

# Stochastic Effects in LMC Models

Josiane Courteau and Sabin Lessard

Département de mathématiques et de statistique, Université de Montréal, C.P. 6128, Succursale Centre-ville, Montréal, Canada, H3C 3J7

Received September 2, 1997

**LMC (local mate competition) was first introduced by W. D. Hamilton to explain extraordinary female-biased sex ratios observed in a variety of insects and mites. In the original model, the population is subdivided into an infinite number of colonies founded by a fixed number of inseminated females producing the same very large number of offspring. The male offspring compete within the colonies to inseminate the female offspring and then these disperse at random to found new colonies. An unbeatable sex ratio strategy is found to be female-biased. In this paper, the effects of having colonies of random size and foundresses producing a random finite number of offspring are considered. The exact evolutionarily stable strategy (ESS) sex ratio is deduced and comparisons with previous approximate or numerical results are made. As the mean or the variance of brood size increases, the ESS sex ratio becomes more female-biased. An increase in the variance of colony size increases the ESS proportion of males when the mean brood size and colony size are both small, but decreases this proportion when the mean brood size or the mean colony size is large.** © 1999 Academic Press

## INTRODUCTION: LMC MODEL AND ESS SEX RATIO

Let us consider the following model known as the local mate competition (LMC) model (Hamilton, 1967): a population is subdivided into an infinite number of colonies founded by a certain number of inseminated females chosen at random in the whole population. These foundresses produce male and female offspring in a certain ratio, and then die. The offspring mate at random within their own colony, every female offspring being inseminated once and only once. Then these newly inseminated females randomly disperse to found new colonies.

In such a model, what is the progeny sex ratio (the expected proportion of males in the progeny) that has higher fitness than any other once fixed in the population? This corresponds to an *evolutionarily stable strategy* (ESS) following Maynard Smith and Price (1973). If the number of foundresses is constant from one colony to another, and denoted by  $n$ , and the number of offspring produced is constant from one foundress to another, and

virtually infinite, then the ESS sex ratio is female-biased and explicitly given by  $(n-1)/2n$  (Hamilton, 1967; Taylor and Bulmer, 1980; Colwell, 1981). When the number of foundresses is a random variable, the ESS sex ratio becomes  $(v-1)/2v$ , where  $v$  represents the average number of foundresses in non-void colonies (Karlin and Lessard, 1986; Nunney and Luck, 1988). When the number of foundresses and the number of offspring produced by a foundress are both random variables, the ESS sex ratio can be approximated by

$$\frac{\mu_K}{2(1+\mu_K)} + \frac{\mu_K}{2\mu_T(1+\mu_K)^2} \left(1 - \frac{\sigma_T^2}{\mu_T}\right) - \frac{\sigma_K^2}{2(1+\mu_K)^3},$$

where  $\mu_K$  and  $\sigma_K^2$  represent the mean and variance for the number of co-foundresses,  $K$ , of a foundress chosen at random, while  $\mu_T$  and  $\sigma_T^2$  represent the mean and variance for the number of offspring,  $T$ , produced by a foundress (Nishimura, 1993). This should be a good approximation if the number of foundresses in each colony or the number of offspring produced by each foundress are large enough, and if variability is small

enough ( $\sigma_K^2$  and  $\sigma_T^2$  small enough). These conditions make it reasonable to ignore the possibility of extinction of a colony due to the absence of offspring of one sex in the colony and to neglect all centered moments of order higher than 2 for the number of foundresses and the number of offspring for each in a Taylor expansion for fitness.

In the case of a fixed number of foundresses and a fixed number of offspring for each, the number of male offspring being fixed (for a "precise" foundress) or following a binomial distribution (for a "binomial" foundress), numerical studies indicate a less female-biased ESS sex ratio as the number of offspring per foundress becomes smaller (Nagelkerke, 1994). This change in the ESS sex ratio in favor of more males is to compensate for the extinction of colonies containing no male, whose probability increases as the number of offspring per foundress decreases.

In this paper, we study the exact ESS sex ratio in the case where the number of foundresses in each colony is a random variable having any distribution and the number of offspring for each foundress is a random variable having a Poisson distribution. Moreover, given the number of offspring, the number of male offspring is assumed to follow a binomial distribution.

