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Fertility assurance and breeding synchrony

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Abstract

Extrapair fertilizations are an important factor in reproduction of many bird species. It has been suggested that pursuit of extrapair fertilizations provides a selective pressure capable of affecting the "ecological" attributes of some bird species. It is known that in some cases the pursuit of extrapair copulations is motivated by fertility assurance. That is, there are populations in which (i) some males and females cannot produce viable offspring, and (ii) there is no pre-copulatory way to choose a compatible mate. In such situations individuals mate for "economic" reasons and attempt to secure reproduction by copulating with multiple partners. Here we formulate and analyze a simple game theoretical model addressing the interplay between environmental constraints and the pursuit of fertility assurance via extrapair copulations in determining breeding synchrony. Our results indicate that breeding synchrony in such cases is determined by the magnitude of the costs (due to environmental constraints) of breeding asynchronously versus the worth of the attendant increase in extrapair opportunities.
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1. Introduction

Female birds become fertile and lay eggs, at approximately daily intervals, until completing the clutch. Ecological factors, such as availability of food, the need to have the fledglings grown for annual migration, etc., determine the optimum dates for the onset of fertility (cf. Welty, 1982). It is reasonable to assume that individual onsets are distributed

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randomly about these optimum dates, and that ecological constraints create selective pressure that narrows the variance.

Thus, we would expect the evolved state to be characterized by a complete overlap of the female periods of fertility within each population. However, observations of real word populations indicate otherwise (cf. Welty, 1982). Thus, we must conclude that environmental conditions are not the only kinds of factors that affect the distribution of female fertility periods around the optimal dates.

With the advent of the molecular techniques used to assign paternity (Jeffreys et al., 1985), it became clear that *extrapair fertilizations* (EPF) play a significant role in reproduction of many socially monogamous species (cf. Griffith et al., 2002). In particular, the interrelations between breeding synchrony and EPF have attracted considerable attention—reviewed by Schwagmeyer and Ketterson (1999). We became interested in the subject when our game theoretical modeling of the extrapair phenomena (Fishman et al., 2003) showed that breeding synchrony may influence extrapair reproductive behavior.

Both the verbal models in Schwagmeyer and Ketterson (1999) and our game theoretical analysis assumed that the degree of breeding synchrony affects the distribution of the gender-specific reproductive strategies, but not vice versa. However, unless one is willing to argue that the differences in timing of the breeding events among individuals and populations are devoid of genetic component(s), we must view the population level breeding synchrony as an outcome of female evolutionarily choices (cf. Saino et al., 1999).

In this paper we use game theoretical methods to study the interrelations between breeding synchrony and extrapair paternity in species/populations where female pursuit of extrapair fertilizations is motivated by seeking fertility assurance—a pursuit that is facilitated by asynchronous breeding (cf. Strohbach et al., 1998). Our results indicate that the degree of breeding synchrony within such populations is determined by the magnitude of the costs, due to environmental constraints, of breeding asynchronously versus the benefits of the attendant increase in extrapair opportunities.

2. The model

As discussed above, we shall focus on populations where female pursuit of EPF is motivated by seeking fertility assurance. That is, populations in which (i) some male/female pairings cannot produce viable offspring, and (ii) there is no pre-copulatory way to chose a genetically compatible mate (cf. Krokene et al., 1998; Kempenaers et al., 1999). Furthermore, for the sake of simplicity in this initial exploration of a very complex subject, we shall restrict attention to species/populations where females lay one egg per breeding season. That is, situations for which the probability density functions for the onset of fertility and the fertility period are the same.

Since we assume that the variance of the onset of fertility around the optimum has a genetic component, the differences in variance can be treated as distinct female reproductive strategies. Hence, we postulate the following.

(a) The reproductive season starts on day 0 and continues to day m inclusive.
(b) The optimal date for fertilization is a day in the range $0 < k^* < m$.

In these terms female strategy is represented by the probability density function $f(k)$: $k = 0, 1, \ldots, m$.

