reproductive behavior of males has long been neglected in the literature, recent studies suggest a renewed interest for this idea. Here we discuss the parallel between male mate-finding and mating strategies in insects and Optimal Foraging Theory, a class of models which formalize the behavior of organisms seeking and exploiting resources, generally food. We highlight the different facets of male mating systems allowing such a parallel, and claim for a unifying approach of foraging behavior. Finally, we discuss novel research perspective emerging from the application of Optimal Foraging Theory to male reproductive behavior.

Keywords

Mating, fitness, optimization, foraging behavior, males, insect

1. Introduction

Since A. J. Bateman's pioneer study on *Drosophila melanogaster* [1], it is expected that male behavior evolves to maximize the number of females they mate as a result of their relatively cheap and numerous gametes. Females, because they invest more energy in gametes and the subsequent production of offspring, are thus considered as the choosy sex: females gain less from multiple copulations than males, but being approached by many competing males, they are expected to select the fittest and/or most compatible mate [2]. In contrast to this common belief, the difference between male and female utility functions appears less dramatic [3–7]: the evolution of reproductive strategies in males must be nuanced by trade-offs between the direct benefits of mating with the maximum number of females and the costs associated with mating. Producing sperm, searching and accessing females after courtship, fighting with rivals, and ensuring paternity when females are polyandrous are well-known examples of reproductive costs in insect males [8–14]. Given these costs, the ultimate causes of male reproductive behavior should be much better understood through an application of the paradigm of optimization.

In this manuscript, we draw a parallel between male mate-finding and mating strategies and Optimal Foraging Theory (OFT), a keystone class of models from behavioral ecology that formalize the behavioral adaptation of organisms seeking and exploiting resource (generally food). We derive the main assumptions and predictions from OFT models to males foraging for females. In the past, optimization analyses of insect male

behavior has been implemented to predict sperm allocation [18] and time allocation to courtship, female-guarding [15–17], or foraging on female patches [19,20]. Given the renewed interest for such approaches, it is time to discuss the relevance of applying rate-maximization models to male reproductive strategy and extending the classic prey and patch with such a perspective.

2. Male foraging behavior with regard to Optimal Foraging Theory

Two basic questions form the core of classic OFT: which food item should a forager select, and when should a forager leave a food patch [21]. Several general assumptions that do not depend upon the specific question underlie the theory (Table 1). Foragers gain energy by consuming food items, but finding and consuming each food item takes a significant amount of time [22,23] so that foragers are selected to maximize the average rate of energy intake during lifetime [21]. Average rate of energy intake is expected to correlate positively with fitness; in the jargon of OFT, average rate of energy intake is a "currency" for fitness. These assumptions can easily be translated in the context of male reproduction (Table 1). The number of females mated is likely correlated with male fitness, probably even more than food items are correlated with forager fitness [1,24] so that males maximizing their lifetime mating rate should be advantaged under natural selection. Searching and mating females are time-consuming activities that males cannot achieve simultaneously. For instance, the time to handle females (i.e. courtship, copulation and post-mating guarding), to recover after mating, to produce another nuptial gift or even to produce more sperm are

many examples of time constraints that should shape the utility function that insect males should maximize [12,16,25]. Moreover, males have a reproductive period limited by their capacity to transfer sperm, such period being temporary (synspermatogenic males) or definitive (prospermatogenic males) as it has recently been pointed out in Hymenoptera [14]. The currency of OFT can thus be adapted to males foraging for females and translate into an average rate at which males find and mate females over a limited period of time.

3. Which type of females to consume? Male strategy in the light of the prey model

The prey model analyses the choice of resource items a forager should include in its diet in order to maximize its long-term average rate of energy intake. It assumes that foragers have to select food items that differ in profitability (measured by the balance between costs and benefits of selecting items of a given type). The decision to select a food item of a given type depends on the rate at which each item is encountered in the environment. How can these assumptions be derived when females are the items that males exploit (Table 1)?

3.1. Females of varying profitability

For a male, the profitability of a female results from the balance between benefits and costs. The profitability of a female results directly from her ability to produce progeny bearing the male's genes. It can be influenced by individual characteristics such as age, body size and metabolic reserves or mating status [2,26–30], which modify the female's fecundity. The benefit males gain from mating varies according to these female attributes, just like the gain

of foragers varies with food quality. Moreover, mating females induce many costs for males; these costs include mate searching and locomotion, mate accession, fights with competitors, insemination, nuptial gifts, etc. These costs could appear as key factors in the evolution of male preferences for a given type of females [11,16,24,31,32], possibly underestimated in the available literature.

