A qualitative model on sexual behaviour: mate guarding and extra-pair copulation in birds

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Abstract

Extra-pair paternity is widespread among avian species, showing high inter and intra-specific variation both in frequency and in typical behaviours. These variations are the result of individual, ecological and phylogenetic influences upon the behavioural searching pattern for extra-pair copulations. A qualitative reasoning model was developed to show how decisions made by females and males could affect the occurrence of extra-pair paternity and fitness. The model demonstrates that population density and the genetic quality of the male with whom the female is mated influences female predisposition to search for extra-pair copulations. Accordingly, high-quality males should have a higher number of within and extra-pair young than low quality males. The model shows that since the interests of males and females are similar, both sexes may achieve an increment in their fitness.

1. Introduction

Monogamy in birds is conceptually defined as a web of complex interactions and conflicts of interest between paired males and females (Westneat and Stewart, 2003). The study of this subject has suffered significant changes with the application of molecular tools, showing it to be less simple than was initially assumed, with a number of hypotheses being suggested to explain the wide variation (0-70%) in the rate of extra-pair fertilization (EPF) among species. Variation in EPF levels must be the result of different ecological, phylogenetic and individual constraints that should have influenced the evolution of this behaviour. The use of a qualitative approach may play an important role in helping to understand the causal relations of this process.

This paper presents a simulation model that intends to increase understanding about the role of individual features and behavioural factors associated with the occurrence of extra-pair paternity (EPP), based on qualitative reasoning (QR) techniques (Weld and de Kleer, 1990). QR models contribute to ecological theory development by determining the logical consistency and the consequences of long and complex chains of ecological reasoning and rapid assessment of assumptions, hypotheses and other ideas (Rykiel, 1989). In the context of EPF studies, QR techniques are useful for establishing causal relations and predicting the system’s behaviour using incomplete knowledge.

The model presented here attempts to answer questions such as: What is the effect of mate quality on female pursuit for extra-pair copulations? Is mate guarding an effective strategy for decreasing paternity loss? Does male genetic quality affect male and female individual fitness?

2. Extra-pair paternity in birds

Despite the variation in the frequency of EPP among species, the determinants of this behaviour are poorly understood. Moreover, it is difficult to separate cause and effect relations, as some variables may have a causal effect on EPP, whereas others may result from the consequences of this behaviour (Westneat and Stewart, 2003). A number of hypotheses have been proposed to explain how such reproductive strategies evolved. These possible explanations include breeding synchrony, need for paternal care, rate of adult mortality, and ecological explanations, such as the relation between breeding density and levels of EPP (Griffith et al. 2002). The breeding density hypothesis states that the proximity to neighbours would increase accessibility to mates for extra-pair copulation (EPC), and would enhance opportunities to evaluate available mates (Birkhead and Møller, 1992).

Considering a bird’s fitness (i.e. a measure of the individual’s ability, relative to others, to leave viable offspring), it is possible for males to increase their reproductive gain without additional parental investment by seeking for EPCs (Birkhead and Møller, 1992). However, the reproductive gain for females is less obvious, because their reproductive capacity is limited by the
number of eggs they can produce. As sexual promiscuity does not increase the number of female offspring, the role of female behaviour in determining the level of EPP is unclear.

According to the good genes hypothesis, if males differ in genetic quality, females paired with low quality males are compensated when searching for EPF with males of higher quality, because this behaviour would improve their offspring’s survival and reproductive chances (reviewed in Jennions and Petrie, 2000). Nevertheless, from the male’s perspective, EPC’s are only valuable for those males that can obtain extra-pair fertilizations, but are unfavorable for those males that lose paternity in their own nest. Thus, males must prevent the occurrence of EPCs by their own females to avoid the future cost of rearing offspring sired by other males. Thus, males develop counterstrategies to avoid, or at least interfere with extra-pair behaviour of their females (Trivers, 1972). The more commonly used for the males is mate guarding, which consists of following the female during her fertile period, to prevent them from copulating with other males (Birkhead and Møller, 1992). On the other hand, males also try to increase their fitness through EPCs, but with this, they incur the risk of losing paternity by leaving their female unguarded, since 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 mating and reproductive effort depend on the attractiveness, or quality of their mates as well as their own quality (reviewed in Magrath and Komdeur, 2003). Thus, it is reasonable to expect that low quality (LQ) males invest more in mate guarding than high quality (HQ) males, and also that females mated with HQ males are less likely to search for EPCs. The level of EPP in a population reflects the response to a series of possible conflicts between females, their social mates, and one or more extra-pair males (Lifjeld et al., 1994).

