Punishment of polygyny

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We investigated the evolution of monogamy (one male, one female) and polygyny (one male, more than one female). In particular, we studied whether it is possible for a mutant polygynous mating strategy to invade a resident population of monogamous breeders and, alternatively, whether a mutant monogamy can invade resident polygyny. Our population obeys discrete-time Ricker dynamics. The role of males and females in the breeding system is incorporated via the harmonic birth function. The results of the invasibility analysis are straightforward. Polygyny is an evolutionarily stable strategy mating system; this holds throughout the examined range of numbers of offspring produced per female. So that the two strategies can coexist, polygyny has to be punished. The coexistence of monogamy and polygyny is achieved by reducing the offspring number for polygyny relative to monogamy. This yields long-term persistence of the strategies for all offspring numbers studied. An alternative punishment is to increase the sensitivity of polygynous breeders to population density. The coexistence is possible only with a limited range of offspring produced. The third way to achieve coexistence of the two mating strategies is to assume that individuals live in a spatially structured population, where dispersal links population subunits to a network. Reducing the dispersal rate of polygynous breeders relative to that of monogamous individuals makes the coexistence feasible. However, for monogamy to persist, the number of offspring produced has to be relatively high.

Keywords: sexual reproduction; monogamy; polygamy; coexistence; evolutionarily stable strategy; spatially structured population

1. INTRODUCTION

In the domain of ecology, the rich variety of mating systems is one of the most captivating naturalistic observations and also a great challenge in terms of solid evolutionary explanations (Clutton-Brock 1989; Davies 1991). For example, in birds up to 90% of all species have monogamy as the predominant mating strategy (Lack 1968). This is particularly true for insectivorous passerines, but less so for seed-eating and frugivorous subfamilies where approximately one-quarter of the subfamilies are polygynous (Lack 1968). We, as so many others, are interested in the evolution of polygyny as a mating system. Polygyny is used here as a term for a mating system where one male can monopolize several females.

Contrary to others (reviewed by Clutton-Brock (1989) and Davies (1991)), we did not look for the ultimate fitness benefits of polygyny or monogamy. Rather, we looked for whether a rare polygynous breeding strategy has any chance of invading a population with a dominant monogamous breeding strategy. Thus, we shall assume that mutation takes place in a population obeying pure monogamy as a mating system. Our objective is to introduce the mutant polygynous breeding strategy into the population of monogamous individuals and analyse the conditions under which the mutant strategy can establish itself and increase in numbers in the population. Thus, we are looking to see whether one of the two strategies is an

evolutionarily stable strategy (ESS) (Maynard Smith 1982) and, if not so, under what conditions monogamy and polygyny can coexist as alternative mating systems. In our study, the two strategies are treated as pure strategies.

2. MALES, FEMALES AND POLYGYNOUS REPRODUCTION

Everything of relevance in population biology revolves around two fundamental processes: births and deaths, both being density dependent. For many temperate species, births are restricted to a short season of the annual cycle. To acknowledge this fact we shall take the discrete-time Ricker equation as a representative of the population renewal process. Our focus is on the evolution of the mating systems and, therefore, we need a way of explicitly incorporating the female (F) and male (M) roles into the population dynamics. For this purpose, we shall adopt the harmonic birth function

$$B(X_F, X_M) = \frac{kX_F X_M^2}{X_F h^{-1} + X_M}, \quad (1)$$

where X_F and X_M denote the number of females and males, respectively. In this equation, the total number of offspring per female is k , half of which are females and the other half males (we shall use k from 1 to 50). Parameter h takes into account the mating system. For $h=1$ we have monogamy and for $h>1$ we have polygyny. The value of parameter h indicates the number of fertile

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Figure 1. The number of offspring per female after the harmonic birth function plotted against the sex ratio in a population of 20 individuals for monogamous (filled symbols) and polygynous (open symbols) breeding strategies (h is the number of fertile females a male can monopolize and $k=5$).

females a single male is capable of monopolizing. The harmonic birth function assumes that every female mates only once per breeding season, which is not a rare event in the animal kingdom (e.g. Clutton-Brock 1989; Höglund & Alatalo 1995). The number 2 in the numerator is simply due to the harmonic mean (Sokal & Rohlf 1981).