Since we are trying to qualify general trends, we choose as the female pure strategies the two extreme cases.[1]

$\mathbf{F}_S$, where S stands for *synchronized*, represents zero variance. That is, the fertility period of $\mathbf{F}_S$ players is always on day k^*.

$\mathbf{F}_U$, where U stands for *unsynchronized*, represents maximum variance. That is, the fertility period of $\mathbf{F}_U$ players is equally likely to happen on any day of the breeding season.

Consequently, the respective probability density functions are given by

$$f_S(k) = \delta(k, k^*) \equiv \begin{cases} 1 & \text{if } k = k^* \\ 0 & \text{otherwise} \end{cases} \tag{1a}$$

and

$$f_U(k) = \begin{cases} \dfrac{1}{m+1} & \text{if } k = 0, \ldots, m \\ 0 & \text{otherwise.} \end{cases} \tag{1b}$$

In principle, we should have subdivided $\mathbf{F}_S$ and $\mathbf{F}_U$ strategists into females who seek extrapair fertilizations and females who do not. However, it is easy to verify that, at least in the context of the current model, females that do not accept extrapair fertilizations always have lower (Darwinian) fitness than females that do. That is, female pursuit of extrapair fertilizations becomes fixed in the population. Similarly, we omit male strategies that do not involve pursuit of EPF opportunities.

For males, pursuit of *extrapair copulations* (EPC) and defense of in-pair paternity are mutually exclusive (cf. Birkhead and Møller, 1992; Chuang-Dobbs et al., 2001). Thus, the possible male strategies are (i) pursuit of EPF opportunities throughout the breeding season and (ii) pursuit of EPF opportunities only when it does not conflict with in-pair paternity defense (cf. Fishman et al., 2003). To decide which of these two male strategies is more appropriate in the current context, we reason as follows.

- As discussed, we focus on situations where the selection of a (genetically) compatible mate is due to female control over the post-copulatory *sperm competition* (cf. Møller and Briskie, 1995; Birkhead and Pizzari, 2002). In such circumstances, both genders improve their chances of gaining viable offspring by copulating with multiple partners. In particular, guarding one's social mate at the expense of passing up extrapair opportunities may not be a viable male strategy (cf. Fishman et al., 2003). Thus, in the current paper, we assume that mated males focus on the pursuit of EPF opportunities at the expense of their in-pair paternity defense.

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[1] We recall that in evolutionary games *pure* strategies—such as the two defined above—do not have to represent observable behavioral phenotypes. Rather, they may represent extreme cases delimiting the range of the pertinent behavior.

Let us denote the frequency of $\mathbf{F_S}$ players by $0 \leq x \leq 1$. As discussed above, we assume that all males pursue EPF opportunities throughout the pertinent period. Thus the ratio of EPF-seeking females to EPF-seeking males (operational sexes ratio) on the kth day, $r(x, k)$, is simply the fraction of females that are fertile on that day. That is, for $k = 0, \ldots, m$, we have

$$r(x, k) = x f_S(k) + (1 - x) f_U(k) = \begin{cases} \dfrac{mx + 1}{m + 1} & \text{if } k = k^* \\ \dfrac{1 - x}{m + 1} & \text{if } k \neq k^*. \end{cases} \tag{2}$$

To derive the expected payoffs for the two kinds of female strategists we reason as follows. Let $0 < q < 1$ be the probability that any randomly selected pair is genetically incompatible (i.e. the probability that a female who has no extrapair partners has a viable offspring is $1 - q$). Thus, let us define the probability that a female that has coupled with n males ($n = 0, 1, \ldots$) in addition to her social mate gains a fertilization by $\alpha_n(q)$: here $\alpha_n(q)$ is monotone increasing in n, monotone decreasing in q, and $\alpha_0(q) = 1 - q$. Finally, let the probability that a female that is fertile on day k^* copulates with n males ($n = 0, 1, \ldots$) in addition to her social mate be defined by $G(r(x, k^*), n) = g_n(x)$, and the corresponding probability for a female that is fertile on any one of the $m(k \neq k^*)$ days be defined by $G(r(x, k), n) = h_n(x)$. Thus, the probability that a female that is fertile on day k^* has a viable offspring is given by

