

A THEORETICAL APPROACH TO UNDERSTANDING MATE SEARCHING BEHAVIOR IN FEMALES**Perla Catalina Chaparro Pedraza****Advisor: Juan Manuel Cordovez****Coadvisor: Daniel Cadena****ABSTRACT**

While searching for mates, females are faced with the tradeoff of maximizing their benefit (finding high-quality males) while reducing the search costs in the face of limitations posed by cognition in terms of memory and accuracy in the perception of male traits signaling quality. Searching females may use various strategies, including sequential search, best-of-n, and Bayesian search. Most studies investigating mate choice have focused more in the result (i. e. traits of selected males) and less in the process, and the fitness consequences of alternative strategies have not been assessed. Because studying mate-searching behavior through experimental manipulation in wild populations is difficult, we proposed a theoretical approach to studying female mate choice using an agent based model (ABM) to quantify the effect on female and male fitness of parameters of variation in female exigency, age, memory and perception. The model was parameterized with data from species in the avian family Pipridae (manakin), which have been extensively studied as models in sexual selection. We found that old (i.e. experienced) females had higher fitness than young ones, and that increases in female exigency leads to decreases in female fitness and increases in male fitness. Fitness of males and females were negatively related under various scenarios, suggesting that variation in female behavior may result in sexual conflict. Variation in memory and perception influenced fitness when females could select among all males, but did not affect fitness when males exhibited dominance hierarchies.

INTRODUCTION

According to classical sexual selection theory, in species with a biased operational sex ratio individuals of the sex not restricted by available mates and having greater parental investment should be choosier than individuals of the other sex; in turn, individuals of the sex constrained by mating opportunities should experience intrasexual competition for mates (Trivers , 1972; Emlen & Oring, 1977). As a consequence of mate choice and intrasexual competition, traits of individuals of the non limiting sex are expected to be under sexual selection, which often leads to the evolution of ornaments, armaments and behaviors allowing individuals to gain access to

individuals of the limiting sex (Darwin, 1871; Emlen & Oring, 1977). Typically, females are the choosier sex because they often show greater parental investment derived from egg production, gestation, and offspring defense and feeding (Emlen & Oring, 1977).

When mating, females must gather and process information about prospective mates, and then select mates based on mating preferences (Castellano & Cermelli, 2011). However, spatial and temporal constraints may preclude the full assessment of all potential mates, and limited perceptual ability and memory may affect quality assessment (Fisher et al, 2002). Hence, females are faced with the tradeoff of maximizing their benefit (i.e., choosing the best possible male based on incomplete information) while minimizing costs. It is thus expected that females would adopt a search strategy optimizing their fitness return (Real, 1990; Reynolds & Gross, 1990).

Several theoretical models have been proposed to describe search strategies employed by females while assessing and choosing mates; in this study we focus on three of these models: sequential search, best-of-n, and Bayesian search (Janetos, 1980; Real, 1990; Luttbeg, 1996). A female using sequential search visits males sequentially until a male with some fixed minimum quality is encountered and selected (Real, 1990). In the best-of-n strategy, females visit and evaluate a fixed number of males and then select the best mate among them (Janetos, 1980). In both sequential search and best-of-n strategies, females obtain sufficient information about the quality of potential mates during a single visit and therefore do not revisit males (except to mate with the best male in best-of-n). In the Bayesian search strategy, females visit males and then revisit them subsequently to refine information before selecting a mate (Luttbeg, 1996). Recently, variants of the above models have incorporated a degree of uncertainty in male assessments conducted by females owing to females being unable to control the accuracy of acquired information due to perceptual and cognitive limitations (Phelps et al, 2006). To our knowledge, model variations have not yet taken into consideration that females may retain information acquired during one breeding season on to subsequent breeding seasons; in systems where males maintain their territories or display arenas across breeding seasons, females may locate their preferred males using information from previous breeding seasons and perform little to no additional searching (DuVal, 2013).

Mate-searching behavior determines the likelihood of finding high-quality males, which, in turn, increases female fitness through accrued direct and indirect benefits. However, spatial and temporal constraints and unreliable information available during the mate-choice process may increase costs and thus reduce fitness. Despite the important consequences of mate-searching behavior for female fitness, most studies on mate choice have focused largely on the outcome of the process, namely on identifying the traits exhibited by preferred mates. In contrast, few studies have investigated the mechanisms leading females to choose a particular mate and the consequences of such mechanisms for organismal fitness (Andersson, 1994; Ryan et al, 2007).

