Short communication

Effects of Biparental Inbreeding on the Evolution of Gynodioecy: A Model and a Case Study in *Chionographis japonica* var. *kurohimensis*

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To examine the evolution of gynodioecy under biparental inbreeding, we developed a new theoretical model and tested it by estimating parameters incorporated in the model in a gynodioecious population of *Chionographis japonica* var. *kurohimensis*. The model and the results showed biparental inbreeding affects the evolution of gynodioecy, but the effect is very small.

Key words: Biparental inbreeding — Gynodioecy — Inbreeding depression — Selfing

Since Uyenoyama (1986) claimed that biparental inbreeding reduces the meiotic cost of biparental reproduction and introduces the possibility of an optimal selfing rate, increased attentions have been paid to estimate the rate of biparental inbreeding (Waller and Knight 1989; Holtsford and Ellstrand 1990) and evaluate the effect of biparental inbreeding on the mating system evolution in plants (Yahara 1992; Lloyd and Lively MS).

For theoretical aspects, Schemske and Lande (1987) criticized the assumption of constant inbreeding depression in the Uyenoyama model and claimed that mixed mating is not evolutionarily stable if inbreeding depression decreases with mean selfing rate. Using a kin selection formulation, Yahara (1992) showed that mixed mating can be evolutionarily stable under covariation of levels of inbreeding depression and biparental inbreeding with mean selfing rate. Using estimates of genotypic correlations between outcrossing mates obtained by Holtsford and Ellstrand (1990), he showed that genetic cost of outcrossing decreases with mean selfing rate. His formulation is, however, criticized by Lloyd and Lively (MS) who developed a more exact formulation of fitness under biparental inbreeding. Using the new formulation, Lloyd and Lively showed that the decreased cost of meiosis by biparental inbreeding almost cancels with inbreeding depression through biparental inbreeding.

As is shown by Lloyd and Lively, the meiotic cost decreases not due to outcrossing between any relatives, but due to outcrossing between particular relatives which share the mutant allele. In this respect, it is interesting to examine the effect of biparental inbreeding on the evolution of gynodioecy, because male sterile mutants never cross with each other.

For gynodioecious species of Hawaiian *Bidens*, Sun and Ganders (1988) found that the estimates of outcrossing rates of female plants are often significantly lower than unity, suggesting the occurrence of biparental inbreeding. Citing Uyenoyama's theory, they suggested that the gynodioecy in Hawaiian *Bidens* could be evolutionarily stable under biparental inbreeding. Maki (1993) also estimated outcrossing rates of female plants in gynodioecious populations of *Chionographis japonica* var. *kurohimensis* and found the occurrence of biparental inbreeding as in Hawaiian *Bidens*. Because hermaphrodites in gynodioecious populations are usually highly selfing (Sun and Ganders 1988, Maki 1991), and selfing enhances biparental inbreeding (Uyenoyama 1986), biparental inbreeding is supposed to be common in gynodioecious populations. It is, however, uncertain whether biparental inbreeding promotes the evolution of female or not. The purpose of this note is to fill this deficiency. Firstly, we develop a simple model and examine the effect of biparental inbreeding on the evolution of gynodioecy. Secondly, we estimate level of biparental inbreeding in a gynodioecious population of *Chionographis japonica* var. *kurohimensis*. Based on the model and the fact, we argue that biparental inbreeding has negative effect on the evolution of gynodioecy.

We assume that male sterility is determined by a dominant allele of nuclear genome. In the population, seed production of hermaphrodites is standadized as 1 and females produce 1 + k seeds. k expresses a reproductive advantage of females. Hermaphrodites self- and cross-fertilize at frequencies s and 1 - s. The average fitness of progeny from cross-fertilization between non-relatives is standadized as 1. The progeny from biparental inbreeding has decreased fitness 1 - d_s and that from selfing has fitness 1 - d_s. d_s is smaller than d_s. Outcrossing gametes are identical by descent at a probability of m. The progeny from outcrossing of females and hermaphrodites has mean fitness m(1 - d_s) + (1 - m) = 1 - md_s. Then, hermaphrodits and females which occur at frequencies
1 − x and x have fitness $W_n$ and $W_i$ as follows.

