

Trade up polygyny and breeding synchrony in avian populations

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Abstract

The advent of the molecular techniques used to assign paternity has focused attention on the differences between the social and the genetic mating systems of sexual species. In particular, the interrelations between *breeding synchrony*—the degree to which the fertility periods of individual females in a population overlap and the degree of extrapair paternity (EPP) in that population, has become a subject of a lively debate. Investigation of the subject can be facilitated by examining the criteria that females use in choosing extrapair partners. These preferences constitute a continuum ranging between two extremes. At one end, there are situations wherein all the females in a population exhibit a preference for males with particular phenotypic markers, and females mated to males lacking such “quality” markers seek extrapair fertilizations from males that do — *trade up polygyny*. At the other extreme, there are situations wherein females seek to maximize the total number of male partners, rather than secure fertilization by males of particular type — *indiscriminate polygyny*.

Previously, we used game theoretical methods to model the interrelations between breeding synchrony and EPP in the context of indiscriminate polygyny. Here we present an analogous investigation in the context of trade up polygyny. Our results for the two cases, which delimit the range of the possible behavior, are similar. That is, we see that it is the pursuit of extrapair fertilizations opportunities that determines breeding synchrony of populations, rather than the vice versa as has been previously suggested.

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1. Introduction

Female birds become fertile and lay eggs, at approximately daily intervals, until completing their clutch. Thus, *breeding synchrony* of an avian population is determined by recording the egg laying times of the females in that population and calculating the variance around the mean. When this variance is small, the population is considered to be “synchronous” and vice versa (cf. Stutchbury and Morton, 1995). It is reasonable to assume that 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). Furthermore, we

would expect that individual onsets are distributed randomly about these optimum dates, and that ecological constraints create selective pressure that narrows the variance.

However, available evidence indicates that environmental constraints cannot be the only selective force affecting breeding synchrony. To wit, comparative analysis across bird species shows that breeding synchrony appears to be proportional to the intensity of the environmental constraints (cf. Spottiswoode and Møller, 2004). This indicates existence of selective forces that promote asynchronous breeding, and that observed situations represent a balance between these two opposing selective forces.

With the advent of the molecular techniques used to assign paternity (Jeffreys et al., 1985), it became clear that *extrapair paternity* (EPP) plays a significant role in

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reproduction of many socially monogamous species (cf. Griffith et al., 2002). In particular, the interrelations between breeding synchrony and EPP have attracted considerable amount of attention (reviewed by Schwagmeyer and Ketterson, 1999). These investigations are complicated by the fact that the observable attributes of EPP vary extensively between species and populations (cf. Petrie and Kempenaers, 1998). As we have discussed elsewhere (Fishman and Stone, 2002; Fishman et al., 2003; Fishman and Stone, 2004), to a considerable degree this variation is interpretable in terms of the criteria that females use in choosing extrapair partners.

These criteria are prescribed by the type of the female benefits for having extrapair young. When raising offspring requires an extensive male parental investment, females must form an exclusive social bond in order to secure such an investment. However, females who secure both paternal care and superior *genetic* endowment for their offspring have higher (Darwinian) *fitness* than females that only secure paternal care. Thus, *extrapair fertilizations* (EPF) provide a viable evolutionary compromise between the female quest for optimal *genetic* partners, and the need to secure an extensive male parental investment. As we formalize shortly, the probability of a females gaining fertilization is reduced by the presence of other EPF-seeking females. Consequently, in the presence of a subpopulation of synchronized females it will be more advantageous for EPF-seeking females to breed asynchronously. It is to be expected that the more limiting the number of extra pair partners the greater the tendency for asynchrony.

Female choices in extrapair partners are classifiable in terms of two distinct classes of preference (cf. Jennions and Petrie, 2000).

- **Trade-up polygyny.**¹ When all females in a population have the same type of optimal genetic partners, we can expect them to evolve ability to recognize males with such optimal genotypes through phenotypic markers. That is, females will have a scale to measure male quality. And, in particular, mated females will accept EPF (as distinct from *extrapair copulations*—EPC) only from males who are superior to their social mate (cf. Strohbach et al., 1998).

Example. In some species where reproductively active males fall into distinct age classes, there is a well-documented female preference for older males as extrapair partners — a preference that, moreover, appears to be independent of any possible non-

genetic (direct) benefits (Wetton et al., 1995; Kempenaers et al., 1997; Stutchbury et al., 1997; Richardson and Burke, 1999).

