



# Bet-hedging against male-caused reproductive failures may explain ubiquitous cuckoldry in female birds



Yukio Yasui<sup>a,\*</sup>, Jin Yoshimura<sup>b,c,d</sup>

<sup>a</sup>Laboratory of Entomology, Faculty of Agriculture, Kagawa University, Miki-cho, Kagawa, 761-0795, Japan

<sup>b</sup>Graduate School of Science and Technology and Department of Mathematical and Systems Engineering, Shizuoka University, 3-5-1 Johoku, Naka-ku, Hamamatsu, 432-8561, Japan

<sup>c</sup>Marine Biosystems Research Center, Chiba University, Uchiura, Kamogawa, Chiba, 299-5502, Japan

<sup>d</sup>Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, Syracuse, NY 13210 USA

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## ABSTRACT

The origin and maintenance of polyandry is one of the key unresolved questions in evolutionary biology. In particular, extra-pair paternity (EPP) due to polyandry is observed in most (socially-) monogamous female birds and the frequency of EPP is surprisingly high (up to 72% in a clutch on average in some species). Many case-by-case hypotheses have been presented to explain this phenomenon but a ubiquitous explanation is still lacking. One possible general explanation is bet-hedging, which is a strategy to avoid the risk associated to mating with a single unsuitable male and thus to minimize the chances of complete reproductive failure by the female. Here, we present a mathematical solution to demonstrate that bet-hedging polyandry becomes highly effective if the risk of extinction of a female lineage attributable to male deficiencies is high in small subpopulation or under limited mate availability. Therefore, cuckoldry or polyandry may be a female strategy to spread the risk of extinction of her genotype over multiple males. The results agree well with the observed EPP frequencies in natural populations and the results of a meta-population simulation model. Our theory contributes new insights applicable not only to birds but also to a broad taxonomic range of animals.

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## 1. Introduction

In the late 1980s, DNA fingerprinting technology revealed that extra-pair mating is extremely widespread in many socially monogamous birds (Birkhead and Møller, 1992; Dixon et al., 1994; Griffith et al., 2002; Westneat and Stewart, 2003). On average, more than 11% (range of across species averages 0–72%) of eggs in a clutch are sired by extra-pair males across birds (Dixon et al., 1994; Griffith et al., 2002). This phenomenon has been questioned because cuckoldry is expected to be very risky and costly to a female if discovered by her pair male (e.g., aggression, mate desertion or reduction of parental investment in offspring by the pair male) (Birkhead and Møller, 1992; Dixon et al., 1994; Petrie and Kempenaers, 1998; Osorio-Beristain and Drummond, 2001; Westneat and Stewart, 2003). Extra-pair mating by females is a type of polyandry (female mating with multiple males within the same reproductive season) and numerous hypotheses (Birkhead and Møller, 1992; Petrie and Kempenaers, 1998; Yasui, 1998; Jennions

and Petrie, 2000; Yasui, 2001; Akçay and Roughgarden, 2007) have been presented to explain this phenomenon. These include direct (non-genetic or environmental) benefits (nuptial gift, sperm supply, and avoidance of infertility) (Gonzalez-Solis et al., 2001; Hasson and Stone, 2009); indirect (genetic) benefits (good genes and avoidance of incompatibility) (Yasui, 1998; Jennions and Petrie, 2000; Yasui, 2001; Akçay and Roughgarden, 2007) and sexual conflict (forced copulation by males) (Arnqvist and Rowe, 2005). The ability of a specific hypothesis to explain extra-pair mating depends on the species, suggesting the involvement of a variety of factors. However, extra-pair copulation is widespread in monogamous birds, implying that this phenomenon is ubiquitous. Therefore, it is worth considering general rather than case-by-case explanations.

