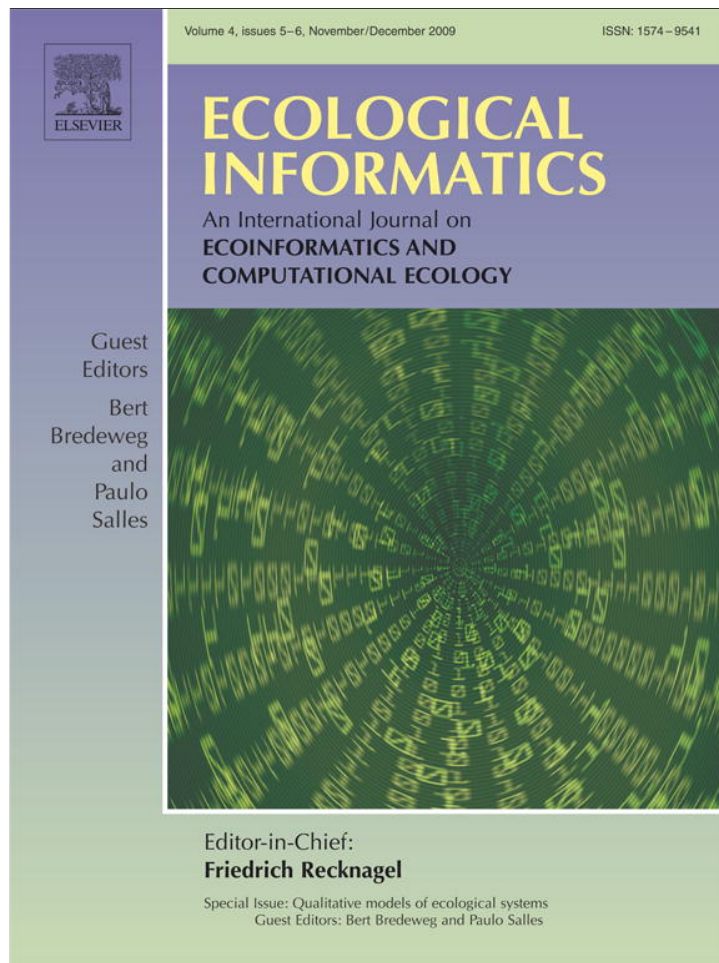


Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Contents lists available at ScienceDirect

Ecological Informatics

journal homepage: www.elsevier.com/locate/ecolinf

Mate guarding and searching for extra-pair copulations: Decision-making when interests diverge

R.I. Dias^{a,*}, P. Salles^b, R.H. Macedo^c

^a Programa de Pós-Graduação em Ecologia, Universidade de Brasília, Brasília, Brazil

^b Institute of Biological Sciences, University of Brasília, Brasília, Brazil

^c Departamento de Zoologia, Universidade de Brasília, Brasília, Brazil

ARTICLE INFO

Article history:

Received 1 December 2008

Received in revised form 3 September 2009

Accepted 8 September 2009

Keywords:

Paternity

Mate choice

Sexual conflict

Modeling

Qualitative reasoning

ABSTRACT

Extra-pair paternity is widespread among avian species, and large variations in frequency occur both within and among species. These variations result from individual, ecological and phylogenetic influences that impinge upon the strategies used in searching for extra-pair copulations. We used qualitative reasoning to evaluate how the decision-making process for each sex could affect the occurrence of extra-pair paternity and fitness. We demonstrate that the quality of the female's mate influences the female's inclination to search for extra-pair copulations. Also shown is the result that high quality males produce a higher number of within-pair and extra-pair young. Since the interests of males and females converge in certain aspects, both sexes achieved an increment in fitness. The model presented in this paper suggests that the conflict of interests between the sexes is influenced by the willingness of females to engage in extra-pair copulations and by the quality of the male to which the female is mated.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

The study of monogamy in birds changed greatly with the application of molecular tools, showing that monogamy is much more complex than initially suggested. Monogamy has been conceptually redefined as a web of complex interactions between paired males and females that typically have conflicts of interest (Westneat and Stewart, 2003). The overall result of such interactions, evaluated on a wide scale, is a high variation in the level of extra-pair fertilization (EPF) among species, ranging from 0 to 70% (Griffith et al., 2002).

Several hypotheses have been suggested to explain this large variation. Among the first hypotheses proposed was that of breeding density, which suggests that a closer proximity to neighbors could facilitate extra-pair copulations (EPC) as well as enhance the opportunities to evaluate potential mates (Birkhead and Møller, 1992; Møller and Birkhead, 1993). Although intuitively appealing, this hypothesis has not been well supported at the intra-specific level (*Uria aalge*, Hatchwell, 1988; *Agelaius phoeniceus*, Gibbs et al., 1990; *Hirundo rustica*, Møller, 1991; *Dendroica petechia*, Yezerinac et al., 1999), and other studies have failed to demonstrate a relation between density and EPF among species (Westneat and Sherman, 1997; Wink and Dyrce, 1999).

It is clear that males can increase their reproductive gain without any additional parental investment by seeking for EPCs (Westneat, 1990; Birkhead and Møller, 1992). However, the reproductive gain for

females is less obvious, because females are limited by the number of eggs they can produce (Trivers, 1972). Thus, females cannot enhance the number of offspring through promiscuous behaviour. This fact raises some concern about the role of female behaviour in determining rates of extra-pair paternity. On the other hand, recent studies have demonstrated that females of different socially monogamous species actively search for EPCs (Petrie et al., 1998; Griffith et al., 2002; Westneat and Stewart, 2003). Females that engage in EPCs could gain direct benefits, such as access to resources controlled by the extra-pair male as well as parental investment (Otter et al., 1994; Gray, 1997). Also suggested are indirect benefits that could be gained, such as high quality genes (Hasselquist et al., 1996) and improved genetic compatibility (Johnsen et al., 2000).