The fitness consequences of alternative mate-searching behaviors are difficult to study through observation or experimental manipulation, and this may explain why studies on this issue are so scarce despite their importance. To overcome such difficulties, we here employ a theoretical

approach using an agent-based model (ABM) to evaluate the fitness consequences, for both females and males, of variation in parameters related to cognitive processes in females (i.e., quality of perception, memory) and in the degree of female exigency given the three search strategies described above. To build our models, we used biological information on birds in the manakin family (Pipridae), which have been thoroughly studied as a sexual selection model.

METHODS

Study system

Lek-mating systems are appropriate models for studying sexual selection (Hoglund & Alatalo, 1995). Almost all species in the manakin family exhibit lek-mating systems in which females select males upon examination at display arenas (Prum, 1994; Snow, 2004). In most species with lek-mating systems, females only receive indirect benefits (males only contribute genes and females must raise offspring on their own) and reproductive success among males is highly skewed (DuVal & Kempnaers, 2008). Manakins often exhibit marked sexual dimorphism and strong reproductive skew in males driven by female mate choice or by male-male interactions leading to social hierarchies (Foster, 1977; Mc Donald, 1989a; DuVal, 2007). Several studies have examined traits associated with reproductive success in male manakins (Foster, 1981; Shorey, 2002; Stein & Uy, 2006; Ryder et al, 2010; Duraes et al, 2009), but information on mate-searching behavior by females is scarce. A recent observational study documented the occurrence of several search strategies within a population of Long-tailed Manakins (*Chiroxiphia linearis*) (Ward, 2012), but the fitness consequences of employing different strategies have not been examined.

Model setup

We implemented an ABM that positions a fixed number of males in a rectangular grid of fixed area. Males are stationary and each has a phenotype signaling its quality; trait values are assigned to individual males based on a zero-truncated normal distribution with mean 5 and standard deviation 1 (continuous traits are often normally distributed; (Falconer & Mackay, 1996). Leks are groups of variable size, and number of males is randomly selected from a normal distribution centered in 8 with deviation 2 and truncated at 3 and 13; these values were established based on existing field data for *C. linearis* (Ward, 2012). Leks are randomly distributed within the grid. In simulations in which social hierarchies exist, the highest quality male in each lek is defined as the alpha male, which is the only male allowed to mate with females visiting the lek.

The model separates females by age into young and old. When searching for mates, young (i.e., inexperienced) females are assumed not to have information on the spatial location of high-quality males, so they start their searches at a random location in the grid; in contrast, old (i.e., experienced) females begin searching in close proximity of a good-quality male, assuming they retain information from previous breeding seasons that helps them locate the best males (DuVal, 2013). Females are able to move freely from the initial site and visit locations occupied by males to evaluate them and eventually mate; when moving from one male's location to another, females always move to the male in closest proximity. Female movement depends on established rules

based on the alternative mate-searching strategies. Females using the sequential search strategy visit males until a male with a quality greater than a defined threshold is encountered and selected. Females using the best-of-n strategy visit a fixed number of males or search during a fixed time. Finally, females using Bayesian search construct a probability distribution of male quality based on which they estimate the probability of finding a better male than those encountered before based on previous observations; with each new observation, females update the probability distribution and determine whether they continue visiting new males or if they revisit previously visited males. When they decide to revisit, they reexamine the top third of previously visited males to refine information and finally mate with the highest-quality male in the subset of revisited males.

The model simulates the assessment process conducted by females: when females arrive at a male's location they spend time assessing him; good-quality males are visited for longer relative to low-quality males (time spent assessing is proportional to quality following a linear relation). The assessment process ends when females assign an observed quality to a particular male. The value for observed quality is sampled from a normal distribution centered in the real quality (i.e., the phenotypic trait indicating quality) and with standard deviation inversely proportional to time spent in observation (we assume that greater time of observation allows for greater accuracy in assessment). When using the best-of-n and Bayesian search strategies, the prospective mate is selected based on comparison among observations; thus, females have to remember the quality of all assessed males. Remembered quality is sampled from a normal distribution with mean equal to observed quality and standard deviation depending on number of observations and elapsed time; we assume that memory becomes less reliable as females visit more males or as they spend more time searching.