$$g(x) = \sum_{n=0}^{\infty} \alpha_n(q) g_n(x). \tag{3a}$$

And the corresponding expression for a female that is fertile on day $k \neq k^*$ is given by

$$h(x) = \sum_{n=0}^{\infty} \alpha_n(q) h_n(x). \tag{3b}$$

Since $r(x, k)$ represents the effective *female to male* ratio, $G(r, n)$ is a monotone decreasing function of r. Hence, by Eq. (2), for any $n \geq 0$: $g_n(x)$ are monotone decreasing-and $h_n(x)$ are monotone increasing in x. Thus, since $\alpha_n(q)$ are positive for any $n \geq 0$, $g(x)$ is monotone decreasing-and $h(x)$ is monotone increasing in x. Thus, since $h(0) = g(0)$, $h(x) > g(x)$ for $0 < x \leq 1$. Let us define

$$\phi(x) = \frac{h(x) - g(x)}{h(x)}. \tag{4a}$$

It is easy to see that

$$\phi(0) = 0 \qquad \text{and} \qquad \phi'(x) > 0 \qquad \text{for } x \geq 0. \tag{4b}$$

The function $\phi(x)$ thus represents the relative advantage (fertility assurance-wise) of asynchronous over synchronous breeding, and Eq. (4b) has a straightforward interpretation.

- The number of copulations that a male is capable of in a day is not unlimited. Thus, since a female's probability of gaining fertilization increases with the number of

copulation partners, the probability of gaining fertilization is adversely affected by a presence of other EPF-seeking females. Consequently, when a population has a non-negligible fraction of $\mathbf{F_S}$ females, there is an advantage (fertility assurance-wise) to *not* being fertile on day k^*; that is, to breeding asynchronously. Moreover, this advantage increases as the fraction of synchronous breeders increases. Finally, when all the females in a population breed asynchronously ($x = 0$), there is no advantage to *not* being fertile on any particular day. Thus, $\phi(0) = 0$.

We see that fertility assurance selects for asynchronous breeding. On the other hand, as discussed above, environmental constraints select for synchronous breeding. To see how these two selective forces interact, we proceed as follows.

Regardless of the nature of the environmental factors that determine the optimum date for fertilization, diverging from these optima should have fitness costs, e.g., decreased offspring survival, or decreased chances of breeding again. Let the net benefits of conceiving on the optimal date (the fitness benefits of having a viable offspring minus the fitness costs of raising it) be $A > 0$, and let the *additional* costs of raising an offspring *not* conceived on the optimum date be $0 < B < A$.[2] In these terms, the respective payoffs to (average) $\mathbf{F_S}$ and $\mathbf{F_U}$ strategists are given by

$$\pi_S(x) = g(x)A \qquad \text{and} \qquad \pi_U(x) = \frac{1}{m+1}[g(x)A + mh(x)(A - B)]. \tag{5a}$$

We recall that an $\mathbf{F_U}$ female has a $1/(m + 1)$ chance of being fertile on day k^*.

Hence, the population-average payoff, $\pi(x)$, is

$$\pi(x) = x\pi_S(x) + (1 - x)\pi_U(x). \tag{5b}$$

Now, fitness represents the per capita reproductive rate. Thus, if the fitness of the $\mathbf{F_S}$ players is less than the population average, their frequency in a population will decrease, and vice versa. In fact, it can be shown (cf. Hofbauer and Sigmund, 1988) that the dynamics of x (the frequency of the $\mathbf{F_S}$ players in a population) are prescribed by

$$x' = [\pi_S(x) - \pi(x)]x = [\pi_S(x) - \pi_U(x)]x(1 - x)$$
$$= \frac{mA}{m+1}h(x)[b - \phi(x)]x(1 - x). \tag{6}$$

Since $\phi(0) = 0$ and $h(x), \phi(x)$ are monotone increasing, system (6) has two possible convergence points (*evolutionarily stable strategy*, ESS, solutions) on $0 \leq x \leq 1$.