The bet-hedging polyandry hypothesis (Watson, 1991; Yasui, 1998, 2001; Schmoll et al., 2007; Garcia-Gonzalez et al., 2015) enables females to spread the risk of complete reproductive failure attributable to male effects over multiple males. Polyandrous clutches should include offspring of more variable phenotypes and within-clutch mean fitness (e.g. embryo survivorship; Garcia-Gonzalez et al., 2015) may be intermediate by offsetting between fit and unfit half-sib offspring within a clutch, whereas the mean fitness within monandrous clutch could be variable among

\* Corresponding author.

E-mail addresses: [yyasui@ag.kagawa-u.ac.jp](mailto:yyasui@ag.kagawa-u.ac.jp), [aaa32330@pop06.odn.ne.jp](mailto:aaa32330@pop06.odn.ne.jp) (Y. Yasui), [yoshimura.jin@shizuoka.ac.jp](mailto:yoshimura.jin@shizuoka.ac.jp) (J. Yoshimura).

clutches (some clutches are good and others are bad due to the quality of each single sire). Therefore, if the number ( $n$ ) of females of the same genotype (strategy) in a population is sufficiently small ( $n \leq 20$ ), geometric mean fitness across generations should be higher for the polyandrous strategy than the monandrous strategy because the former effectively suppresses fitness fluctuation between generations (Yasui, 1998, 2001). In large populations including many monandrous female lineages, however, the chances that all monandrous females mate with bad males are low, and thus, the geometric mean fitness of this strategy across generations may be comparable to that of polyandrous strategy (i.e. bet-hedging does not work effectively in large populations; Yasui, 2001). However, Yasui and Garcia-Gonzalez (2016) showed that this “small population” constraint is overcome in metapopulations consisting of many small patches, each containing only several females of the same genotype. Based on individual-based simulations, Yasui and Garcia-Gonzalez (2016) showed that the polyandrous genotype tends to win over the monandrous genotype in each patch and can spread over metapopulations via dispersal (gene flow). Nevertheless, the mathematical background of bet-hedging polyandry remains unclear. Yasui (1998, 2001) demonstrated that the between-generation fitness variance should be smaller in polyandrous genotype than monandrous competitor using a mathematical model but did not compare geometric mean fitness itself between the two strategies. Yasui and Garcia-Gonzalez (2016) presented a simulation model rather than an analytical model. Here, we develop an analytical model of extra-pair mating using a geometric mean fitness approach.

### 1.1. Geometric mean fitness approach for bet-hedging polyandry

We imagine the case that a single polyandrous mutant female invades a population occupied by a monandrous wild type. In this case, the initial reproductive success of this mutant female is very important because it determines the fate of the entire polyandrous genotype. If she successfully produces multiple offspring, her lineage branches into multiple lineages, however, if she fails to reproduce, the mutant genotype goes to extinction. If these descendant lineages occupy the entire population (and if they do not allow the reinvasion of monandrous genotype), polyandry represents an ESS (evolutionarily stable strategy). In this paper, we focus on whether polyandry is advantageous or not in this first stage of genotype invasion using a geometric mean fitness approach.

For the invading mutant female, the persistence of her descendants over generations is fundamental. She should avoid the risk of the extinction of her genotype. We suppose that natural animal populations contain a certain proportion of infertile or unproductive males due to various temporal or permanent / genetic (mutational or compatibility-related) or environmental causes (see Garcia-Gonzalez, 2004; Yasui and Garcia-Gonzalez, 2016). Because of the possibility of choosing such an unsuitable mate, she has a chance of losing all her offspring. To avoid this extinction problem of her genotype, mating with other males may be adaptive. This is the basic condition for ubiquitous risk-spreading polyandry.