We shall first have a brief look at the behaviour of the birth function. For the numerical exercise we selected 20 as the population size, $k=5$ and varied h from monogamy ($h=1$) to modest polygyny ($h=2$) and to a relatively high harem size ($h=10$). We explored equation (1) through a full range of female numbers (figure 1). It is apparent that over a wide range of sex ratios the polygynous mating strategy is better off than monogamy. Against this information, a natural question arises: Why are there monogamous species in nature?

(a) *Non-structured populations*

To address the question above we proceed in step and order. First, the dynamics for a two-sex population will be written as

$$\begin{aligned} X_F^{t+1} &= 0.5 \times B(X_F, X_M) \exp[-(X_F^t + X_M^t)] \\ X_M^{t+1} &= 0.5 \times B(X_F, X_M) \exp[-(X_F^t + X_M^t)] \end{aligned} \quad (2)$$

where t denotes time ($t=0, 1, 2, \dots$) and the birth function B is given in equation (1). We now turn our question into a research programme and ask whether polygyny—or monogamy for that matter—is an unbeatable breeding strategy, i.e. an ESS (Maynard Smith 1982). For this purpose, we have to modify equation (2) such that the population system renders it correct for an invasibility analysis. In practice, we shall set either monogamy or polygyny as the resident (common) strategy and examine under what conditions the other rare strategy, polygyny or monogamy, can invade the population. Thus, the

Figure 2. The relationship between offspring number for monogamous females (k_m) and polygynous females (k_p) allowing stable coexistence of the two mating strategies in a non-structured population. The slight wobbling and jerkiness in the symbol lines is due to the fact that the offspring were counted in integers (the broken line indicates equal offspring numbers for the two breeding systems).

resident strategy is left to establish itself after equation (2) for 10 000 generations. Then a rare (10^{-8}) mutant of the other strategy attempts to invade the population. The task is to analyse whether the invasion is successful or not. Under these conditions the dynamics of the coupled system become

$$\begin{aligned} X_{\bullet, m}^{t+1} &= 0.5 \times B(X_{m, F}, X_{m, M}) \exp[-\mu_{\bullet, m} (\sum X_{\bullet, m}^t + \sum X_{\bullet, p}^t)] \\ X_{\bullet, p}^{t+1} &= 0.5 \times B(X_{p, F}, X_{p, M}) \exp[-\mu_{\bullet, p} (\sum X_{\bullet, m}^t + \sum X_{\bullet, p}^t)] \end{aligned} \quad (3)$$

Here m refers to monogamy ($h=1$ in equation (1)) and p refers to polygyny ($h>1$). The symbol $\bullet$ refers to either females or males. Thus, in equation (3) we have two equations for females and two for males. The first summation in the parentheses is over monogamous females and males while the second summation is over polygynous females and males, that is individuals of the two strategies are matched in terms of competition. The success of an invasion is checked after 10 000 time-steps of the joint dynamics have passed. A sample of the next 100 steps is taken for this analysis.

The term μ in equation (3) gives the sex-specific sensitivity to density dependency. Data exist to indicate that females and males may differ in their demography. In particular, in polygyny sexually sized dimorphic species males often suffer from a higher mortality risk than females (Clinton & LeBoeuf 1993; Anholt 1997; Jorgenson *et al.* 1997), while in monogyny the sex differences are often less severe and more variable (Berger & Cunningham 1995; Cooch *et al.* 1996; Gaillard *et al.* 1997). Thus, we have a natural choice of parameter values: $\mu_{F, m} = \mu_{M, m} = 1$, $\mu_{F, p} \geq 1$ and $\mu_{M, p} > 1$; it is also possible that $\mu_{F, p} = \mu_{M, p}$.