(a) If $\phi(1) < b$, then $x' > 0$ for $0 < x < 1$. Thus, $x(t)$ converges to unity if $x(0) > 0$. That is, $\mathbf{F_S}$ is the unique ESS solution of system (6).

(b) If $\phi(1) > b$, there exists a unique $0 < \xi < 1$ such that $\phi(\xi) = b$. Consequently we have (i) $\phi(x) < b$ for $0 < x < \xi$, implying $x' > 0$, (ii) $x' = 0$, if $x = \xi$, and (iii) $\phi(x) > b$, i.e. $x' < 0$ when $\xi < x < 1$. Thus, $x(t)$ converges to ξ if $0 < x(0) < 1$. That is, a mixed strategy solution, $\mathbf{F_S} \oplus \mathbf{F_U}$, where the frequency of the $\mathbf{F_S}$ behavior

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[2] If $B > A$, then the relative fitness of asynchronous breeders will always be less than the relative fitness of synchronous breeders. That is, a modeled population will always breed synchronously.

(on either an individual or a population level[3]) is ξ, is the unique ESS of system (6).

Finally, since $\phi(\xi) = b$, by the *implicit function theorem*: $\partial\xi/\partial b > 0$. That is, the degree of breeding synchrony in the population increases with the intensity of the environmental constraints.

3. Example

Let us illustrate the, somewhat abstract, considerations above with an example. For the purposes of illustration, let us assume copulation with at least one genetically compatible partner assures fertilization, i.e., $\alpha_n(q) = 1 - q^{n+1}$. And let us also assume that the probability of gaining $n \geq 0$ extrapair copulations on the kth day is given by a *Poisson* distribution with the parameter $\lambda(x, k) = c/r(x, k)$.[4] In these terms we have

$$g(x) = \sum_{n=0}^{\infty}(1 - q^{n+1})e^{-\lambda(x,k^*)}\frac{[\lambda(x, k^*)]^n}{n!}$$
$$= 1 - q \exp\left[-(1 - q)\frac{m + 1}{mx + 1}c\right] \tag{7a}$$

and

$$h(x) = 1 - q \exp\left[-(1 - q)\frac{m + 1}{1 - x}c\right]. \tag{7b}$$

And, therefore,

$$\phi(x) = q\frac{\exp\left[-(1 - q)\frac{m+1}{mx+1}c\right] - \exp\left[-(1 - q)\frac{m+1}{1-x}c\right]}{1 - q \exp\left[-(1 - q)\frac{m+1}{1-x}c\right]}. \tag{7c}$$

Thus, the existence/stability conditions for the mixed ESS are

$$b < b^* \equiv \phi(1) = qe^{-(1-q)c}. \tag{8}$$

We illustrate these results in Fig. 1.

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[3] As discussed above, strategies such as $\mathbf{F_S}$ and $\mathbf{F_U}$ which are represented by the integer values zero and one of x in the current model are known as *pure* strategies, whereas strategies for which x takes fractional values—in effect "mixing" the pure strategies—are known as *mixed* strategies. There are two kinds of real word situations that give raise to mixed strategies.

- *Population level polymorphism*—wherein each individual exhibits a specific pure strategy, but there is more than one pure strategy present on the population level.
- Alternatively, individuals may exhibit behavior corresponding to different pure strategies at different times *despite similar circumstances*. In such situations, it is useful to think of pure strategies as extreme cases delimiting the range of the possible individual behavior.