Note that the measure of fitness here should be the future persistence (sustainability of the genotype over generations), instead of the average reproductive success among females of the same genotype in each generation, that is, the usual arithmetic mean fitness (Slatkin, 1974; Gillespie, 1977; Philippi and Seger, 1989; Hopper, 1999; Yasui, 2001; Yasui and Garcia-Gonzalez, 2016). The future persistence of the mutant female's offspring is measured by the between-generation geometric mean fitness that is the multiplicative growth of her own lineage (Lewontin and Cohen, 1969; Yoshimura and Clark, 1991; Yoshimura and Jansen, 1996; Yoshimura et al., 2009). The geometric mean fitness is used for an adaptation either against environmental stochasticity (e.g. change

of the “fittest” male genotype across generations) or demographic stochasticity (e.g. sampling error of mates within a patch) (Garcia-Gonzalez et al., 2015; Yasui and Garcia-Gonzalez, 2016). In the current case, the latter demographic stochasticity is the main problem, since in small patches there is a possibility that all monandrous females choose bad males, resulting in complete reproductive failures and extinction of the genotype (Yasui, 1998, 2001; Yasui and Garcia-Gonzalez, 2016).

Geometric mean fitness  $G(r_x)$  of genotype  $x$  across  $T$  generations is equal to  $T$ th root of the products of growth rates ( $r_x(t)$  = number of individuals ( $n_x$ ) in generation  $t + 1$  /  $n_x$  in generation  $t$ ) of the genotype over  $T$  generations, such that

$$G(r_x) = \left\{ \prod_{t=0}^{T-1} \frac{n_x(t+1)}{n_x(t)} \right\}^{1/T} = \left\{ \prod_{t=0}^{T-1} r_x(t) \right\}^{1/T} \quad (1)$$

(see Yoshimura and Clark, 1991; Yoshimura and Jansen, 1996).

It is useful to know that the logarithm of geometric mean fitness  $G(r_x)$  across  $T$  generations is also transformed into the arithmetic mean ( $E$ ) of logarithmic growth rates ( $r_x$ ) over  $T$  generations, such that

$$\log G(r_x) = (1/T) \sum \log r_x = E \{ \log r_x \} \quad (2)$$

(Yoshimura and Clark, 1991; Yoshimura and Jansen, 1996). This transformation from geometric mean to arithmetic mean makes analyses easier. Indeed, the logarithmic transformation of parameters, which is routinely performed in empirical studies to adjust to the normal distribution requirements of statistics, implies that geometric mean analyses have been already used widely (without due consideration).

Recently, several bet-hedging studies (such as Starrfelt and Kokko, 2012; Holman, 2016) have adopted a variance-discount method (or “Gillespie's measure”; Gillespie, 1977) instead of the cross-generational geometric mean fitness. However, Gillespie's measure is problematic because this approximation presupposes very small variance (fluctuation) of fitness around its mean (Yoshimura and Jansen, 1996; Yoshimura et al., 2009). For example, samples including zero fitness value (complete reproductive failure in a generation) correctly lead to zero geometric mean fitness (lineage extinction) but incorrectly translate into a positive Gillespie's measure (no extinction). Therefore, Gillespie's measure is not applicable to cases when extinction of a genotype (strategy) in a small patch frequently occurs due to intrinsic and/or extrinsic fitness fluctuation (see Yoshimura and Jansen, 1996; Yoshimura et al., 2009 for verification). In this study, the geometric mean fitness approach demonstrates that a bet-hedging strategy works effectively to avoid the risk of extinction of a female genotype, which cannot be avoided by a purely monandrous mating pattern.

## 2. Model

### 2.1. A model for bet-hedging polyandry

Suppose that an individual female parent of semelparous species produces offspring by mating with her pair male and/or an extra-pair male in a patch belonging to a large metapopulation. Each patch contains only a few females of the same genotype, thus demographic stochasticity works prominently. The probability of offspring survival depends on the quality of male partners. This quality is determined by some temporal or permanent / genetic (mutational or compatibility-related) or environmental causes, occurring recurrently in every generation (for details see Garcia-Gonzalez 2004; Yasui and Garcia-Gonzalez, 2016). The offspring survival of good males is  $f_g$  (set: = 1) and that of bad males is  $f_b$  (set:  $\ll 1$ ). The frequencies of good males and bad males in metapopulation are  $p_g$  and  $p_b$ , respectively ( $p_g + p_b = 1$ ). For the

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