According to the “good genes hypothesis”, if males differ in genetic quality, females paired with low quality males could improve their fitness by obtaining EPCs from males of higher quality than their partner, improving the survival and reproductive chances of their offspring (Jennions and Petrie, 2000). Nevertheless, from the male's perspective, EPCs are only valuable for those males that obtain EPFs, but are disastrous for those males that lose paternity in their own nests. Thus, males must attempt to prevent their females from engaging in EPCs to avoid a future cost of rearing offspring sired by other males. As a result, males developed counterstrategies to prevent or decrease the chances that their females engage in EPCs (Trivers, 1972). The tactic commonly used by males takes the form of mate guarding, which consists of following the female during her fertile period to prevent copulation with other males (Birkhead and Møller,

* Corresponding author. Tel.: +55 61 3307 2265.

E-mail address: raphaeligor@unb.br (R.I. Dias).

1992). While males also try to increase their fitness through EPCs, they incur a higher risk of losing paternity by leaving their own female unguarded; in other words, males cannot maximize within and extra-pair paternity simultaneously (Hasselquist and Bensch, 1991). The result is that males must decide how much time to allocate to these two mutually exclusive activities, and must adjust mate guarding behaviour according to the risk of being cuckolded.

Males and females must follow adaptive rules of differential allocation, where the reproductive and mating effort depend on their own attractivity (i.e., quality) and that of their mates (Magrath and Komdeur, 2003). Thus, it is reasonable to expect that low quality males should invest more in mate guarding compared to high quality males, and that females mated with high quality males are less likely to search for EPCs. The level of extra-pair paternity in a population reflects the response of a series of possible conflicts between females, their social mates, and one or more extra-pair males (Lifjeld et al., 1994). The conflict between females and their partners depends especially upon whether EPCs and EPFs are costly or beneficial for females.

This paper presents simulation models based on qualitative reasoning (QR) to generate predictions about the evolution of EPC, the role of specific characteristics and behavioural factors that impinge upon the occurrence of extra-pair paternity, evaluating their possible effects on fitness. Models based on QR allow a clear definition of the structure of a system, represent causality and predict the potential behaviour of the system in response to induced changes. QR offers a technique to create and simulate models in a compositional way, applying well accepted ecological knowledge that is still not adequately synthesized (Salles and Bredeweg, 2003; Bredeweg et al., 2009). The main objective of this study is to represent the mechanisms associated with the trade-off between mate guarding and searching for EPCs. More specifically, we describe the mechanisms that: (1) explain the differences observed in strategies of high and low quality males; (2) explain possible variations in the strategies of females mated with these different males; and (3) evaluate the effects of these variables upon fitness.

The proposed model should be capable of answering the following questions:

- 1 – What is the effect of mate quality on female pursuit of extra-pair copulations?
- 2 – Is mate guarding an effective strategy for defending paternity?
- 3 – Is there variation in terms of male and female individual fitness, when the quality of the male is high or low?

When discussing the model we will particularly explore the causal dependencies determining the interactions between males and females to provide explanatory answers to the questions enumerated above.

2. Modeling using qualitative reasoning

The model presented in this study was implemented using elements of ontology provided by the qualitative process theory – QPT (Forbus, 1984). According to QPT, changes in the system are always initiated by processes and their effects propagate to the whole system via causal relations. Processes, which are causal for changes, are modeled as direct influences ($I+$ and $I-$), and propagation of processes, representing a consequence, are modeled with qualitative proportionalities ($P+$ and $P-$). Both direct influences and proportionalities express causal dependencies and mathematical functions (Forbus and de Kleer,

Table 1
Configurations included in the model.

Entity	Configuration	Entity
Population	Includes	Male
Population	Includes	Female
Female	Mate with	Male

Table 2
Quantity representations and respective quantity spaces.

Entity	Quantity	Quantity space	QS
Population	Growth rate	{minus, zero, plus}	Mzp
Population	Density	{zero, low, medium, high}	Zlmh
Male	Mate guarding	{zero, low, medium, high, max}	Zlmhm
Male	Search for EPC	{zero, low, medium, high, max}	Zlmhm
Male	N of within partner chicks (female)	{zero, low, medium, high}	Zlmh
Male	N of extra-pair chicks	{zero, low, medium, high}	Zlmh
Male	Male fitness	{zero, low, medium, high}	Zlmh
Female	Fecundity rate	{minus, zero, plus}	Mzp
Female	N of within partner chicks (male)	{zero, low, medium, high, max}	Zlmhm
Female	N of extra-pair chicks	{zero, low, medium, high}	Zlmh
Female	Fitness variation rate	{minus, zero, plus}	Mzp
Female	Female fitness	{zero, low, medium, high}	Zlmh

1993). Dynamics are captured by differential equations, where constraints are placed on the derivative of a quantity, rather than on the quantity itself. In QPT this is modeled by means of direct influences, which are defined as follows: the relation $I+(Y,R)$ means that R is a rate that represents the magnitude of change in Y in a certain period of time, so that $dY/dt = (... + R...)$. Similarly, $I-(Y,R)$ means that $dY/dt = (... - R...)$. Note that, eventually, the magnitude of R is added to Y (if the relation is $I+$) or subtracted from Y (if the relation is $I-$).