[4] The reader may wish to think of c as the number of EPC that an average male can "manage" on the average day—the *Casanova* factor.
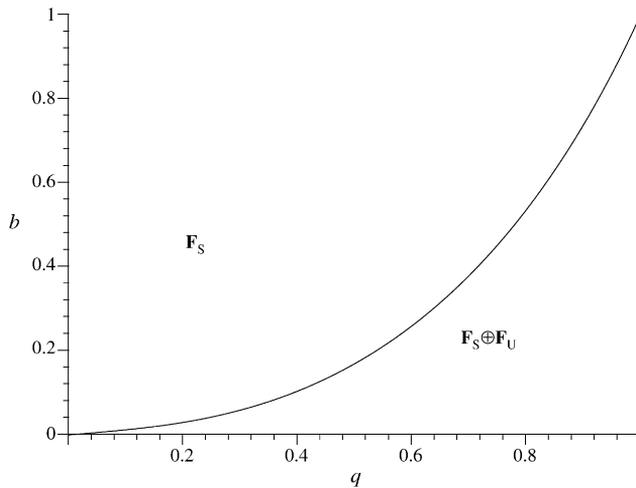
Fig. 1. The conditions on the model's parameters for evolutionary stability of the two possible ESS solutions. If $b < b^*$, the model has a unique mixed ESS: $\mathbf{F}_S \oplus \mathbf{F}_U$ (the modeled population exhibits a degree of asynchronous breeding). Otherwise, $\mathbf{F}_S$ (representing a completely synchronous breeding) is the unique ESS. Here $c = 2$.

Furthermore, as discussed above, even when a population exhibits an ESS with a degree of breeding asynchrony, the extent of this asynchrony decreases with the intensity of the environmental constraints, b (see Fig. 2).

4. Discussion

With the advent of the molecular techniques used to assign paternity (Jeffreys et al., 1985), it became clear that in dealing with avian mating systems we must distinguish between social and genetic monogamy. Although 95% of bird species are socially monogamous (Lack, 1968), genetic monogamy only occurs in 14% of the surveyed passerine species, and the average frequency of extrapair offspring among socially monogamous species is 11.1% of offspring and 18.7% of broods (Griffith et al., 2002).

Thus, extrapair fertilization is an important factor in the lives of many bird species. In particular, it has been suggested (cf. Wagner, 1993) that pursuit of EPF opportunities provides a selective pressure capable of affecting the "ecological" attributes, such as population density, of these species. Here we study the possible effects of the pursuit of EPF opportunities on breeding synchrony.

Our results indicate that when female ability to gain extrapair fertilizations is constrained by the availability of male partners (cf. Strohbach et al., 1998), breeding synchrony will be determined by the relative magnitudes of the two opposing selective pressures: environmental constraints—favoring synchronization—and the pursuit of extrapair opportunities—favoring asynchrony (cf. Westneat and Gray, 1998). If environmental constraints are large relative to extrapair benefits, breeding will be synchronous. Otherwise, the degree of asynchrony will increase until the attendant extrapair benefits equal the costs
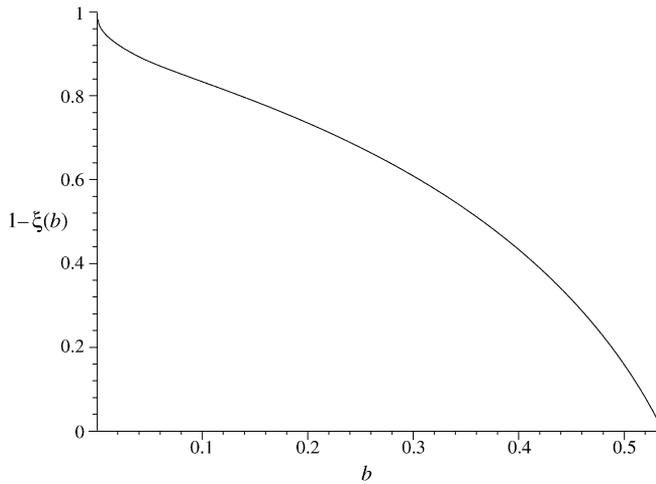
Fig. 2. The degree of asynchrony in the mixed ESS, $\mathbf{F}_S \oplus \mathbf{F}_U$, as a function of the (relative) intensity of environmental constraints. Here $q = 0.8$, $m = 30$, and $c = 2$.

of the environmental constraints. Thus, our results indicate that, under appropriate conditions, pursuit of extrapair fertilizations determines breeding synchrony of avian populations, rather than vice versa.

Acknowledgements

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