Estimating fitness consequences of mate-searching behavior

Male and female fitness is expressed in terms the number of viable offspring given an amount of energy invested. In our model, offspring quality depends on male quality; females selecting high-quality males would have high-quality offspring because these would inherit "good genes" (or genes enhancing attractiveness). Female costs are computed considering energy spent in the assessment process, taking into consideration the distance traveled and the time spent searching. Male costs depend on their quality; because displays are energetically costly and male traits have been shown to be honest indicators of quality in manakins (Duraes et al, 2009), we assumed that energy expenditure is proportional to male quality. To quantify benefits and costs to males and females, we used information derived from various studies on manakin biology summarized in Table 1.

Table 1. Parameters used to estimate benefits and costs of different mate-searching strategies. Error terms indicate standard deviations.

Parameter	Species	Parameter value		Reference
Basal metabolic rate of males	<i>Manacus vitellinus</i>	60±3.73	kJ/day	(Barsk et al, 2011)
Metabolic rate of displaying males	<i>Manacus vitellinus</i>	120±2.9	kJ/day	(Barsk et al, 2011)
Basal metabolic rate of females	<i>Manacus vitellinus</i>	72.7	kJ/day	Calculated based on (Vleck & Vleck, 1979) with data from (Barsk et al, 2011)
Time spent in mate searching	<i>Chiroxiphia linearis</i>	3	hours/day	(Ward, 2012)
Number of leks visited	<i>Chiroxiphia linearis</i>	4.02	leks/day	(Ward, 2012)
Increase in home range during breeding season	<i>Pipra pipra</i>	3 times home range		(Thery, 1992)
Mean time spent foraging at each tree	Several species of frugivorous Neotropical birds	4	min/tree	(Wheelwright, 1991)
Fruits eaten in foraging	Several species of frugivorous neotropical birds	3	fruits/tree	(Wheelwright, 1991)
Dry pulp eaten	<i>Manacus vitellinus</i>	0.046	g dry pulp/fruit	(Worthington, 1989)
Energy in dry pulp	<i>Manacus vitellinus</i>	14.3	kJ/g dry pulp	(Worthington, 1989)
Efficiency in energy assimilation	<i>Manacus vitellinus</i>	61%		(Worthington, 1989)
Clutch size	Several species of manakins	2		(Snow, 2004)
Nesting success	<i>Manacus vitellinus</i>	13.8%		(Brawn et al, 2011)
Survival rate of adults	<i>Manacus vitellinus</i>	47%		(Karr et al, 1990)

Female benefits

To estimate number of offspring we assumed clutch size and nesting success as constants in the model. Survival rate of offspring was set to be related linearly to the quality of the selected male (i.e., the sire). Thus, female benefits are described as:

$$female\ benefit = Clutch\ size \times nesting\ success \times survival\ rate \quad (1)$$

Female costs

Females incur in costs associated to energy expenditure while assessing mates. We here consider the cost resulting from traveling to leks and from the associated reduction in foraging time (Gibson & Bachman, 1992). Female Long-tailed Manakins (*Chiroxiphia linearis*) spend an average of three

hours per day searching for males and they visit a mean of 4.02 leks per day (Ward, 2012). Given an estimate of the basal metabolic rate of females, we assumed the average increase in metabolic rate during mate searching is three times that of the nonbreeding season because female manakins are known to expand their home range by a factor of three during the mating season (Thery, 1992). In our model, females visiting the average of 4.02 leks were assigned the average 3x increase in metabolic rate resulting from traveling. We assumed females visiting no leks do not spend any energy in searching, and used a linear relationship with average increase (3x) in metabolic rate for 4.02 leks and 0 kJ for 0 leks. Based on the consideration of the above variables, this linear relation leads to the following function:

$$\text{female cost of traveling} = 4.517 \text{ kJ/lek} \times \text{number of leks visited} \quad (2)$$

The cost associated to the reduction in foraging time (eq. 3) is assumed to be proportional to the time spent assessing males and to the energy females could potentially gain during this time if they were foraging. The potential energy gain is computed based on the product of an estimate of number of fruits eaten per tree, the average energy content in dry pulp per fruit, and energy assimilation efficiency. According to data in Table 1 this product is 1.20 kJ/tree; because females roughly spend a mean of 4 minutes foraging in each tree, we estimate that they fail to earn 0.30 kJ/min while searching for and assessing mates:

$$\text{female cost caused by less time foraging} = \text{time spent in assessment} \times 0.30 \text{ kJ/min} \quad (3)$$