Qualitative proportionalities carry much less information than direct influences. For example $P+(ZX)$ means that there is some function (f) which determines Z , that depends at least on X and is increasing monotonically in its dependence on X , such that $Z=f(...X...)$ and $dZ/dX > 0$. In this case, if X is increasing, then Z will increase as well, and if X is decreasing, Z changes in the same direction. Similarly, $P-(ZX)$ means that if X is increasing, then Z will decrease with the implicit function being decreasing monotonically.

Causality is always expressed in a directed way: both expressions $I+(Y,R)$ and $P+(ZX)$ mean that R and X cause changes respectively in Y and Z , and not the opposite. Combined, direct influences and proportionalities build up a representation of causal chains. For example, the statements $I+(Density, Population\ growth\ rate)$ and $P+(Mate\ guarding, Density)$ express the following causal flow:

Population growth rate \rightarrow Density \rightarrow Mate guarding

More than one influence is actively influencing a quantity, and their effects should be combined. This operation is called *influence*

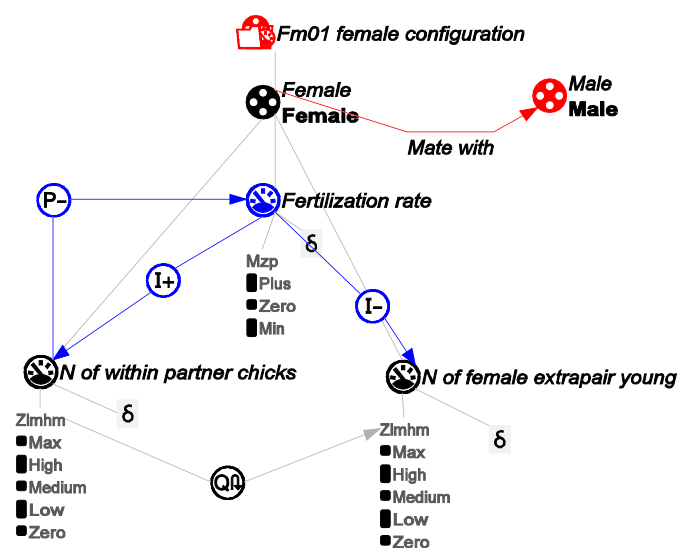


Fig. 1. Model fragment 'Female reproduction'.

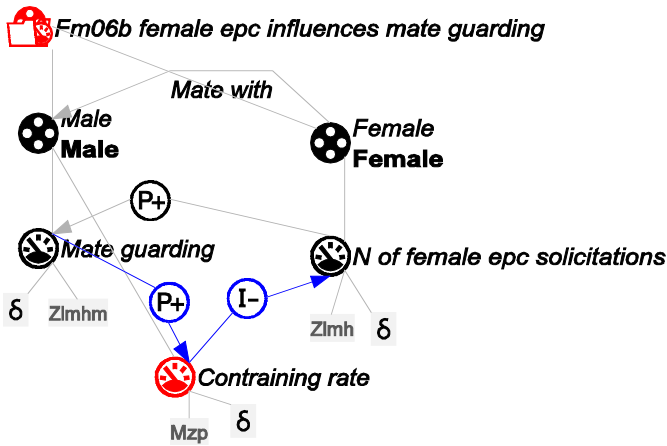


Fig. 2. Model fragment 'Constraint on female behaviour'.

resolution. Direct influences combine via addition. If they have the same sign or if we know their relative magnitudes, it is possible to determine how the influenced quantity will change. If their actual values are not known, the qualitative reasoning engine tries all the possibilities and a number of possible outcomes may be produced.

Influence resolution involving proportionalities follows the same procedure but is often more complex, as this is not necessarily done via addition (it may involve a product or an exponential function). The final result of this ambiguity may cause qualitative simulations to become unmanageable. Possible solutions include introducing more knowledge into the model to solve these ambiguities, the use of assumptions, and other modeling primitives, such as correspondences (see below).

The model presented in the paper is implemented in the qualitative simulator Garp3 (Bredeweg et al., 2009). Following the compositional

modeling approach (Falkenhainer and Forbus, 1991), the model was developed by creating a library of reusable components, and model fragments. Static model fragments are used to model events that do not change with time, while process and agent model fragments implement system components that define dynamic aspects of the system. Scenarios provide the context of the initial values from where the simulations progress. Once quantity values and relations are defined, the simulator generates states. Transitions between states are determined by transition rules and options defined by the user, and each sequence of states created during the simulation is a behaviour path. The collection of all the states produced by the simulation is denominated state graph. With Garp3 functionalities, it is possible to inspect the causal model, the equation history and the quantity value history. This approach has been used in different ecological studies (for example, Salles et al., 2003; Salles and Bredeweg, 2006; Salles et al., 2006).

3. The model

3.1. Assumptions

In our model we assume that males cannot maximize both within-pair paternity and extra-pair paternity simultaneously (Hasselquist and Bensch, 1991). Thus, we assume that mate guarding can only be totally efficient if it occurs continuously (Chuang-Dobbs et al., 2001). However, we assume that males vary in quality (high or low) and that the propensity of females to search for EPCs is related to the quality of their partner. We assume that mate guarding varies as a function of the male's attractiveness. We ignore the possibility that females could obtain direct, non-genetic benefits from extra-pair mating.

We assume that density and the number of female extra-pair young have a positive effect on mate guarding. Although it is known that the number of EPCs is not directly related with the number of EPFs, the latter was used as an indicator of female behaviour for simplification.