- **Indiscriminate polygyny.** Since genetic incompatibility leads to infertility, there can be a variation in what constitutes an ideal genetic partner for an individual female. When females have to assure fertility, but are incapable of a pre-copulatory choice of a compatible genetic partner, we would expect the attendant material benefits to be the sole criterion for the selection of social mates. Because a social mate selected in such fashion may not be genetically compatible, we expect females to solicit EPC from diverse extrapair males—and use *in copula* and/or *post-copulatory* mechanisms to select compatible genetic partners (Zeh and Zeh, 1996, 1997).

Previously, we used the methods of evolutionary game theory to investigate the interrelations between breeding synchrony and EPP in the context of indiscriminate polygyny. Here we present an analogous investigation in the context of trade-up polygyny. Our results for the two cases, which delimit the range of the pertinent behavior, are similar. That is, we see that it is the pursuit of extrapair fertilizations opportunities that determines breeding synchrony of populations, rather than the vice versa as was suggested by other authors (cf. Stutchbury, 1998).

In retrospect, the similarity between indiscriminate and trade-up polygyny cases should not be surprising. In both cases there is a possibility of female–female competition: to maximize the number of extrapair partners in the indiscriminate polygyny case vs. gaining EPF from one of the limited number of “high-quality” males in the trade-up polygyny situations. In both cases, the intensity of the female–female competition is decreased by asynchronous breeding.

2. Formulation of the model

As discussed above, in the current model, we focus on populations where female choice of extrapair partners is motivated by the pursuit of superior genetic endowment for their offspring. This emphasis on trade-up polygyny is reflected in the following features of the current model.

1. From the female point of view, the reproductively active males within the modeled population fall into two distinct classes: *desirable* (high quality) and *undesirable* (low quality).
2. The modeled population is monogamous, and unpaired females do not breed. Thus, some females have to accept low-quality social mates.

¹Some texts use the term “polyandry” in lieu of the term “polygyny”. However, since in previous usage (in the context of social mating) the term polyandry represents a situation wherein several males associate exclusively with one female, we prefer the term polygyny.

- 3. Male quality differences have a genetic component(s), and therefore the offspring of high-quality males are more valuable.

Since, under trade-up polygyny, females accept EPF only from males who are superior to their social mate (cf. Strohbach et al., 1998), we have the following.

- 4. Females mated to low-quality males accept/seek extrapair fertilizations, whereas females mated to high-quality males do not.

For males, pursuit of EPC and defense of in-pair paternity are mutually exclusive (cf. Birkhead and Møller, 1992; Chuang-Dobbs et al., 2001). Since attribute#4 above implies that low-quality males cannot gain EPF whereas high-quality males are not in risk of being cuckolded, male extrapair vs. in-pair behavior becomes quality dependent. That is:

- 5. Low-quality males focus exclusively on defending their in-pair paternity; whereas high-quality males focus exclusively on the pursuit of extrapair opportunities.

Finally, unless one is willing to argue that the differences in the timing of the breeding events among individuals and populations are devoid of genetic components, we must view the population-level breeding synchrony as an outcome of female evolutionary choices (cf. Saino et al., 1999). That is:

- 6. The probability density functions for the onset of fertility/duration of fertility periods can be treated as distinct female reproductive strategies.

We note that the current paper is an *initial* exploration of the general principles of the interrelations between breeding synchrony and EPP, rather than a description of the pertinent situation in any specific species/population. The modeling approach is a simplification that allows us to effectively explore the critical features of the phenomena. In other words, ours is a strategic qualitative model rather than a predictive model (May, 1975). Consequently:

- 7. We restrict the model 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 fertility period are the same. Since multi-egg clutches are usually laid on consecutive days, we feel that modeling a multi-egg case will add a dimension of algebraic complexity without changing the essential properties of the model.

- 8. The form of the (onset of fertility) probability distributions may vary among species/populations. In particular, our model focuses on showing how the relative fitness of the distinct female strategies depends on the variance, rather than on a particular form, of such probability distributions.

Since we assume that the variance of the onset of fertility around the optimum has a genetic component,

the differences in this 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 day $0 < k^* < m$.