3. Qualitative models

The model presented in this study was implemented in the qualitative simulator Garp3 (Bredeweg et al., 2006), using elements of ontology provided by the qualitative process theory (Forbus, 1984). Following the compositional modelling approach (Falkenheimer and Forbus, 1991), the model was developed by creating a library of reusable components, model fragments, used to represent processes, agents and static views of the modeled system. Causal relations are captured by means of relations between the quantities, direct influences (I+ and I-) for representing processes and qualitative proportionalities (P+ and P-) for propagating the effects of processes to other parts of the system. 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), but not in behavioural ecology.

4. The model

Relevant assumptions in this model are: (a) males cannot maximize both within-pair and extra-pair paternity simultaneously. Accordingly, mate guarding can only be totally efficient if it occurs continuously throughout the entire period of female fertility; (b) males can be of either high (HQ) or low quality (LQ) and female propensity to search for EPC is related to the quality of their mates; (c) mate guarding varies as a function of male quality; (d) females do not obtain other non-genetic benefits from an extra-pair mating.

The current version of the model consists of three entities associated to 16 quantities, that express properties of the entities and ultimately characterize the states of the system under study. The system structure is organized around entities and the configurations ‘Female’ mates with ‘Male’ and these two entities are included in the ‘Population’. Quantities associated to the entity ‘Population’ represent aspects of population dynamics. Growth rate represents the population growth process, and population Density is a proxy for the concept of breeding density. The entity ‘Male’, is associated to the quantities Mate guarding and Search for EPC. These quantities have quantity spaces spanning from zero to maximum, to capture the idea that a male has a limited amount of time to expend in each of these behaviours. The quantity Control rate, which is motivated by mate guarding, represents the level of control males have regarding female behaviour. The quantity N of within partner chicks represents offspring produced with the male’s pair and its quantity space includes a maximum point because the number of chicks produced is constrained by the number of eggs a female can lay. Females are also associated to the quantity N of within partner chicks with the same quantity space. The quantities
related to the number of extra-pair young produced by males (N of male extra-pair young) and females (N of female extra-pair young) have different quantity space for a simple reason; males can fertilize a high number of females, while females are again constrained by the number of eggs they produce. Therefore, only the female’s quantity space includes the value maximum. The Fertilization rate refers to the rate of female fertilization. The quantity N of female EPC solicitations represents female extra-pair behaviour – solicitations for extra-pair copulation, that may result in fertilization. Male and female fitness are calculated in different ways (see specific fragments below), in relation to number of chicks produced (for males) and the quality of chicks produced (for females). Female fitness changes are seen as the result of a process, with a Fitness variation rate that varies according to the levels of within pair and extra-pair behaviour.

The library consists of 33 model fragments, 13 of them representing ecological processes (population growth, female reproduction, constraining female behaviour, and female fitness variation). Reproduction of females 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). An inverse correspondence between the quantity spaces of the two types of offspring assures that increase in one of them corresponds to decrease in the other, given the limited number of eggs produced by the female in her lifespan. This representation expresses the idea that females exert some control over the offspring produced.

Mate guarding is a central concept for the control of EPP. It is assumed that, given that the male’s time and energy budgets are limited, there is a tradeoff between mate guarding and search for EPC, so that low quality males invest more in the former and less in the latter, while high quality males invest more in the search for EPC. This hypothesis is captured by model fragments that represent male fitness variation. 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’, a process that constrains females from engaging in EPC.

The most important model fragments are those related to the fitness variation of females and males. Female fitness changes due to a process, represented in the model fragment ‘Female fitness variation’, which introduces the relation I+(Female fitness, Fitness variation rate). The rate of this process is influenced both by N of within partner chicks and by N of female extra-pair young. As mentioned above, females mated with low quality males may increase their fitness via EPC. This idea is captured by the model fragment ‘Fitness of female mated with low quality male’ (Figure 1) that shows a negative proportionality between N of within partner chicks and Fitness variation rate, and a positive one linking N of female extra-pair young and the rate. This model fragment also shows the assumption ‘Female fitness variation rate follows the n of extra-pair young’ related to the correspondence between derivatives, causing the rate to follow the direction of change of female extra-pair offspring.