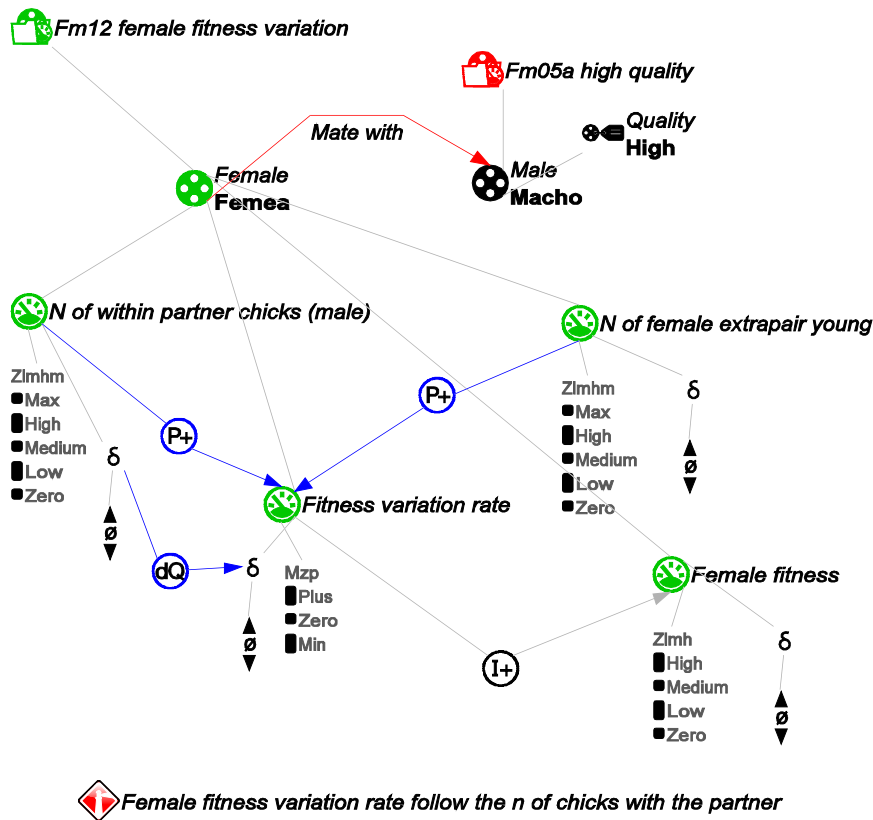


Fig. 3. Model fragment 'Female fitness when mated with a high quality male'.

The density effect discussed in the literature (Griffith et al., 2002) is well known for increasing the risk of extra-pair paternity and for modulating the intensity of mate guarding (Alatalo et al., 1987).

To predict male fitness, we assume that fitness is the sum of the young obtained with the social mate and with extra-pair mates, independently of male quality. For females, on the other hand, we assume that fitness varies with the number of chicks the female had with her partner and through extra-pair copulations, but taking into consideration her mate's quality. For example, it is expected that females mated with low quality males with a high number of within-pair young have a lower fitness.

3.2. Model configuration

The model consists of the following entities: “population”, “male” and “female” (Table 1). These entities were created to represent the interactions between the sexes in a population that may vary in densities.

The entities were associated to quantities, which express characteristics that can facilitate the understanding of the problem under study. Qualitative values, that represent important qualitative states to describe the behaviour of the system, were associated to the quantities (Table 2).

The model library consists of 26 model fragments. Two model fragments are used to represent the ecological processes of population growth, and variation in population density. Other fragments represent the configurations of males and females. Reproduction of females (Fig. 1) is represented by a model fragment in which there are two

opposite direct influences: $I+$ (N of within partner chicks, Fertilization rate) and $I-$ (N of female extra-pair young, Fertilization rate). In fact, the Fertilization rate quantity space, {minus, zero, plus}, captures the balance between fertilization by the paired male and by extra-pair copulation: the value *plus* means that fertilization within-pair > extra-pair; *minus* means that fertilization within-pair < extra-pair; and *zero* means they are equal. An inverse correspondence between the quantity spaces of the two types of offspring assures that an increase in one of them corresponds to a decrease in the other, given the limited number of eggs produced by the female. This representation expresses the idea that females exert some control over the offspring produced.

Mate guarding is a central concept for the control of extra-pair paternity (EPP). It is assumed that males must allocate their time between two mutually exclusive activities: mate guarding and searching for EPCs. Thus, we represented high quality males as individuals that invest more in EPCs, since their high quality guarantees access to EPP without losing much paternity at home. This occurs, of course, because mates of high quality males presumably do not need to search for other copulation opportunities given that they already have a high quality male siring their young. This behaviour is captured by model fragments that represent male fitness variation (see Fig. 4). In this model, the quantity *Mate guarding* is determined by breeding *Density* and by the quantity *N of female EPC solicitations*. The male reaction is captured by the model fragment ‘Constraint on female behaviour’ (Fig. 2), a process that constrains females from engaging in EPC.