In these terms female strategy can be represented by the probability density function

$$f(k) : k = 0, 1, \dots, m.$$

Firstly, as discussed above, we recall that all females accept EPF only from males that are superior to their social mates. Since we are trying to qualify general trends, we choose as the female pure strategies the two extreme (delimiting) cases:²

F_S , where S stands for *synchronized*, represents zero variance. That is, the fertility period of F_S players is always on day k^* .

F_U , where U stands for *unsynchronized*, represents maximum variance. That is, the fertility period of F_U players is equally likely to happen on any day of the breeding season.

Consequently, the probability density functions (corresponding to the minimum vs. maximum variance) are given by

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

and

$$f_A(k) = \begin{cases} \frac{1}{m+1} & \text{if } k = 0, \dots, m, \\ 0 & \text{otherwise.} \end{cases} \quad (1b)$$

Here the subscript A stands for asynchronous (breeding).

As discussed, we are dealing with situations wherein females have a *pre-copulatory* criteria for choosing an optimal mate. Thus, given that individual females appear to have a degree of control over the timing of their breeding events (cf. Saino et al., 1999), there is a possibility of individuals “adjusting” the timing of their fertility periods. We represent this possibility as the third strategy:

F_C , where C stands for *conditional*. F_C strategists breed on k^* day, when mated to high-quality males, and breed asynchronously when mated to low-quality males.

Now we note that F_C and F_U strategists mated to low-quality males, exhibit identical behavior, and thus have

²To recollect, 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.

the same fitness. However, since — as discussed below — asynchronous breeding is more costly than synchronous breeding, F_C strategists mated to high quality males have higher fitness than F_U strategists in the same situation. Thus, given a population with male heterogeneity, F_C strategists have higher average fitness than F_U strategists. In formal game theoretical terms; F_C strictly dominates F_U , and therefore the latter can be excluded. Thus, we retain two female strategies: F_S vs. F_C .

It remains to define the pertinent costs and benefits.

- Let us denote the fraction of the high quality among the paired males by $0 < p < 1$. Thus, a fraction $1 - p$ of females is paired with undesirable mates and, consequently, is receptive toward extrapair fertilization by high-quality (desirable) males.
- Let the net (benefits minus costs) female payoff for having an offspring by a low-quality male be $A > 0$. And let the corresponding benefits for having an offspring by a high-quality male be $A + B$, where $B > 0$.
- Finally, 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 us denote the average, additive cost of breeding on $k \neq k^*$ day by $D_k > 0$.

Let us denote the frequency of the F_S strategists by $0 \leq x \leq 1$. Since a fraction $1 - p$ of the females are mated to low quality males, the fraction of females that seek extrapair fertilizations on k th day is given by $(1 - p)[xf_S(k) + (1 - x)f_A(k)]$. Thus, the ratio of EPF seeking females to EPF seeking males on the k th day of the breeding season, $r(x, k)$, is given by

$$r(x, k) \equiv \frac{(1 - p)[xf_S(k) + (1 - x)f_A(k)]}{p} = \begin{cases} \frac{1-p}{p} \frac{mx+1}{m+1} & \text{if } k = k^*, \\ \frac{1-p}{p} \frac{1-x}{m+1} & \text{if } k \neq k^*. \end{cases}$$

Female probability of gaining an EPF is adversely affected by female–female competition for acceptable extrapair partners. Since this competition increases as $r(x, k)$ increases, it is reasonable to assume that the probability that a female seeking EPF on the k th day will succeed, decreases with $r(x, k)$. Thus, we can define the functional dependence of the female’s probability to gain an EPF on the k th day on $r(x, k)$ by $G(r(x, k))$, where

$$G(0) = 1, G(z) \xrightarrow{z \rightarrow \infty} 0 \quad \text{and} \quad G'(z) < 0 \text{ for } z \geq 0 \tag{3}$$

Since the value of $r(x, k)$ is the same for all $k \neq k^*$ days, we shall simplify the subsequent discussion by writing $r(x, 0)$ whenever we wish to indicate the value of $r(x, k)$ on one of the $k \neq k^*$ days.

Since $r(x, 0) < r(x, k^*)$ for $x > 0$, Eq. (3) implies $G(r(x, 0)) > G(r(x, k^*))$ whenever $x > 0$. That is, unless a population does not have any F_S females, female pursuit of extrapair fertilizations is facilitated by not being fertile on k^* day i.e. by breeding asynchronously.