![Figure 1](image)

5. Simulations

The model has 31 scenarios, from simple simulations exploring only population dynamics and male or female features to complex interactions between HQ and LQ males and female within-pair and extra-pair reproduction and the effects of mating success and mate quality on their fitness. The initial scenario ‘Female mated with a HQ male’ produces the most complex simulation within this model. The following assumptions hold in this scenario: ‘Female fitness variation rate follow the n of chicks with the partner’ and ‘N of within partner chicks are the same for males and females’. In this scenario, population Growth rate starts with the value <plus,>, Density with <medium,>, and the trade off between male Mate guarding and Search for EPC have initial values in the interval <low,> and <high,> respectively. All the other quantities started with the value <medium,>, except the rates that have value <zero,>. The simulation produced three initial states; the full simulation, 166 states. The causal model, as it appears in state 10, is presented in Figure 2. It shows that an increase in Density propagates to
**Mate guarding**, which has three influences: (a) it negatively affects the male Search for EPC, reducing the **N of male extra-pair young**; (b) it positively affects **Constraining rate**, triggering the feedback loop that reduces the **N of female EPC solicitations** and causes Mate guarding to decrease; and (c) it positively affects **Fertilization rate**, causing **N of within partner chicks** to increase and **N of female extra-pair young** to decrease. These two quantities influence the female **Fitness variation rate**, but given that there is a derivative correspondence, the rate will take the derivative of **N of within partner chicks**.

In the behaviour path explored above, **Male fitness** followed the derivative of **N of within partner chicks**, but there are behaviour paths in which it follows the derivative of **N of male extra-pair young** and is decreasing. In fact, **Male fitness** may enter a cyclic path, and oscillate between the values low and high, as shown in Figure 4:

![Figure 4. Cyclic behaviour expressed by the quantity Male fitness in a simulation starting with the scenario ‘Female mated with a high quality male’](image)

**6. Discussion**

Qualitative reasoning models may contribute to the development of ecological theories in many ways. They can be used to formalize scientific hypotheses, or qualitative theories about particular domains, that may support the development of new ideas that explore applications or further theoretical developments of those theories. The model described in this paper also has the potential to support further studies on sexual selection. As genetic polyandry with extra-pair offspring seems to happen in approximately 90% of bird species (Griffith et al., 2002) it is of great interest to understand why such sexual behaviour evolved and how these traits may affect bird fitness. However, modelling sexual behaviour in birds presents new challenges for qualitative reasoning models. Among them, the need for representing interactions involving phenomena that occur in different time scales, and in different generations. Integration of changes in successive generations in phylogenetic studies will require the implementation of evolutionary mechanisms such as mutation, adaptation and natural selection that may explain why current generations of birds behave as they do.

The model presented here was designed to help students and researchers interested in behavioural ecology, especially in sexual selection, to understand processes involved in evolution of extra-pair paternity on a narrow scale, based on individual decisions. Although not evaluated so far by end users, the model was evaluated by an expert in animal behaviour in a step-by-step procedure, during which relevant concepts, model fragments, scenarios and simulation results were presented and discussed (Rykiel, 1996). The expert made comments and suggestions to improve knowledge representation, which were included in the model, and the results obtained were considered satisfactory and potentially useful.
7. Conclusions

In this paper, qualitative reasoning techniques are used to formalize representations of hypotheses related to sexual behaviour and extra-pair paternity in avian species, expressing cause – effect relations and exploring complex chains of reasoning about system behaviour. The answers provided by the model to the questions formulated in the introduction are based on the most relevant mechanisms identified in the literature to explain extra-pair paternity in birds, such as the trade-off between mate guarding and male search for EPC and the use of different strategies for increasing fitness in females mated to high and low quality males.

Ongoing work includes improving representations of both male and female behaviour and of the factors that affect their fitness. For males, current modelling effort aims to improve the representation of mate guarding and paternal care; for females, the goal is to explore alternative hypotheses about how their own interests would drive behaviour and influence the level of extra-pair paternity.

The results obtained so far confirm the potential of QR modelling contribution to the ecologists’ understanding of the theoretical basis of complex aspects of sexual selection in birds.

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References


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