Our study shows how the standard results on the ESS sex ratio in LMC models are affected in the face of stochasticity, of both foundress and offspring numbers. Although our approach and mathematical methods could be applied to a wide variety of LMC models, we concentrate on the case of diploid populations with no dispersal of males before mating and complete dispersal of females after mating. We refer the reader interested in the effect of haplodiploidy to Hamilton (1979), Taylor and Bulmer (1980), Wilson and Colwell (1981), and Herre (1985), who dealt with the case in which the number of foundresses can be assessed by each one. This assumption is not made in this paper. For dispersal models, see, e.g., Bulmer (1986), Karlin and Lessard (1986), and Taylor (1994).

## EXACT ESS SEX RATIO WITH A POISSON BROOD SIZE

In the LMC model, let the number of offspring produced by a foundress be represented by a random variable  $T$ . Suppose that the variable  $T$  has a Poisson distribution with mean  $\lambda$  and that all such variables are independent. Moreover let every foundress in the population be such that each offspring in the progeny is male

with probability  $r$  independently of all other offspring. Then  $r$  is the expected proportion of males in the progeny, called the *progeny sex ratio*, and is fixed in the population.

Now assume that a foundress chosen at random in the population mutates such that each offspring in her progeny is male with probability  $\hat{r}$ , instead of  $r$  for a non-mutant foundress, independently of all other offspring. We want to compare the fitness of such a mutant foundress to the fitness of a non-mutant foundress.

Let us define the fitness of a foundress as her expected contribution to the next generation through her sons and daughters, this expected contribution being the expected number of her inseminated daughters plus the expected number of female offspring inseminated by her sons. This definition of fitness should be appropriate at least for diploid populations. If  $\hat{m}$  and  $\hat{f}$  represent the numbers of sons and daughters, respectively, produced by a mutant foundress, and  $M$  and  $F$  the total numbers of sons and daughters, respectively, produced by all the other (non-mutant) foundresses of the same colony, then the fitness of the mutant foundress is the expected value of the variable

$$W = \begin{cases} \hat{f} + \hat{X} & \text{if } \hat{m} + M \geq 1 \\ 0 & \text{if } \hat{m} + M = 0 \end{cases} \quad (1)$$

where  $\hat{X}$ , which denotes the number of female offspring inseminated by the sons of the mutant foundress, follows a binomial distribution with parameters  $\hat{f} + F$  and  $\hat{m}/(\hat{m} + M)$  in the case  $\hat{m} + M \geq 1$ , that is, in the case where there is at least one male offspring in the colony. In the case  $\hat{m} + M = 0$ , none of the female offspring is inseminated.

We are interested in finding a progeny sex ratio  $r^*$  such that, if every non-mutant foundress produces a progeny sex ratio  $r = r^*$ , then any mutant foundress producing a progeny sex ratio  $\hat{r} \neq r^*$  will have a lesser fitness than a non-mutant foundress. Therefore we look for a progeny sex ratio  $r^*$  such that the expected value of  $W$ ,  $E[W]$ , satisfies the conditions

$$\left. \frac{\partial}{\partial \hat{r}} E[W] \right|_{\hat{r}=r^*} = 0 \quad (2)$$

and

$$\left. \frac{\partial^2}{\partial \hat{r}^2} E[W] \right|_{\hat{r}=r^*} < 0. \quad (3)$$

If the solution to conditions (2) and (3) is unique, then the corresponding progeny sex ratio  $r^*$  is better than any

other once fixed in the population. This corresponds to an ESS *sex ratio* (Maynard Smith and Price, 1973). A sex ratio that satisfies condition (2) is said to be a *critical sex ratio*.

In order to calculate the expectation of  $W$  for a mutant foundress,  $E[W]$ , it will be convenient first to calculate the conditional expectation of  $W$  given the number  $K$  of co-foundresses of the mutant foundress,  $E[W|K]$ , and then to take the expectation of this variable.

First of all, note that, given  $\hat{m}, \hat{f}, M, F$  and the formula for the expected value of a binomial distribution, the expected value of  $W$  is

$$E[W|\hat{m}, \hat{f}, M, F] = \begin{cases} \hat{f} + \frac{\hat{m}}{\hat{m} + M} (\hat{f} + F) & \text{if } \hat{m} + M \geq 1 \\ 0 & \text{if } \hat{m} + M = 0. \end{cases} \quad (4)$$