Let us define

$$\phi(x) = G(r(x, 0)) - G(r(x, k^*)). \tag{4a}$$

That is, the function $\phi(x)$ represents the relative advantage, with respect to gaining EPF from high-quality males, of not breeding on the k^* day i.e. *the advantage of asynchronous breeding*.

When a population does not have any F_S players, female–female competition for desirable extrapair partners on the k^* day is no more intense than on any other day i.e. $r(0, 0) = r(0, k^*)$, and therefore

$$\phi(0) = 0. \tag{4b}$$

Since the intensity of the competition for desirable extrapair partners increases for females breeding on the k^* day and decreases for females breeding on any other day as the fraction of F_S players in the population increases: $G(r(x, 0))$ is monotonically increasing, and $G(r(x, k^*))$ is monotonically decreasing in x . Consequently,

$$\phi'(x) > 0 \text{ for } x \geq 0. \tag{4c}$$

Finally, it is reasonable to assume that the advantage of asynchronous breeding, $\phi(\dots)$ increases with the length of the breeding season and decreases as the fraction of high-quality males in the population increases. Thus, we must have

$$\frac{\partial \phi}{\partial m}(x; m, p) > 0 > \frac{\partial \phi}{\partial p}(x; m, p) \text{ for } 0 < x \leq 1. \tag{4d}$$

Now,

$$\frac{\partial \phi}{\partial m}(x; m, p) = \frac{1 - p}{p} \frac{1 - x}{(m + 1)^2} [G'(r(x, k^*)) - G'(r(x, 0))]$$

and

$$\frac{\partial \phi}{\partial p}(x; m, p) = \frac{1}{p^2} \frac{1}{m + 1} [(mx + 1)G'(r(x, k^*)) - (1 - x)G'(r(x, 0))]. \tag{4e}$$

And therefore, the function $G(\dots)$ must satisfy

$$G'(r(x, 0)) < G'(r(x, k^*)) < \frac{1 - x}{mx + 1} G'(r(x, 0)) \text{ for } 0 < x \leq 1. \tag{4f}$$

The information necessary for postulating an explicit form for $G(\dots)$, and hence for $\phi(\dots)$, is not available at present. Moreover, there is no *a priori* reason to assume that different species and populations exhibit the same functional form of $G(\dots)$. Thus, we shall restrict the current analysis to the most general form possible i.e. the one delimited by the minimal necessary constraints of Eqs. (3) and (4).

We see that pursuit of trade-up polygyny selects for asynchronous breeding. On the other hand, as discussed above, environmental constraints select for synchronous breeding.

The respective payoffs to the (average) F_S and F_C strategists are given by

$$\pi_S(x) = (1 - p)[A + G(r(x, k^*))B] + p(A + B) \quad (5a)$$

and

$$\pi_C(x) = (1 - p) \left[A + \frac{G(r(x, k^*)) + mG(r(x, 0))}{m + 1} B - \frac{m}{m + 1} D \right] + p(A + B)$$

where

$$D = \frac{1}{m} (D_0 + \dots + D_{k^*-1} + D_{k^*+1} + \dots + D_m).$$

To recollect, an asynchronously breeding female has a $1/(m + 1)$ chance of being fertile on k^* day.

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

$$\pi(x) = x\pi_S(x) + (1 - x)\pi_C(x) \quad (5b)$$

Finally, fitness represents the *per capita* reproductive rate. Thus, if the fitness of the 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 F_S players in a population) are described by

$$\begin{aligned} x' &= [\pi_S(x) - \pi(x)]x = [\pi_S(x) - \pi_C(x)]x(1 - x) \\ &= \frac{m(1 - p)B}{m + 1} [d - \phi(x)]x(1 - x), \end{aligned} \quad (6)$$

where $d = D/B$ i.e., the parameter d represents the costs of breeding asynchronously relative to (additive) benefits of gaining fertilization by a high quality male.

Thus, system (6) has two possible convergence points (*evolutionary stable strategy*, ESS, solutions) on $0 \leq x \leq 1$, depending on the magnitude of d relative to $\phi(1) = \text{maximum value of } \phi(\bullet)$.