Male benefits

As for females, to estimate number of viable offspring sired by males we assumed clutch size and nesting success to be constant (Table 1). Again, offspring survival rate was related linearly to the sire's quality. Male benefits (eq. 4) are thus computed by multiplying these parameters by the number of matings:

$$\text{male benefit} = \text{Clutch size} \times \text{nesting success} \times \text{survival rate} \times \text{number of matings} \quad (4)$$

Male costs

We assume that male displays are energetically expensive and that males of higher quality exhibit better (i.e., more costly) displays (displays are honest indicators of male quality). We assume that average males in the model (those with assigned quality of 5) increase their energy expenditure while displaying in 60 kJ, the difference between basal metabolic rate and metabolic rate of displaying males (Table 1). Males with quality located at one standard deviation from the mean (i.e., quality of 6) were assumed to spend 2.9 kJ/day more than those of mean quality (2.9 kJ/day is the standard deviation of the estimated metabolic rate of displaying males) (Barsk et al, 2011). We assumed the relation between display cost and male quality to be an exponential function defined based on energy expenditure of males, and calculated this function's parameters based on data for males of mean quality and males with values one standard deviation from the mean. We

assumed the function to be exponential reasoning that at increasing values of male quality, improving quality in a fixed amount would require greater relative investment in energy.

$$\text{male cost} = 43.45\text{kJ} \times 1.067^{\text{quality}} \quad (5)$$

With the above information, we computed benefits/costs ratios (hereafter BCR) as proxy of fitness for females and males for each run of our model with varying parameters (see below). Hereafter, we use these estimates of BCR (expressed in units of number of offspring per kJ invested) to examine the fitness consequences of alternative search strategies for females and males under various circumstances.

Assessing the influence of female exigency, perception, memory and prior experience, and of male hierarchies

We used our ABM to investigate the fitness consequences of parameters related to female traits including their degree of exigency in mate-selection decisions, the accuracy of their perception of male quality, and their ability to memorize male quality. We also examined the effect of social organization by considering the fitness consequences of alternative search strategies.

- **Female exigency:** We modeled the effect of variation in the degree of female exigency under each alternative search strategy. For females using sequential search, we varied the threshold (i.e., minimum quality) of selected males between 4 and 8 at intervals of 0.1. For females using the best-of-n strategy, we varied (1) the fixed number of males visited from 2 to 20 considering all integer values or (2) the fixed time devoted to search between 300 and 3000 seconds with intervals of 50 seconds. For females using Bayesian search, we allowed exigency to vary (i.e., to increase) by subtracting a value between 0 and 0.5 (at intervals of 0.05) from the probability of revisiting estimated by females.
- **Prior experience:** We examined fitness separately for young (inexperienced) and old (experienced) females.
- **Perception:** As described above, observed male quality is offset from its real quality to an extent defined by an inverse linear relation with the time spent in assessment. We introduced variation in perceptual ability by changing the slope of the linear function used to describe decay in the accuracy of perception with decreasing assessment time. The slope is calculated by multiplying a constant 1/3 by integers between 20 and 500, with intervals of 20 (i.e., 20, 40, ..., 180, 500). The value of 1/3 was selected empirically to result in meaningful values of the deviation of observed quality from real quality.
- **Memory:** In the model, remembered quality is offset from observed quality to an extent defined by the direct relation with the time elapsed and the number of observations. Variation in ability to memorize was introduced by changing the slope of the linear function used to describe above relation. The slope is calculated by dividing a constant 1/1000 by numbers from 1 to 15, with intervals of 0.5. The value of 1/1000 was selected

empirically to result in meaningful values of the deviation of remembered quality from observed quality.

- Hierarchies: We considered scenarios in which any male could be selected by females to mate (i.e., without hierarchies) and scenarios in which there is an alpha male in each lek; alphas were the only males mating with visiting females. In the latter scenarios, females only selected among alpha males in the grid.

Model implementation and statistical analysis

We implemented the model in MATLAB Mathworks. We simulated a single breeding season with 150 females and 160 males and replicated it 1000 times for each combination of parameters. To evaluate male fitness, males were classified into five groups according to their quality. Benefits and costs of males and females in each breeding season were saved to build plots with 95% confidence intervals. To analyze the effect of hierarchies when there is variation in memory we used Kolmogorov-Smirnov tests to compare the distributions of fitness across different parameters describing memory and between situations with and without hierarchies. The linear relation between perception and female fitness allowed us to use an ANCOVA test to determine the effect of perception in fitness with the presence of hierarchies as covariable. These analyses were repeated for each of the three search strategies.