The most important model fragments are those representing the effect on the fitness of males and females, exemplified by fragments

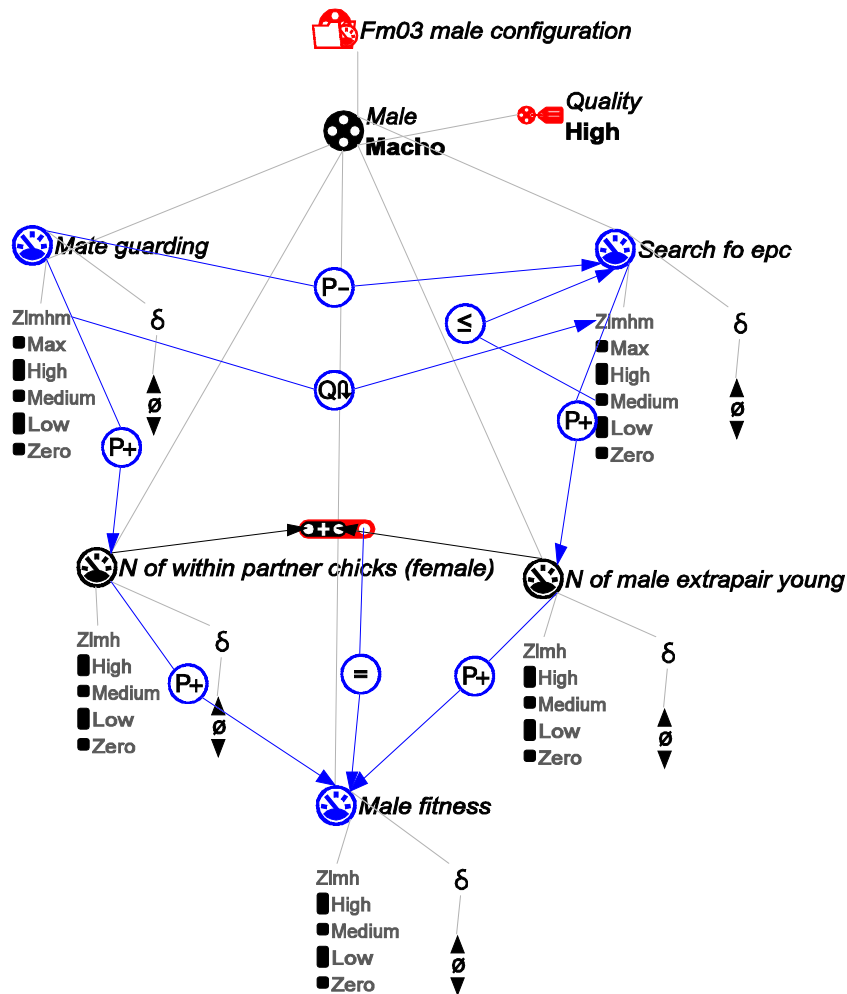


Fig. 4. Model fragment 'Fitness of the high quality male'.

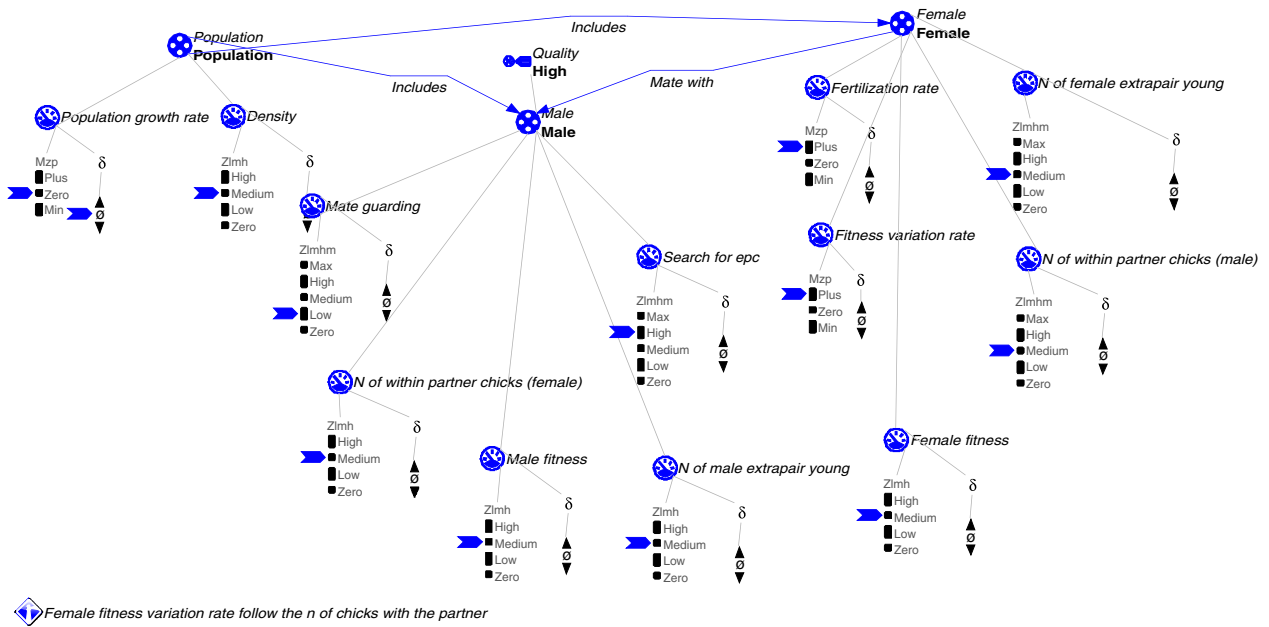


Fig. 5. Initial scenario 'Female mated with a high quality male'.

Fm12a and Fm13a (Figs. 3 and 4, respectively). The model fragment Fm12a represents the fitness of a female mated with a high quality male. In this case, there is a positive influence on the fitness variation rate, both from the number of within-pair young and extra-pair young. Fragment Fm13a represents the fitness of a high quality male. For males, the effect on fitness is more easily calculated, since male fitness results from the sum of within-pair young plus extra-pair young.