- (a) Since $d > \phi(0) = 0$, $d < \phi(1)$ implies existence of $0 < \xi < 1$ such that $\phi(\xi) = d$. That is: (i) $x' > 0$ if $0 < x < \xi$; (ii) $x' = 0$ if $x = \xi$; and (iii) $x' < 0$ if $\xi < x < 1$. Hence, $x(t)$ converges to ξ whenever $0 < x(0) < 1$

That is, a mixed strategy solution, $F_S \oplus F_C$, where the frequency of synchronous breeding (on either individual or a population level³) is ξ , is the unique ESS of system (6) if $d < \phi(1)$.

- (b) If, $\phi(1) < d$, then $d > \phi(x)$ for $0 < x < 1$ i.e. $x' > 0$ for $0 < x < 1$. Thus, system (6) converges to $x = 1$. And therefore, F_S is the unique ESS solution of system (6).

Note. By *implicit function theorem* and Eqs. (4), it is easy to see that

$$\frac{\partial \xi}{\partial d} > 0, \frac{\partial \xi}{\partial m} < 0, \text{ and } \frac{\partial \xi}{\partial p} > 0. \quad (7)$$

Hence the degree of synchrony in the population increases with the relative cost of breeding asynchronously and the intensity of environmental constraints. It decreases with the length of the breeding season.

Let us define the steady state frequency of F_S players by x_{ESS} ,

$$x_{\text{ESS}} = \begin{cases} \xi & \text{if } d < \phi(1), \\ 1 & \text{if } d \geq \phi(1). \end{cases} \quad (8a)$$

Then the fraction of females that breed on the optimal date, σ , is given by

$$\begin{aligned} \sigma &= x_{\text{ESS}} + p(1 - x_{\text{ESS}}) + \frac{1 - p}{m + 1} (1 - x_{\text{ESS}}) \\ &= \begin{cases} \frac{mp+1}{m+1} + m \frac{1-p}{m+1} \xi & \text{if } d < \phi(1), \\ 1 & \text{if } d \geq \phi(1). \end{cases} \end{aligned} \quad (8b)$$

Using Eqn. (7) it is straightforward to show that σ is monotone increasing in d and p and monotone decreasing in m when $d < \phi(1)$. We depict these results in Fig. 1 below, where — for illustration purposes only — we take an arbitrary function that satisfies

³As discussed above, strategies such as F_S and F_C , 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 types of real world situations that give rise 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.

