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

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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, and a number of hypotheses have been suggested to explain the huge variation (0-70%) in the rate of extra-pair fertilization (EPF) among species. According to the *breeding density hypothesis*, for example, a proximity to neighbors 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, defined as a measure of individual 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 extra-pair paternity 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 EPC with males of higher quality, because this behaviour would improve their offspring's survival and reproductive chances [reviewed in Jennions and Petrie, 2000]. Nevertheless, males cannot maximize the search for EPC and mate guarding simultaneously, as these behaviours are mutually exclusive. Therefore, EPC is only valuable for males with good chances of extra-pair fertilization, but may be undesirable for those who lose paternity in their own nest. To avoid losing paternity males apply different tactics, with *mate guarding* probably occurring most commonly [Birkhead and Møller, 1992].

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, based on qualitative reasoning (QR) techniques [Weld and de Kleer, 1990]. QR models contribute to ecological theory development with rapid assessment of assumptions, hypotheses, and other ideas by representing the system structure, establishing causal relations and predicting the system behaviour using incomplete knowledge [Salles and Bredeweg, 2003]. QR has been used in different ecological studies [e.g. Salles *et al*., 2006], none of which has focused on bird sexual behaviour. This model attempts to answer questions such as: *What is the effect of mate quality on female pursuit for promiscuous copulations? Is mate guarding an effective strategy for decreasing paternity loss? Does male genetic quality affect male and female individual fitness?*

The model was implemented in Garp3 [Bredeweg *et al.*, 2006], using direct influences (*I+ and I–*) and proportionalities (*P+ and P–*) as defined by the qualitative process theory [Forbus, 1984], and following a compositional modelling approach [Falkenhainer and Forbus, 1991]. Relevant assumptions in this model are: (a) males cannot maximize both within-pair and extra-pair paternity simultaneously. Thus, mate guarding can only be totally efficient if it occurs throughout the entire period of female fertility; (b) males can be of either high or low quality and female propensity to search for EPC is related to the quality of their mates; (c) mate guarding varies as a function of male genetic quality; (d) females cannot obtain other non-genetic benefits from an extra-pair mating; (e) density and the number of female extra-pair offspring have a positive effect (P+) on mate guarding.

The current version of the model consists of the entities 'population', 'male' and 'female', which are associated to 12 quantities. The library consists of 26 model fragments, three of them representing ecological processes: population growth, increase of female fertilization rate and female fitness variation. Influences of male quality on female behaviour are captured in two groups of model fragments: with high quality (HQ) males, offspring from both within-pair and extra-pair copulations result in positive influences on *fitness variation rate*; and with low quality (LQ) males, within-pair offspring have a negative influence, while extra-pair offspring have a positive influence on *fitness variation rate*. The model has 21 scenarios, from simple simulations exploring only HQ and LQ male or female features to complex interactions between HQ and LQ males and female within-pair and extra-pair reproduction and the effects of sexual behaviour on their fitness. For example, the scenario 'High quality male and female fitness with steady population' establishes the following initial conditions: density stable at the value medium; for the males, low mate guarding and high search for EPC; medium values for the quantities within-pair and extra-pair offspring and male fitness. For the females, medium values for the quantities within-pair and extra-pair offspring and female fitness, while the fertilization and fitness variation rates are positive. Figure 1 shows a causal model and relevant quantity values in the behaviour path [3→4→27] of this simulation.

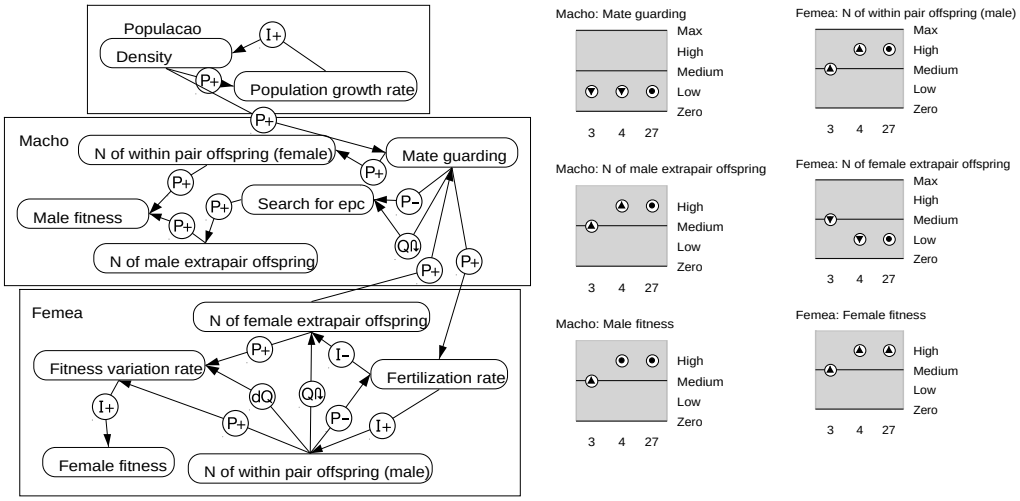

Figure 1. Causal model in state 1 and value history diagrams of relevant quantities.

Figure 1 describes the causality flow in the model: *mate guarding* is influenced both by population *density* and by changes in female *extra-pair offspring*, and influences female *fertilization rate*, which in turn determines the value of *extra-pair offspring*. This feedback mechanism controls the reproductive behaviour in both males and females. For example, when *mate guarding* decreases, the search for EPC increases and so do extra-pair offspring, while

within-pair offspring decreases in males. Male fitness results from positive influences both from within-pair and extra-pair offspring. For females, *Fertilization rate* directly influences both their within-pair and extra-pair offspring values; it encompasses an inverse correspondence relation such that when a certain number of eggs is used for within-pair reproduction, a corresponding number is no longer available for EPC. The two types of offspring positively influence *fitness variation rate* (in this case) and this quantity finally determines the value of female fitness. Simulation with this scenario produces all the expected behaviours. Mating with HQ male should only improve female offspring, both from within and extra-pair fertilizations. Accordingly, female fitness increases in all the behaviour paths. Male fitness, however, expresses three possible behaviors: it may remain stable, when both within and extra-pair offspring influences are equivalent; it may decrease, when within-pair offspring is decreasing and its influence is stronger than the influence from extra-pair offspring; and it may increase, when the influence of extra-pair offspring is stronger, as shown in the behaviour path [3→4→27]. In this case, an ideal situation is shown: *mate guarding* is small, decreasing and stabilizing; male extra-pair offspring is increasing and stabilizing; female within-pair offspring is increasing and stabilizing, and extra-pair offspring is decreasing and stabilizing. Both male and female fitness increase.

The answers provided by the model to the questions formulated above are based on the most relevant mechanisms identified in the literature to explain sexual behaviour in birds, such as the use of different strategies for increasing fitness in females, and HQ and LQ males and the trade-off between mate guarding and EPC. Accordingly, males´ decisions are based on their own genetic quality and females take into account their mate's quality. In the model, males decide between mate guarding and searching for EPC. For females, it is the mate quality that influences their extra-pair behaviour. Females mating with HQ males are not stimulated to search for EPC, as the costs associated with this behaviour may outweigh the benefits. Ongoing work includes improving representations of both male and female behaviour. For males, current modelling effort aims at including the energetic investment in mate guarding and EPC; 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 our understanding of the theoretical basis of complex aspects of sexual selection in birds.

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