Figure 3. Bifurcation graphs of resident (*a–c*) (i) and invader (*a–c*) (ii) reproductive strategies in a non-structured population. The data are taken after 10 000 generations have elapsed since the introduction of the invading strategy. The relevant parameters are (*a*) (i) monogamy and (ii) polygyny, $h=2$ and $\mu_{M,p}=1.2$; (*b*) (i) polygyny, $h=2$ and $\mu_{M,p}=1.25$ and (ii) monogamy; (*c*) (i) monogamy and (ii) polygyny, $h=5$ and $\mu_{M,p}=1.4$. The panels are paired so that (*a*) (i) and (ii), (*b*) (i) and (ii) and (*c*) (i) and (ii) are of the same simulations. The dots in the panels indicate the population size for each k given. For example, in (*a*) (ii) the dynamics are stable up to $k=12$ and two-point periodic from then on up to $k=20$; from this onwards the period number increases until complex or chaotic dynamics are achieved from $k>25$. In the region of k where the population sizes are plotted for one strategy only, this strategy is the ESS (e.g. in panel pairs (*a*) (i) and (ii) polygyny is an ESS with $k<35$). When population sizes are indicated for both reproductive strategies long-term coexistence is possible (e.g. in panel pairs (*a*) (i) and (ii) the range of coexistence is $35\leq k\leq 43$).

(b) Spatially structured populations

We shall next extend our invasibility analysis into a spatially structured system, i.e. we will have a number of populations ($n=100$) obeying Ricker dynamics under the current domain of the harmonic birth function. The subpopulations will be coupled by dispersing individuals. For simplicity, we shall restrict our analysis to implicit space (e.g. Allen *et al.* 1993; Heino *et al.* 1997; Ranta *et al.* 1999) where the distances between subpopulations do not matter. Thus, with monogamy and polygyny as breeding strategies we will have four new parameters setting the dispersal rate (d =the proportion of individuals leaving the focal subpopulation) of females and males: $d_{F,m}$, $d_{M,m}$, $d_{F,p}$ and $d_{M,p}$. In order to limit the number of parameter combinations to the minimum we shall take $d_{F,m}=d_{M,m}$ and $d_{F,p}=d_{M,p}$.

The invasibility analysis was performed with equations (2) and (3) iterated for the resident breeding strategy for 10 000 generations and then we introduced a rare mutant (10^{-8}) of the opposite strategy in one randomly chosen population. Using the dispersal-linked version of equation (3) we allowed another 10 000 generations to elapse and then the next 100 were used to check the success of the invasion.

3. RESULTS

The invasion analysis revealed the following fact. All other things being equal, polygyny is a superior breeding strategy. It is an ESS and can always invade a monogamous resident population and take it over, whereas a monogamous breeding system cannot invade a polygynous population. These conclusions hold for both non-structured and spatially structured populations.

As there are reportedly species using monogamy as a breeding strategy (see Clutton-Brock (1989) and Davies (1991) for reviews) we shall devote our efforts to looking at when monogamy and polygyny are able to coexist as alternative mating systems. In this search we are actually looking for the level of punishment polygyny has to take in order to be able to coexist with monogamy. Under natural conditions the punishment can either be in terms of reduced fecundity ($k_p < k_m$), density dependence ($\mu_{\bullet,p} > \mu_{\bullet,m}$) or the costs of dispersal ($d_{\bullet,p} > d_{\bullet,m}$) (in spatially structured populations only).

We first discuss our findings in the case of non-structured populations. Invasion by polygynous (or monogamous) breeders into a population of monogamous (or polygynous) breeders is successful when k_p is

Figure 4. Bifurcation graphs of (a,b) (i) resident and (a,b) (ii) invader reproductive strategies in a spatially (implicitly) structured population. The data are taken after 10 000 generations have elapsed since the introduction of the invading strategy in one of the 100 subpopulations. The relevant parameters are (a) (i) monogamy, $d_{M,m}=0.3$ and (ii) polygyny, $h=2$, $\mu_{M,p}=1$ and $d_{M,p}=0.05$; (b) (i) polygyny, $h=5$, $\mu_{M,p}=1$ and $d_{M,p}=0.05$ and (ii) monogamy, $d_{M,m}=0.3$. The panels are paired so that (a) (i) and (ii), (b) (i) and (ii) and (c) (i) and (ii) are of the same simulations.

sufficiently smaller than k_m . For a few polygyny levels ($h=2, 5$ and 10) we looked for k_p to make both invasion and coexistence possible for the two strategies. The coexistence of the two breeding systems is achievable by a constant reduction in k_p relative to k_m ; this reduction has to be greater with the number of females a male can monopolize (figure 2).