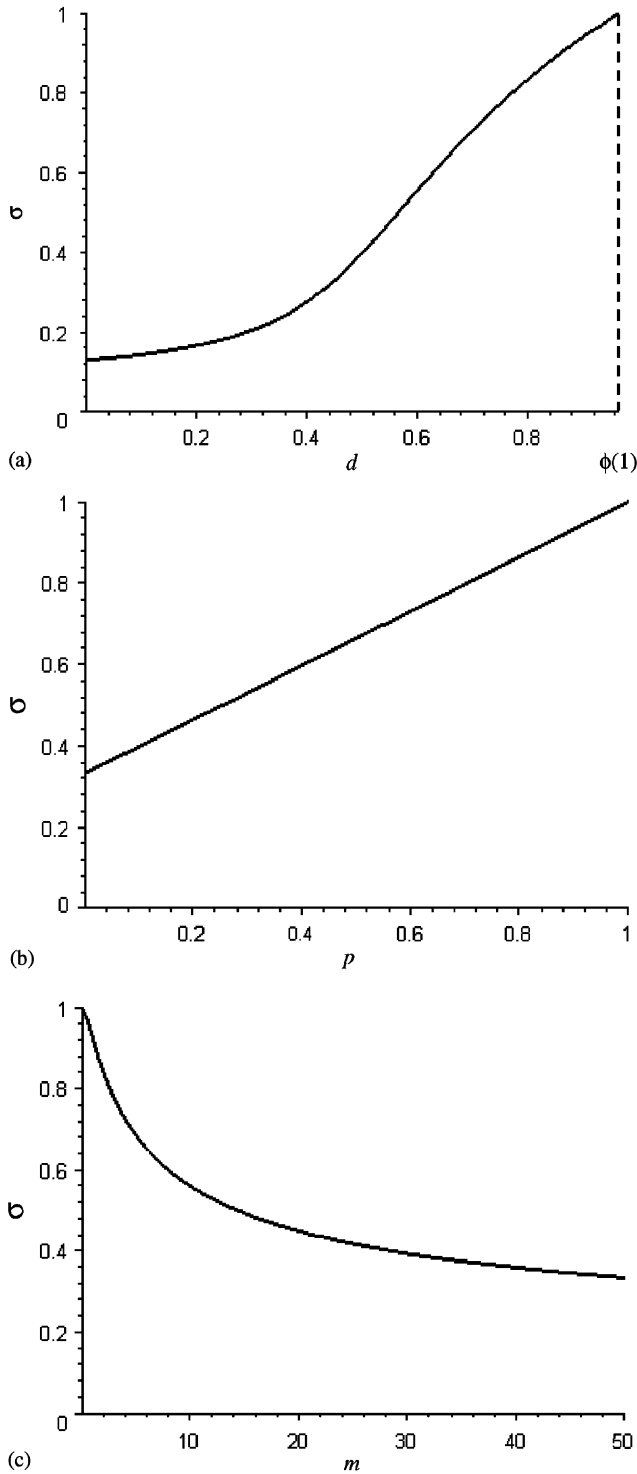


Fig. 1. The fraction of females breeding on the optimal date (the degree of breeding synchrony) when

$$G(r(x, k)) = \frac{1}{1 + \left[\frac{m+1}{1-p} \right] p e^{-p/(m+1)} r(x, k)}$$

We depict three functional relations. (a) Breeding synchrony vs. the (relative) intensity of environmental constraints ($p = 0.1$ and $m = 29$). (b) Breeding synchrony vs. the frequency of high-quality males in the population ($d = 0.5$ and $m = 29$). (c) Breeding synchrony vs. the length of the breeding season ($d = 0.5$ and $p = 0.1$).

conditions (3) and (4).

$$G(r(x, k)) = \frac{1}{1 + \frac{m+1}{1-p} p e^{-p/(m+1)} r(x, k)} = \begin{cases} \frac{1}{1+(mx+1)e^{-p/(m+1)}} & \text{if } k = k^*, \\ \frac{1}{1+(1-x)e^{-p/(m+1)}} & \text{if } k \neq k^*. \end{cases}$$

In these terms

$$\sigma = \begin{cases} \frac{(1-p) \left[\sqrt{(m+1)Q + (m-1)d(1+\pi)} \right] + 2(m+1)p - m}{2(m+1)d\pi} & \text{if } d < \phi(1), \\ 1 & \text{if } d \geq \phi(1) = \frac{(m+1)\pi}{1+(m+1)\pi}. \end{cases}$$

$$Q = (m-1)[d(1+\pi) - 1]^2 + 2d^2(1+\pi)^2 + 2,$$

where

$$\pi = e^{-p/(m+1)}.$$

3. Discussion

Given that roughly 95% of bird species are classified as ‘monogamous’ (Lack, 1968), some might claim that the class *Aves* is short on mating system diversity. However, with the advent of the DNA fingerprinting techniques (Jeffreys et al., 1985), it became clear that in dealing with avian mating systems we must distinguish between social- and genetic monogamy. Recent evidence indicates that genetic monogamy occurs in only 14% of surveyed passerine species, with the average frequency of extrapair offspring among socially monogamous bird species being 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 bird species.

Previously (Fishman and Stone, 2005), we have analysed the interrelations between EPP and breeding synchrony in the context of indiscriminate polygyny. Here we studied the same issue in the context of trade up polygyny. In both cases we have seen that breeding synchrony 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 of the environmental constraints.

In retrospect these interrelations between breeding synchrony and environmental constraints should not be surprising. Though under indiscriminate polygyny all females compete for maximizing the number of different male partners, whereas under trade up polygyny females mated to undesirable males compete for extrapair fertilization by one of the limited number of desirable males; in both cases asynchronous breeding decreases the intensity of the female–female competition while incurring costs due to synchrony-compelling environmental constraints.

As discussed in the introduction, indiscriminate- and trade-up polygyny are extreme cases, delimiting the range of pertinent female behavior. That is, we expect the bulk of actual populations to exhibit some state intermediate between these two extremes. Nevertheless, the fact that the results at the two extremes are so similar lends a degree of credence to the conclusion that, under appropriate conditions, pursuit of extrapair fertilizations determines breeding synchrony of avian populations, rather than the vice versa.

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