



The male mate search: an optimal foraging issue?

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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 (OFT), 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 OFT to male reproductive behavior.

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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 [3,4*,5*,6,7]: 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 [8–13,14*]. 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.

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

Table 1

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

Assumptions of the OFT	Transposition to males foraging for females
<i>General assumptions</i>	
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.
<i>Assumptions of the prey model</i>	
Different prey types can be found in the environment and provide different profitability levels for the forager.	Different female types (i.e. virgin, mated, etc.) 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.
<i>Assumptions of the patch model</i>	
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.

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.

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)?

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.

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 (Table 1). 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^{*},34–39,40^{*}]. 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

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