$$W_n = s(t - d_s) + \frac{1}{2} \left( 1 - s \right)(1 - md_b) + \frac{1}{2} \left( 1 - s \right)(1 - md_b)(1 - x) + \frac{1}{2} \left( 1 + k \right)(1 - md_b)x$$

$$= s(1 - d_s) + (1 - s)(1 - md_b) + \frac{1}{2} \left( 1 + k \right)(1 - md_b) \cdot \frac{x}{1 - x}.$$  \hspace{1cm} (ta)

$$W_i = \frac{1}{2} \left( 1 + k \right)(1 - md_b).$$  \hspace{1cm} (tb)

Let $s (1 - d_s) = W_s$ and $(1 - s)(1 - md_b) = W_o$. $W_s$ is a fitness component of the hermaphrodite through selfing and $W_o$ is a fitness component of the hermaphrodite through outcrossing with the other hermaphrodites. Let equilibrium frequency of females is $x^*$. Biparental inbreeding changes $x^*$ by decreasing both $W_o$ and $W_i$. By substituting $x$ by $x^*$ in the equation $W_n = W_i$,

$$W_s + W_o + W_i + \frac{x^*}{1 - x^*} = W_i,$$  \hspace{1cm} (2)

$$\frac{x^*}{1 - x^*} = 1 - \frac{W_s + W_o}{W_i},$$

$$= 2 \left[ 1 - s d_s - (1 - s) md_b \right],$$  \hspace{1cm} (3)

$$\frac{W_i}{W_s} = \frac{W_i(1 - d_s)}{W_s + W_o},$$

$$= \frac{(1 + k)(1 - md_b) - 2(1 - s d_s) + 2md_b(1 - s)}{2k(t - md_b) + s(d_s - md_b)}.$$  \hspace{1cm} (4)

The numerator of rhs is always positive because $md_s < 1$ and $md_b < d_s < d_b$. Thus, if the numerator is positive, female can co-occur with hermaphrodites. If there is no biparental inbreeding $(m = 0)$, the numerator is $2sd_b + k - 1$, and $sd_b > (1 - k)/2$ is the condition required for female to persist in the population (Charlesworth and Charlesworth 1978).

Biparental inbreeding has positive or negative effect on the numerator depends on whether $(1 - k)/2$ is larger than $s$ or not. In addition, biparental inbreeding increases $x^*$ by decreasing the denominator. This effect results from a decrease of male fitness of hermaphrodites by crossing with females. To examine a net effect of biparental inbreeding on $x^*$, we consider some particular cases below.

For females to co-occur stably with hermaphrodites, both $s$ and $d_s$ are required to be very large when $k$ is small, and $k$ is required to be close to 1 when $sd_k$ is small. Let consider the following three cases with two extremes: (1) $s = 1, d_s = 0.5, k = 0.2$, (2) $s = 0.6, d_s = 0.7, k = 0.5$, and (3) $s = 0.2, d_s = 0.9, k = 0.8$. We assume $md_s = 0.1$. Then, $x^*$ increases from 0.286 to 0.293 in case 1, from 0.370 to 0.398 in case 2, and from 0.163 to 0.176 in case 3 in comparison with the expectations under no biparental inbreeding. Thus, biparental inbreeding increases the equilibrium frequency of females when the condition for females to be maintained is satisfied. However, the effect is small in all three cases examined.

As a case study, we estimated $m$ in a population (HAM) of Chionographis japonica var. kurohimensis for which Maki (1993) estimated $s = 0.95, d_s = 0.34,$ and $k = 0.17$. To estimate $m$, we estimated fixation index of parent population, $f_p$, and that of progeny population from female, $f_i$. In equilibrium,

$$f_i = \frac{m(1 + f_p)}{2},$$

$$m = \frac{2f_i}{1 + f_p}.$$  \hspace{1cm} (5)

Using these formula, $f_p, f_i,$ and $m$ are estimated to be 0.50, 0.25 and 0.34. Thus, there is recognizable biparental inbreeding in the population examined. Using the estimates, $s = 0.95, d_s = 0.34, k = 0.17,$ and $m = 0.34$,

$$x^* = \frac{-0.18 - 0.09 d_s}{2(0.49 - 0.38 d_s)}.$$  \hspace{1cm} (6)

The numerator is negative and biparental inbreeding decreases the numerator, although only slightly. For the population examined, the effect of biparental inbreeding does not contribute to enhance the evolution of gynodioecy. Because the numerator is negative but females do exist in the population, some additional factors enhancing the evolution of gynodioecy should work in the population. Maki (1993) suggests that $d_s$ and $k$ could be underestimated.

As a conclusion, biparental inbreeding does affect the evolution of gynodioecy, but the effect is generally very small. The other factors seem to be more important to maintain females with hermaphrodites in gynodioecious populations.

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References


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