But, given that the mutant foundress produces  $T$  offspring, the random variables  $\hat{m}$  and  $\hat{f}$  have a binomial distribution with parameters  $T, \hat{f}$  and  $T, 1 - \hat{f}$ , respectively, since the  $T$  offspring of the mutant foundress are male with probability  $\hat{f}$  and female with probability  $1 - \hat{f}$ , independently of one another. Similarly, given  $K$  non-mutant co-foundresses producing  $T_1, \dots, T_K$  offspring, the random variables  $M$  and  $F$  have a binomial distribution with parameters  $S_K, r$  and  $S_K, 1 - r$ , respectively, where

$$S_K = T_1 + \dots + T_K.$$

Under the assumption that the numbers of offspring produced by the foundresses are independent Poisson random variables with mean  $\lambda$ , the variables  $\hat{m}, \hat{f}, M$ , and  $F$ , conditionally on  $K$ , are independent random variables having a Poisson distribution with means  $\lambda\hat{f}$ ,  $\lambda(1 - \hat{f})$ ,  $K\lambda r$ , and  $K\lambda(1 - r)$ , respectively (see Appendix 1). Therefore, we have

$$\begin{aligned} E[W|K] &= E[W|\hat{m} + M \geq 1, K] P(\hat{m} + M \geq 1 | K) \\ &\quad + E[W|\hat{m} + M = 0, K] P(\hat{m} + M = 0 | K) \\ &= E\left[\hat{f} + \frac{\hat{m}}{\hat{m} + M} (\hat{f} + F) \mid \hat{m} + M \geq 1, K\right] \\ &\quad \times P(\hat{m} + M \geq 1 | K). \end{aligned}$$

But since  $\hat{m}, \hat{f}, M$ , and  $F$  are conditionally independent random variables, it follows that  $\hat{m}/(\hat{m} + M)$  and  $\hat{f} + F$  are

also conditionally independent random variables, so that

$$\begin{aligned} &E\left[\frac{\hat{m}}{\hat{m} + M} (\hat{f} + F) \mid \hat{m} + M \geq 1, K\right] \\ &= E\left[\frac{\hat{m}}{\hat{m} + M} \mid \hat{m} + M \geq 1, K\right] E[\hat{f} + F | K]. \end{aligned}$$

Moreover, since  $\hat{m}$  and  $M$  conditionally on  $K$  are not only independent but have also a Poisson distribution, we have

$$P(\hat{m} + M = 0 | K) = P(\hat{m} = 0) P(M = 0 | K) = e^{-\lambda(\hat{f} + Kr)}$$

and (see, e.g., Lemire and Lessard, 1997)

$$E\left[\frac{\hat{m}}{\hat{m} + M} \mid \hat{m} + M \geq 1, K\right] = \frac{E[\hat{m}]}{E[\hat{m}] + E[M | K]}.$$

We conclude that

$$\begin{aligned} E[W|K] &= \left[ E[\hat{f}] + \left( E\left[\frac{\hat{m}}{\hat{m} + M} \mid \hat{m} + M \geq 1, K\right] \right. \right. \\ &\quad \left. \left. \times E[\hat{f} + F | K] \right) \right] (1 - P(\hat{m} + M = 0 | K)) \\ &= \left[ \lambda(1 - \hat{f}) + \left( \frac{\hat{f}}{\hat{f} + Kr} \right) (\lambda(1 - \hat{f}) + \lambda K(1 - r)) \right] \\ &\quad \times (1 - e^{-\lambda(\hat{f} + Kr)}) \\ &= \lambda \left[ (1 - \hat{f}) + \frac{\hat{f}((1 - \hat{f}) + K(1 - r))}{\hat{f} + Kr} \right] (1 - e^{-\lambda(\hat{f} + Kr)}). \end{aligned}$$

Finally, we get

$$\begin{aligned} E[W] &= E[E[W|K]] \\ &= E\left[\lambda \left[ (1 - \hat{f}) + \frac{\hat{f}((1 - \hat{f}) + K(1 - r))}{\hat{f} + Kr} \right] \right. \\ &\quad \left. \times (1 - e^{-\lambda(\hat{f} + Kr)}) \right]. \end{aligned}$$