3.3. Scenarios

The current version of the model includes 21 scenarios that separately simulate processes such as population growth, mate guarding and reproduction, and which together generate more complex scenarios that encompass all these processes. The most representative scenarios are those that present the effect of changing values upon the fitness of both sexes. The scenario Sce11c presents the fitness of a high quality male and a female. The initial values for this scenario include a constant population growth, with density stabilized at the level medium; low mate guarding and a high search effort for EPCs for the males, due to an inverse correspondence present on the fragment model; the number of within and extra-pair young as well as male fitness presented medium values initially. For the females, the number of within and extra-pair young and female fitness also presented medium values initially, while fertilization rate and fitness variation rate were positive (Fig. 5).

4. Results

The information used in this study was acquired from the literature. The model went through calibration processes and conceptual validation. The calibration process of a model concerns producing a model that is as consistent as possible relative to the database from which parameters were estimated. On the other hand, conceptual validation requires correctness of the theory and assumptions that support the conceptual model (Rykiel, 1996). The simulation produced three initial states, which generated a total of 34 states, including 25 end states. The causal model presented in state 10 is shown in Fig. 6. The causal chain is initiated by the population growth rate, which has

a positive influence on population density, which influences mate guarding. The variable mate guarding, which is positively influenced by the number of female extra-pair young (which indicates the female's propensity for searching for copulations with other males), generates positive influences on fertilization rate and on the number of male within-pair young. However, since mate guarding and search for EPCs are mutually exclusive, they are linked by an inverse correspondence together with a negative proportionality. Male fitness is affected by the number of within and extra-pair young. Females present a limited number of eggs to be fertilized, so they are represented by an inverse correspondence between the number of within and extra-pair young. Finally, female fitness when mated with a high quality male is affected by the fitness variation rate that is positively influenced by the number of within and extra-pair young.

The behavioural trajectory shown in Fig. 6 illustrates the result of this simulation, showing that when a female is mated with a high quality male, there is a resulting increase in female fitness. Alternatively, these males tend to invest more in searching for EPCs, thereby reducing mate guarding and enhancing the number of EPFs and, consequently, levels of fitness (Fig. 7). Theoretically, a male that invests more in EPCs would leave his female unguarded for longer periods, leading to fewer within-pair chicks. Nevertheless, as the female strategy differs from that of the male, and as the number of within-pair young must be a result of a combination of both male and female strategies, the simulation result suggests that females mated with high quality males should produce a higher number of within-pair chicks, since they do not need to search for good genes from other males.

5. Discussion and Conclusion

Paternal investment in offspring not sired by the male is an important cost to the male's fitness (Trivers, 1972) that must have favored the evolution of strategies to avoid the presence of extra-pair young. One such likely strategy is that of mate guarding. However, as demonstrated in the results of this simulation, mate quality must influence the female's decision of searching for copulations with other males, generating a

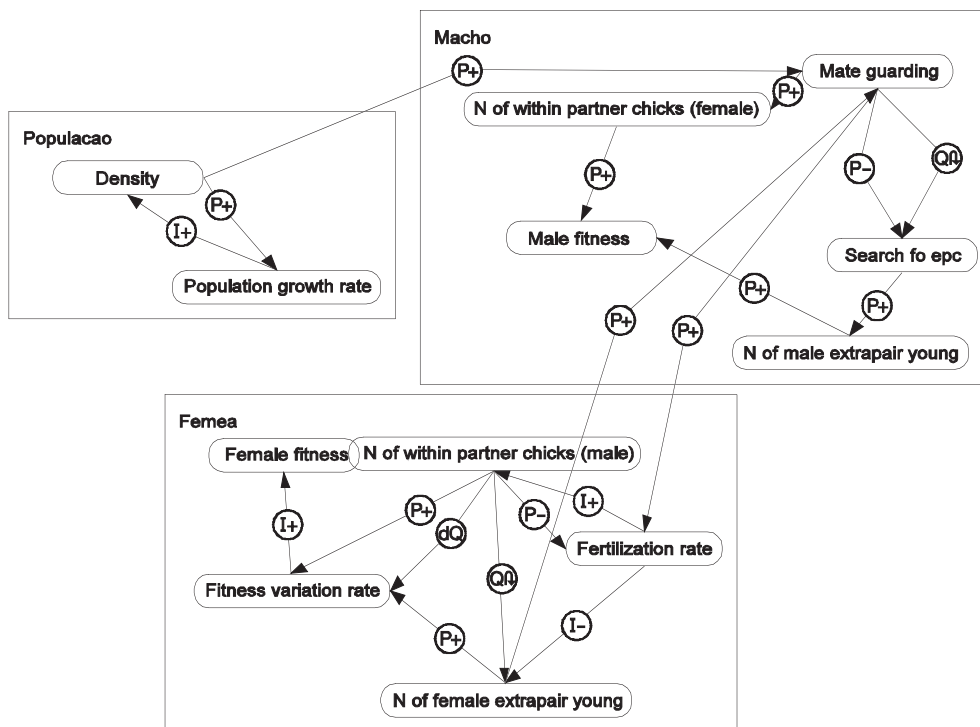


Fig. 6. Causal model obtained on state 10 of the simulation.