Elasticity analysis

We conducted an elasticity analysis to determine the effect of each parameter on our estimates of fitness. To do this we found the maximum change in fitness in relation to the each parameter (i.e., the maximum value of derivative) standardized by the parameter value to allow for comparisons between different functions. Greater values indicate a greater change in fitness when a given parameter varies.

RESULTS

Female exigency

Female exigency affected female and male fitness in different ways given each search strategy (Figure 1). In females, fitness (BCR) was affected differently by exigency under the different search strategies. In sequential search, we observed a sigmoidal relationship in which increases in exigency (i.e., in threshold values for mating) resulted in decreases in female fitness regardless of female age (experience, Figure 1a). In best-of-n, for both variations (fixed number of males and fixed time), the function we obtained fits a hyperbola describing an inversely proportional relation between exigency in decision (i.e., visiting more males or searching for a longer time) and fitness for both young and old females (Figure 1c and 1e). Finally, in Bayesian search, exigency and female fitness were linearly related; this relationship was negative in young females and showed a positive but non-significant trend in old females (Figure 1g).

Overall, high-quality males performed better than lower quality males across all search strategies and parameter values; in fact, we found that males in the two lower-quality groups never mated, and thus we do not show them in plots. As in females, the consequences of female exigency on male fitness differed between strategies, but in contrast to females, males generally increased their fitness when female exigency increased (Figure 1b, 1d, 1f), except in Bayesian search (Figure 1h), where male fitness was unrelated to female exigency. In general, male fitness functions were noisier than female fitness functions.

Prior experience

Overall, old females had higher fitness than young ones, but differences in fitness between old and young females decreased with increases in female exigency, becoming non-significant at high exigency values in sequential search and best-of-n strategies (Figure 1a, 1c, 1e). In Bayesian search, fitness of old females was significantly higher than that of young females for all values of female exigency, and fitness differences increased with increases in female exigency (Figure 1g). The only additional effect of age we detected was the different pattern observed for old females performing Bayesian search given different exigency values described above.

Memory, perception and hierarchies

Hierarchies had an effect on female fitness when there was variation in memory and perception. When hierarchies existed (i. e., leks with alpha male), the variation in memory and perception had no significant effect on fitness ($p > 0.05$) (Figure 2a and 2c). In contrast, when there were no hierarchies, both memory and perception had an effect on female fitness (figure 2b and 2d). Kolmogorov-Smirnov tests comparing the distributions of female fitness across different parameters describing memory between situations with and without hierarchies revealed significant difference for the three strategies ($p < 0.01$; by definition, memory has no importance for sequential search). Without hierarchies, perception had a strong effect on fitness (linear regression from ANCOVA test $p < 0.01$), being stronger for females using sequential search and best-of-n strategies (Figure 2b). With no hierarchies, memory variation had a stronger effect on fitness of females using best-of-n strategy than on females using Bayesian search (K-S test $p < 0.01$) (Figure 2d). The relationship between female fitness and memory was positive logarithmic whereas that with perception was positive linear.

As in female fitness, fitness of males in the highest quality group increased when females have good perception and memory capabilities and there are not hierarchies. Similarly to female fitness, when there were no hierarchies, male fitness was unaffected by variation in memory and perception.

Elasticity analysis

Elasticity analysis showed that parameters related to female exigency (i. e. threshold value, fixed number of males, fixed time to search, revisit decision) had strong effects on female fitness (range 0.99- 1.06 depending on strategy and age). The effects of parameters related to female exigency

were two orders of magnitude greater than those related to memory (0.01-0.04) and perception (0.01-0.05).

DISCUSSION

Female exigency and its consequences on female and male fitness

Regardless of the search strategy employed (except for Bayesian search by old females), simulations based on our ABM indicated that female fitness decreases when females are highly choosy. According to classical sexual theory, females are expected to be choosy (Bateman, 1948), but our model suggests that the choosiest females perceive the lowest fitness because of their high searching costs. In consequence, females should not be choosy when searching costs are high, as reported for some natural systems (Meuche et al, 2013). On the other hand, theory suggests that females exhibiting low exigency should also experience low fitness because of their mating with low-quality males, but we did not observe such pattern. We believe this result may be explained by considering the consequences of alternative search strategies for males, as discussed below.