3.2. Choosy males?

Should the classic prey model apply to male reproduction, the main prediction would be that the decision to mate a female relies on a threshold depending on the rate at which each type of females is encountered (Table1). There is no evidence in the literature that males select females according to their encounter rate with females of different types. However, choosy males have been found in many insects taxa [24,33–40]. In particular, the strength of male preference toward females of a given phenotype depends on the variance in female quality and the costs of mating for males: preference increases when males suffer a higher cost of mating [41,42]. Hence, male behavior is consistent with predictions from the prey model, in the sense that their choice depends on trade-offs between costs and benefits of mating a given type of females. Moreover, the prey model predicts that time to access and exploit mobile resource influences the optimal choice [43]. Females are similarly mobile so that males should adapt their decision to their encounter rate with females.

Obviously, the prey model does not perfectly fit the foraging behavior of males, because it does not consider (i) the response of the resource towards the forager, and (ii) the behavior of the forager after expressing its choice. (i) In the prey model, even if preys or

hosts can respond by escaping or defending themselves, choices are made solely by the forager. Mate choice differs [33], as mating results from the attraction of one sex by the other, with the latter having a control over being "consumed" or not. Hence, the outcome of male choice depends not only on its own choice (true choice) but also on the response of the female (apparent choice) [34,44]. (ii) Copulation duration, guarding duration, sperm quantity and/or quality transferred to the females are many examples suggesting that insect males adapt their investment in females according to their profitability [45–50]. As a consequence, applying the prey model to males foraging for females should not only consider the outcome of the matching between a male and a given type of female, but also the complete sequence of mating, including all behaviors subsequent to copulation.

4. Leaving a hot spot? Male strategy in the light of the patch model

Food items are generally aggregated in the environment. Unexploited patches vary in quality and patch exploitation result in patch depletion, which also contribute the variability among patches. As in the prey model, time is a central constraint: traveling from patch to patch and exploiting a patch takes a significant amount of time acting as a primary constraint in the evolution of patch use behavior. The patch model assumes that foragers visit patches sequentially and allocate time to each patch according to its quality: the higher the patch quality relative to the environment-wide expected intake rate, the longer the patch residence time (Marginal Value Theorem, MVT) [23]. The optimal decision to leave a patch (i.e., the patch residence time maximizing the long-term rate of energy gain) depends

on a threshold intake rate below which the forager should decide to stop exploitation. Can these assumptions and predictions be adapted in the context of males foraging for females (Table1)?

4.1. Sequential visits on female patches.

In insects, females may aggregate into discrete patches for a number of reasons. Females can aggregate (i) if they exploit a resource such as food or hosts that is itself patchily distributed [51], (ii) if social interactions among females or agonistic behaviors of males for females lead them to aggregate [52], or (iii) if females develop and emerge simultaneously in a restricted area [19]. Moreover, depletion may occur in female patches because after mating, females loose a large amount of their profitability for males. The rate of patch depletion results from patch exploitation by males: the number of profitable females decreases with the number of matings [15]. Female patches are nonetheless highly unstable in species where females are highly mobile, which imposes additional costs to the forager, as shown for some parasitoid insects [43]. It is therefore crucial to consider the distribution of females in space and time to understand the forces shaping the behavior of males foraging for patchily distributed females.

4.2. Males adapt their patch residence time.

Do males estimate the quality of female patches and adapt their foraging behavior accordingly? OFT applied to male dung flies show that males adapt copulation time to the quality of females [15,53], and recent research suggests that time allocation is also relevant in the context of males exploiting patches of females. Like foragers on food or host patches,

male insects exploiting female patches use local information such as sexual pheromones or contacts with virgin females [19,54], and adapt patch departure based on proximate mechanism [55,56]. Male decision to leave a female patch relies on information on female density and the number of mated females, which yield patch residence times consistent with predictions from the MVT [57]. Hence male insects can optimize their residence time on female patches.

5. Implication for future research

We argue that applying OFT to male reproduction is relevant, but also point out on peculiarities of underlying behaviors that limit a simple parallel between OFT and male reproduction (Table 1). Male reproductive behavior does not fit a simple maximization criterion. It should be better viewed as a complex optimization problem with specific currencies. The parallel between OFT and male reproductive behavior is worth the debate, but the paucity of strong demonstration to date could make the debate sterile. Rather, this idea should yield testable predictions guiding and inspiring future research.

Suboptimal rate-maximizing strategy?