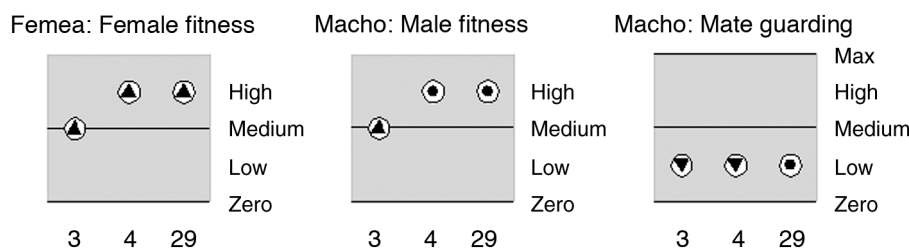


Fig. 7. History value diagram.

more substantial effect upon the number of female extra-pair young than could be generated by simple male guarding behaviour. In our model, we presume that high quality males should invest less in mate guarding, because they have higher chances of success in obtaining EPCs. Thus, males are expected to invest in mate guarding or in searching for EPCs based upon their own characteristics and upon the female's tendency to engage in promiscuous copulations (Kokko and Morrell, 2005). Thus, the trade-off between these two activities must be more intense for low quality males than for high quality ones, because when a female is paired with a high quality male she will be less likely to seek for EPCs. First, because their mates already provide them with "good genes"; second, because searching for copulations with other males is a costly behaviour, possibly generating aggressive behaviour from the cuckolded male (Barash, 1976; Valera et al., 2003), a reduction in paternal investment (Trivers, 1972; Dixon et al., 1994), or increased chances of infection of sexually transmitted diseases (Petrie and Kempenaers, 1998). Other less obvious costs incur due to the possibly elevated costs of searching for and evaluating a partner. As suggested by Kokko and Morrell (2005) and showed in other simulations of our model, a possible combination of male and female behaviour is that high quality males that invest more in searching for EPCs could have lower paternity with their social mate compared to low quality males, since the latter should try to maximize mate guarding.

The main effects that the model presents, concern the decision-making process based on self quality, for males, and based on mate quality, for females. According to our previous discussion, male quality influences his decisions to guard his mate or to search for copulations with other females. For females, the quality of their social pair will affect extra-pair behaviour. Females mated with high quality males are not motivated to search for extra-pair copulations. This happens because the costs associated with such behaviour could outweigh the benefits. A study with *Icterus galbula bullockii* showed that older males lost less paternity in their own nests and gained more extra-pair fertilizations than did sub-adult males (Richardson and Burke, 1999).

In the simulations of the model we observed that males and females present strategies that directly affect their fitness. For males this is a simple sum of the number of within and extra-pair young. For females the situation is not so simple, since the number of young produced is limited, females invest more in quality. Consequently, as demonstrated in the simulation, when a female is paired with a high quality male, both sexes will have an increase in fitness, resulting from the number of extra-pair young for the males, and from both within and extra-pair young for the females. This happens because, possibly, a female mated with a high quality male will only search for EPCs if the extra-pair male is of better quality than her social mate.

Studies suggest that females mated with low quality males obtain EPCs with high quality males, possibly to enhance offspring fitness (Friedl and Klump, 2005). For some species it has been shown that extra-pair young had a higher performance than within-pair young (e.g., *Marmota marmota*; Cohas et al., 2007), or that extra-pair fledglings had higher survival (*Parus caeruleus*; Kempenaers et al., 1997; Charmantier et al., 2004). Another study demonstrated that extra-pair young had a better immune response relative to their half siblings in the nest (Johnsen et al., 2000). Possibly, the conflict of interest between females and their partners depends mainly on

whether the extra-pair copulations are costly or beneficial for the females. However, the probability of a brood containing extra-pair young should be influenced by the behaviours adopted by both sexes.

In conclusion, we believe that the presented model formalizes some ideas that are generally taken for granted in some EPP studies, but that have not been properly evaluated. In addition, the model highlights the importance of additional focusing on female behaviour, as it is an important determinant for fertilization fate. The model also suggests that the importance of mate guarding in within-pair fertilization rate should be viewed differently under various contexts. Future studies of sexual selection must take into consideration the factors that influence decisions of both sexes and how these decisions are integrated within the phenomenon of EPP.

Acknowledgments

This study was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – CAPES and the Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq through student scholarships to R.I.D. and through a research fellowship to R.H.M.

References

- Alatalo, R.V., Gottlander, K., Lundberg, A., 1987. Extra-pair copulation and mate guarding in the polyterritorial pied flycatcher, *Ficedula hypoleuca*. *Behaviour* 101, 139–155.
- Barash, D., 1976. Male response to apparent female adultery in the mountain bluebird (*Sialia currucoides*) – an evolutionary interpretation. *Am. Nat.* 110, 1097–1101.
- Bredeweg, B., Linnebank, F., Bouwer, A., Liem, J., 2009. Garp3 - workbench for Qualitative Modelling and Simulation. *Ecological Informatics* 4 (5–6), 263–281.
- Birkhead, T.R., Møller, A.P., 1992. *Sperm Competition in Birds – Evolutionary Causes and Consequences*. Academic, London. 282 pp.
- Charmantier, A., Blondel, J., Perret, P., Lambrechts, M., 2004. Do extra-pair paternities provide genetic benefits for female blue tits *Parus caeruleus*? *J. Avian Biol.* 35, 524–532.
- Chuang-Dobbs, H.C., Webster, M.S., Holmes, R.T., 2001. The effectiveness of mate guarding by male black-throated blue warblers. *Behav. Ecol.* 12, 541–546.
- Cohas, A., Bonenfant, C., Gaillard, J., Allainé, D., 2007. Are extra-pair young better than within-pair young? A comparison of survival and dominance in alpine marmot. *J. Anim. Ecol.* 76, 771–781.
- Dixon, A., Ross, D., O'Malley, S.L.C., Burke, T., 1994. Parental investment is inversely related to the degree of extra-pair paternity in the reed bunting. *Nature* 371, 698–700.
- Falkenhainer, B., Forbus, K., 1991. Compositional modelling – finding the right model for the job. *Artif. Intell.* 51, 95–143.
- Forbus, K.D., 1984. Qualitative process theory. *Artif. Intell.* 24, 85–168.
- Forbus, K., de Kleer, J., 1993. *Building Problem Solvers*. MIT Press, Cambridge, MA.
- Friedl, T.W., Klump, G.M., 2005. Extrapair fertilizations in red bishops (*Euplectes orix*) – do females follow conditional extrapair strategies? *Auk* 122, 57–70.
- Gibbs, H.L., Weatherhead, P.J., Boag, P.T., White, B.N., Tabak, L.M., Hoysak, D.J., 1990. Realized reproductive success of polygynous red-winged blackbirds revealed by DNA markers. *Science* 250, 1394–1397.
- Gray, E.M., 1997. Female red-winged blackbirds accrue material benefits from copulating with extra-pair males. *Anim. Behav.* 53, 625–639.
- Griffith, S.C., Owens, I.P.F., Thuman, K.A., 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Mol. Ecol.* 11, 2195–2212.
- Hasselquist, D., Bensch, S., 1991. Trade-off between mate guarding and mate attraction in the polygynous great reed warbler. *Behav. Ecol. Sociobiol.* 28, 187–193.
- Hasselquist, D., Bensch, S., von Schantz, T., 1996. Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature* 381, 229–232.
- Hatchwell, B.J., 1988. Intraspecific variation in extra-pair copulation and mate defense in common guillemots *Uria aalge*. *Behaviour* 107, 157–185.
- Jennions, M., Petrie, M., 2000. Why do females mate multiply? A review of the genetic benefits. *Biol. Rev. Camb. Philos. Soc.* 75, 21–64.