Successful coexistence of the two breeding systems is also possible when the density-dependent costs of the polygynous system are larger than those in monogamy. Long-term coexistence of the two strategies is possible only in the range of $1.17 < \mu_{M,p} \leq 1.2$ (figure 3a(i)). Outside this range monogamy and polygyny are exclusively ESSs (figure 3b(ii)); the borderline is strict and the demarcation value of k depends on the value of $\mu_{M,p}$ (or of $\mu_{F,p}$ and $\mu_{M,p}$ if they both deviate from 1.0). The strategy-specific bifurcation graphs after the invasion are symmetrical, i.e. the graphs for monogamous and polygynous breeders are matching independent of which strategy was resident and which one was the intruder. The invasion of the intruding strategy is not very sensitive of the polygyny parameter h (figure 3c(iii)); the parameter of relevance is $\mu_{\bullet,p}$. In addition, polygyny (regardless of the value of h) can invade a resident monogamous population, but their stable coexistence is in a very limited range of k in the area of chaotic population dynamics.

In spatially structured populations, invasion of polygyny into a monogamous population is possible. Here, the system is also symmetrical (it is possible for a monogamous breeding system to invade a polygynous system, the strategy-specific bifurcation graphs being similar in both cases independent of who is the invader). Sex-specific differences in the density-dependent parameter are no longer needed in spatially structured populations ($\mu_{\bullet,m} = \mu_{\bullet,p}$) provided the two strategies differ in their dispersal rates ($d_m > d_p$). However, the difference between the strategy-specific dispersal rates should be substantial (figure 4; the difference in the dispersal rates can be reduced if simultaneously $\mu_{\bullet,p} > \mu_{\bullet,m}$ also). Polygyny is the ESS breeding strategy for low values of k , the number of offspring produced. Long-term coexistence of monogamy and polygyny is only possible in the chaotic range of population dynamics.

4. DISCUSSION

We summarize our major findings as follows. First, polygyny is an ESS breeding system. It can overcome monogamy over a wide range of offspring produced per female. That monogamy and polygyny can coexist as pure strategies in a population requires that individuals using polygyny are punished somehow. A straightforward way of producing stable coexistence of monogamy and polygyny in a population is to reduce the offspring number (k_p) that polygynous females can produce. This works over the entire examined range of offspring numbers produced by monogamous and polygynous females. An alternative path to coexistence is to increase the density-dependent parameter of the polygynous breeder so that $\mu_{\bullet,p} > \mu_{\bullet,m}$. However, this yields a very narrow range of $k_{\bullet}$ and $\mu_{\bullet,p}$ where long-term coexistence is possible. Yet another way to introduce stable coexistence between the two breeding strategies is to assume that both monogamous and polygynous breeders live in a spatially structured population system, which is not an unlikely scenario. The dispersal of individuals ties the subunits into a population network. Making the dispersal rate of polygynous breeders substantially lower than that of monogamous breeders enables coexistence. Of course, it is always possible to use all the different combinations ($k_m > k_p$, $\mu_{\bullet,m} < \mu_{\bullet,p}$ and $d_m > d_p$) in concert. Nevertheless, we cannot escape the conclusion that polygyny has to be punished in one way or another to enable monogamy and polygyny to coexist.

Against these findings it is of interest to note that, in a Spanish house sparrow (*Passer domesticus*) population, polygynous males raised 70% of the nestlings raised by monogamous males (Veiga 1990). Matching observations also came from a Swedish tree sparrow (*Passer montanus*) population where monogamous pairs were capable of raising 4.7 fledglings, while the average for polygynous pairs was 1.0 (P. Rintamäki, personal communication). Thus, it appears that in these passerines polygynous males are punished in terms of offspring raised to independence. It remains to be seen whether there is any evidence for the two other means of punishment, i.e. polygynous breeders being more sensitive to density dependence or dispersing less than monogamous breeders.

We have carried out a straightforward and very basic study of the evolution of mating systems, in particular that of polygynous mating behaviour. We have observed that differential density dependence and dispersal between the sexes and mating systems and differential success in reproduction between mating systems may facilitate the evolution of one or the other type of mating system. These are basic factors in describing how well each mating system is doing in terms of evolutionary advantage. However, we are aware that there are other factors related to breeding systems, such as parental care and territoriality (e.g. Clutton-Brock 1989), which may well appear to be important in the evolution of mating systems.

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