Most theoretical studies of mate-searching strategies have focused on the optimization of benefit/cost ratios resulting in female fitness (Luttbeg, 2002; Wiegmann et al, 2010). A notable result obtained from our model is that males perform better at values of female exigency where females perform worse and vice versa; this was true when females used sequential search and best-of-n strategies, but was not the case of Bayesian search where male fitness was unaffected by female exigency (Figure 1h). The opposite effect of female exigency on female and male fitness is, in fact, quite remarkable. For example, when females use sequential search the relationship between exigency and female fitness has a negative sigmoidal shape; in this case, the relationship between female exigency and fitness of the highest-quality males (which should receive most of the matings) resembles a positive sigmoidal function. Likewise, given the best-of-n strategy, females experience a most steep decrease in fitness with exigency, while the fitness of the highest-quality males increases steeply with exigency describing an inverse rectangular hyperbola.

The inverse correlation between female and male fitness given variation in female exigency suggests a possible "battle of sexes" caused by the conflict of interests between sexes. Sexual conflict has been proposed as a consequence of opposite interests of males and females in terms of parental investment (Trivers, 1972). Thus, the dynamics of sexual conflict in mating systems where females receive direct benefits from males has been well studied (Schustes & Sigmund, 1981). Recently, however, studies have demonstrated that the battle of sexes may also occur in mating systems where females receive only indirect benefits (Cameron et al, 2003), in which mate-choice may have even evolved as a consequence of sexual conflict (Gavrilets et al, 2001). To our knowledge, there are no previous studies where male fitness associated with alternative female mate-searching strategies was estimated. Our results suggesting a potential sexual conflict indicate that consideration of both female and male fitness may be crucial to understanding the evolution of mate-searching behavior.

Females using the best-of-n strategy experienced the steepest decrease in fitness with increasing exigency. Other models have demonstrated that best-of-n is the least optimal strategy for females under various conditions (Wiegmann, 2010), but empirical studies have observed individuals using this strategy when searching for mates (Jennions & Petrie, 1997). A possible explanation for maintenance of this strategy in nature offered by our model is that, despite reducing female fitness, it may be optimal for males. Again, this underscores the importance of considering male fitness in studies of female mate-searching behavior.

An additional difference noted between sexes is that stochasticity seems to play a more important role in male fitness than in female fitness, as shown by the higher variability in plots depicting male fitness given various parameters. High stochasticity could be understood as low predictability and is consistent with the high variance in reproductive success of males in natural populations (Bateman, 1948).

Age

As expected, old females performed better than young females because they have knowledge from previous breeding seasons allowing them to mate with good-quality mates and to minimize search cost. The most marked contrast between old and young females fitness occurred when females use Bayesian search due to old females constructing a prior probability distribution of male quality based on previous knowledge. Our model assumed that the location of male display areas was conserved from season to season; however the model based on young females is applicable to species with unstable display areas.

Memory, perception and hierarchies

We expected that limitations in memory and perception would affect female fitness because of inaccuracy in the assessment process. We found support for this prediction in a mating system without hierarchies, but not when hierarchies existed. This result is attributable to the fact that, with hierarchies, females can select mates only among alpha males, which are good-quality males by definition. Our observation that female exigency has a great effect on female and male fitness even with hierarchies and that any effects of perception and memory disappear when hierarchies exist is consistent with our results in elasticity analysis showing exigency has a much stronger effect on fitness of memory and perception capabilities.

Conclusions

This study provided the first approach to evaluating the effect of alternative mate searching behaviors on both male and female fitness. This allowed us to find unexpected evidence suggesting sexual conflict, and fitness functions suggesting optimal values of female exigency and perceptual abilities not only for females but also for males. Finally, our model allowed us to assess the interaction between cognitive constraints in mate choice, search strategies and the presence of hierarchies in lekking systems in determining fitness; such interactions can hardly be studied via observation or experimentation, highlighting the value of a theoretical approach. Future

developments of our approach should consider simulating populations over long time to determine the effect of results in fitness presented above in evolutionary scales.