- Johnsen, A., Andersen, V., Sunding, C., Lifjeld, J.T., 2000. Female bluethroats enhance offspring immunocompetence through extra-pair copulations. *Nature* 406, 296–299.
- Kempnaers, B., Verheyen, G., Dhondt, A., 1997. Extrapair paternity in the blue tit (*Parus caeruleus*) – female choice, male characteristics, and offspring quality. *Behav. Ecol.* 8, 481–492.
- Kokko, H., Morrell, L.J., 2005. Mate guarding, male attractiveness, and paternity under social monogamy. *Behav. Ecol.* 16, 724–731.
- Lifjeld, J.T., Dunn, P.O., Westneat, D.F., 1994. Sexual selection through sperm competition in birds – male–male competition or female choice? *J. Avian Biol.* 25, 244–250.
- Magrath, M.J.L., Komdeur, J., 2003. Is male care compromised by additional mating opportunity? *Trends Ecol. Evol.* 18, 424–430.
- Møller, A.P., Birkhead, T.R., 1993. Cuckoldry and sociality – a comparative study of birds. *Am. Nat.* 142, 118–140.
- Møller, A.P., 1991. Density-dependent extra-pair copulations in the swallow (*Hirundo rustica*). *Ethology* 87, 316–329.
- Otter, K., Ratcliffe, L., Boag, P.T., 1994. Extra-pair paternity in the black-capped chickadee. *Condor* 96, 218–222.
- Petrie, M., Doums, C., Møller, A.P., 1998. The degree of extra-pair paternity increases with genetic variability. *Proc. Natl. Acad. Sci. U. S. A.* 95, 9390–9395.
- Petrie, M., Kempnaers, B., 1998. Extra-pair paternity in birds: explaining variation between species and populations. *Trends Ecol. Evol.* 13, 52–58.
- Richardson, D.S., Burke, T., 1999. Extra-pair paternity in relation to male age in Bullock's orioles. *Mol. Ecol.* 8, 2115–2126.
- Rykiel, E.J., 1996. Testing ecological models – the meaning of validation. *Ecol. Model.* 90, 229–244.
- Salles, P., Bredeweg, B., 2003. Qualitative reasoning about population and community ecology. *AI Mag.* 24, 77–90.
- Salles, P., Bredeweg, B., 2006. Modelling population and community dynamics with qualitative reasoning. *Ecol. Model.* 195, 114–128.
- Salles, P., Bredeweg, B., Araujo, S., Neto, W., 2003. Qualitative models of interactions between two populations. *AI Commun.* 16, 291–308.
- Salles, P., Bredeweg, B., Bensusan, N., 2006. The ants' garden— qualitative models of complex interactions between populations. *Ecol. Model.* 194, 90–101.
- Trivers, R.L., 1972. Parental Investment and Sexual Selection. In: Campbell, B (Ed.), *Sexual Selection and the Descent of Man*. Aldine Press, Chicago, pp. 136–179.
- Valera, F., Hoi, H., Kristin, A., 2003. Male shrikes punish unfaithful females. *Behav. Ecol.* 14, 403–408.
- Westneat, D.F., 1990. Genetic parentage in the indigo bunting – a study using DNA fingerprinting. *Behav. Ecol. Sociobiol.* 27, 67–76.
- Westneat, D.F., Sherman, P.W., 1997. Density and extra-pair fertilizations in birds – a comparative analysis. *Behav. Ecol. Sociobiol.* 41, 205–215.
- Westneat, D.F., Stewart, I.R., 2003. Extra-pair paternity in birds: causes, correlates, and conflict. *Ann. Rev. Ecol. Syst.* 34, 365–396.
- Wink, M., Dyrce, A., 1999. Mating systems in birds: a review of molecular studies. *Acta Ornithol.* 34, 91–109.
- Yezerinac, S.M., Gibbs, H.L., Briskie, J.V., Whittam, R., Montgomerie, R., 1999. Extrapair paternity in a far northern population of yellow warblers *Dendroica petechia*. *J. Avian Biol.* 30, 234–237.