The main prediction resulting from the theory detailed above is that the reproductive behavior of insect males results in a lower mating rate than the higher rate potentially achieved in the environment. The reason is that male fitness is underpinned by other currencies than a mere mating rate, because males gain to reject females depending on their

quality or availability. We thus suggest that optimal male mating rate should be seen, as for females [2], as reaction norms rather than a constant and evolutionary fixed optimum. Males should consequently adapt their mating frequency to experienced environmental conditions such as mating costs, female quality and spatial / temporal distribution.

Mating patterns and population dynamic depend, in part, on the male choice

Although mate choice is generally attributed to females, male mate choice by males has been recognized for its role in mating patterns and its consequent influence on sexual selection [58]. The optimality perspective developed here may serve to understand the consequences of male choice on population dynamic. For instance, males of some insect species continue to mate after being sperm-depleted [40,59]. Although such a behavior can appear as an evolutionary conundrum, it was hypothesized that such a behavior increases the fitness of sperm-depleted males by having a direct influence on the offspring sex-ratio [40]. From our perspective, we predict that sperm-depleted males exhibit a specific foraging behavior reflecting competition with conspecific males rather than a direct transmission of gametes. Further researches are thus needed to better understand how fertilization potential determines male foraging strategy.

Males exhibit proximate mechanisms of foraging.

If males face an optimal foraging issue, we can predict that they will display proximate mechanisms common to optimal foraging in other contexts. These mechanisms have been thoroughly described in the case of parasitoids foraging for hosts [56,60,61], and recent studies show interesting analogies between female exploiting host patches and male

exploiting female patches [19,20]. For instance, male tendency to leave a female patch depends on the total number of females as well as the number and status of the females encountered, just like the female tendency to leave a host patch depends on the total number of hosts and the number and status of the hosts encountered. Research on the behavioral ecology of parasitoids is fruitful and dynamic [61]. We therefore expect a rising interest for the mechanistic and cognitive underpinnings of male mate choice and patch exploitation.

6. Conclusion

In this paper, we proposed that OFT could be applied to better understand some facets of male reproduction such as male mate choice and male behavior when females are patchily distributed. The underlying idea is that male reproductive strategy is certainly not the result of a simple maximization of the number of matings. Rather, male reproduction is better understood as a complex optimization problem, and OFT is a relevant paradigm to formalize questions and interpret observations. We thus detailed the specific situations where OFT could be applied to male foraging for females (Table 1). We argue that females can be envisaged as resources of varying quality for males, with possible aggregation and depletion, so that classic optimal foraging models such as the prey and patch models are likely relevant for analyzing male reproductive behavior. Reasoning male foraging behavior in terms of optimality nonetheless depends on idiosyncrasies of insect species, including the mating system or the social system. We thus point out that any optimal

behavior is understandable only if all the variables underlying the decision process are considered. For instance, the preference for a given type of female may depend on the female intrinsic quality but also on environment-wide characteristics such as the predictability and distribution of other females. To date, little is known about the way male insects perceive and use information in order to optimize their foraging strategies. We thus hope behavioral ecologists will be interested in the idea that male insects may exhibit optimal foraging behaviors.

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Table 1. Transposition of the main OFT assumptions to males foraging for females.

Assumptions of the OFT	Transposition to males foraging for females
General assumptions	
The currency consists of maximizing long-term average rate of energy intake for the forager.	The male aims at maximizing the number of females mated per unit of time.
Encounters with preys/hosts follow a sequential Poisson process.	The male encounters females one at a time at a constant encountering probability.
The forager has a complete information and recognizes each prey type and patch density.	The male has complete information and recognizes each female type and patch density.
Searching and handling activities are exclusives.	Seeking and mating females are exclusive activities.
Assumptions of the prey model	
Different prey types can be found in the environment and provide different profitability levels for the forager.	Different female types (i.e. virgin, mated….) can be found in the environment and provide different profitability levels for the male.
Encounter without attack is not costly in time and energy.	Encounter with a female without mating is not costly for the male.
The decision of the forager is to attack or not a given prey upon encounter according to the rate at which each prey type is encountered.	The decision of the male is to mate or reject the encountered females according to the rate at which each female type is encountered.
Assumptions of the patch model	
The forager sequentially visits different patch types of varying quality.	The male visits successively a sequence of patches formed by a various number of females or by their quality.
The energy gain obtained in a given patch type is a decelerating function of time due to patch depletion.	The number of females the male mates in a patch increases at a decelerating rate due to mating.
The decision of the forager is to stay or leave the patch at the appropriate time.	The decision of the male is to stay or leave the patch of females at the appropriate time.