FIGURES

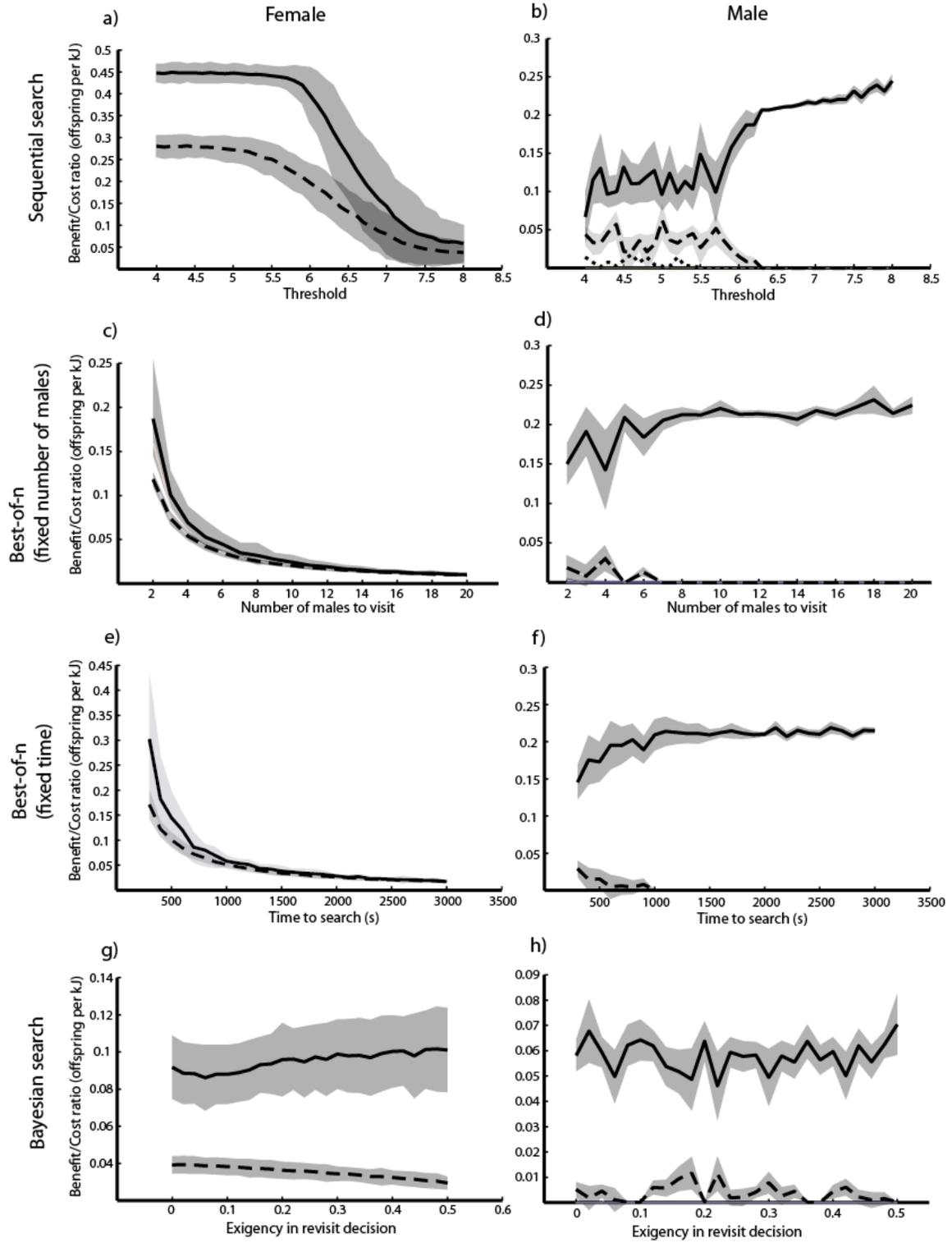


Figure 1. Female benefit/cost ratio (vertical axes of left column) decreases when female exigency increases (horizontal axes), except in Bayesian search g). Male benefit/cost ratios increases (vertical axes of right column) when female exigency increases, except in Bayesian search. Plots show a high inverse correlation between benefit/cost ratio of males and females in each strategy (the first row presents the results when females use the sequential search strategy, the second and third row show the benefit-cost ratio when females employ Best-of-n with a fixed number of males (second) and when they use Best-of-n with a fixed time to search (third), and the fourth row shows benefit-cost ratio when females employ Bayesian search). In general, old females (solid lines in left column graphs) perform better than young females (dashed line). Males of high quality (solid line in right column graphs) perform better when females exigency increases, except in Bayesian search, and males of lower qualities (dashed and pointed lines) decreases their benefit/cost ratio when females exigency increases until they do not mate therefore their benefit/cost ratio is zero.

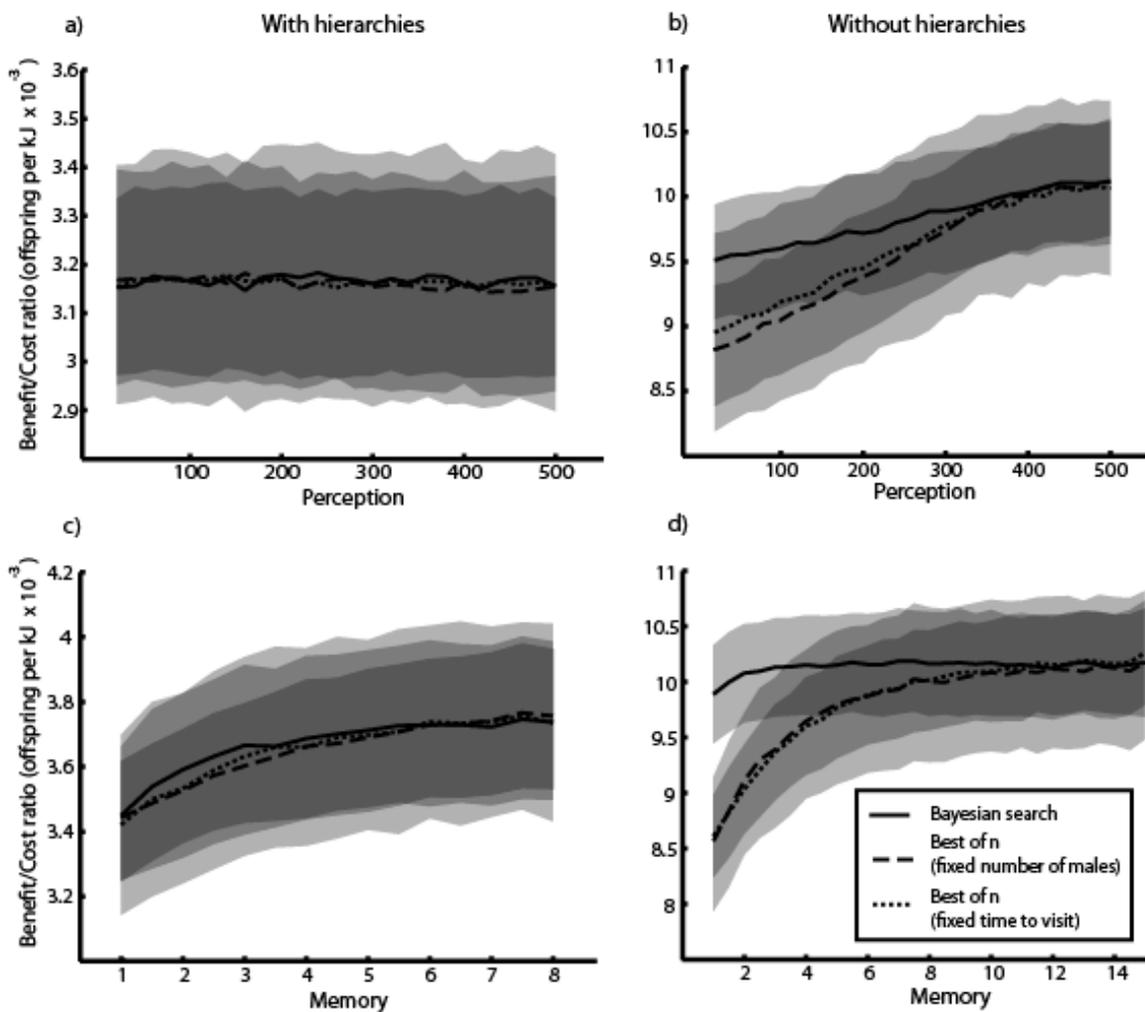


Figure 2. When male hierarchies exist (left column) females do not decrease their fitness (vertical axes) when they have bad perception (first row of plots) and low memory capabilities (second row of plots). Female performance increases when memory and perception capabilities increase only when there are no hierarchies (right column), while the effect of cognitive constraints disappears when hierarchies are present.

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