The partial derivative of  $E[W]$  with respect to  $\hat{f}$  evaluated at  $\hat{f} = r$  is given by

$$\begin{aligned}
& \left. \frac{\partial}{\partial \hat{r}} E[W] \right|_{\hat{r}=r} \\
&= E \left[ \frac{\partial}{\partial \hat{r}} \left( \lambda \left[ (1-\hat{r}) + \frac{\hat{r}((1-\hat{r}) + K(1-r))}{\hat{r} + Kr} \right] \right. \right. \\
&\quad \left. \left. \times (1 - e^{-\lambda(\hat{r} + Kr)}) \right) \right] \Big|_{\hat{r}=r} \\
&= \lambda E \left[ \left( -1 + \frac{(K+1)(1-r)}{(K+1)r} \right. \right. \\
&\quad \left. \left. + r \left( \frac{-(K+1)r - (K+1)(1-r)}{(K+1)^2 r^2} \right) \right) \right. \\
&\quad \left. \times (1 - e^{-\lambda(K+1)r}) + 2(1-r) \lambda e^{-\lambda(K+1)r} \right] \\
&= \lambda E \left[ \left( -1 + \frac{1-r}{r} - \frac{1}{(K+1)r} \right) (1 - e^{-\lambda(K+1)r}) \right. \\
&\quad \left. + 2(1-r) \lambda e^{-\lambda(K+1)r} \right] \\
&= \lambda E \left[ \left( -2 + \frac{K}{(K+1)r} \right) (1 - e^{-\lambda(K+1)r}) \right. \\
&\quad \left. + 2(1-r) \lambda e^{-\lambda(K+1)r} \right] \\
&= -2\lambda(1 - e^{-\lambda r} E[e^{-\lambda Kr}]) + 2\lambda^2(1-r) e^{-\lambda r} E[e^{-\lambda Kr}].
\end{aligned}$$

Thus, we have

$$\begin{aligned}
& \left. \frac{\partial}{\partial \hat{r}} E[W] \right|_{\hat{r}=r} \\
&= -2\lambda(1 - e^{-\lambda r} E[e^{-\lambda Kr}]) + 2\lambda^2(1-r) e^{-\lambda r} E[e^{-\lambda Kr}] \\
&\quad + \frac{\lambda}{r} \left( E \left[ \frac{K}{1+K} \right] - e^{-\lambda r} E \left[ \frac{K}{1+K} e^{-\lambda Kr} \right] \right). \quad (5)
\end{aligned}$$

We can formulate the last equation in terms of the moment-generating function. More precisely, if we let

$$\varphi(t) = E[e^{tK}] \quad \text{and} \quad I(x) = \int_{-\infty}^x e^t \varphi(t) dt, \quad (6)$$

then we have

$$\begin{aligned}
E \left[ \frac{e^{x(K+1)}}{1+K} \right] &= E \left[ \int_{-\infty}^x e^{t(K+1)} dt \right] \\
&= \int_{-\infty}^x E[e^{t(K+1)}] dt = I(x),
\end{aligned}$$

and it is easy to see that

$$E[e^{-\lambda Kr}] = \varphi(-\lambda r), \quad E \left[ \frac{K}{1+K} \right] = 1 - I(0) \quad (7)$$

and

$$E \left[ \frac{K}{1+K} e^{-\lambda Kr} \right] = \varphi(-\lambda r) - e^{\lambda r} I(-\lambda r).$$

Then Eq. (2) is satisfied if and only if  $r^*$  is a solution of the equation

$$\begin{aligned}
& -2r^* + e^{-\lambda r^*} \varphi(-\lambda r^*) (2r^* + 2\lambda r^* (1-r^*) - 1) \\
& \quad + 1 - I(0) + I(-\lambda r^*) = 0, \quad (8)
\end{aligned}$$

where the functions  $\varphi$  and  $I$  are given by (6).

Moreover,  $r^*$  is an ESS sex ratio if it is the unique solution to (8) and if

$$\begin{aligned}
& \left. \frac{\partial^2}{\partial \hat{r}^2} E[W] \right|_{\hat{r}=r=r^*} \\
&= \frac{2\lambda}{r^{*2}} \left[ -E \left[ \frac{K}{(K+1)^2} (1 - e^{-\lambda r^*(K+1)}) \right] \right. \\
&\quad \left. - \lambda r^* E \left[ \frac{e^{-\lambda r^*(K+1)}}{K+1} \right] \right. \\
&\quad \left. + \lambda r^* (1 - 2r^* - \lambda r^* + \lambda r^{*2}) E[e^{-\lambda r^*(K+1)}] \right] < 0. \quad (9)
\end{aligned}$$

A sufficient condition for this to occur is

$$1 - 2r^* - \lambda r^* + \lambda r^{*2} \leq 0.$$

But this is true if and only if

$$\frac{(2+\lambda) - \sqrt{4+\lambda^2}}{2\lambda} \leq r^* \leq \frac{(2+\lambda) + \sqrt{4+\lambda^2}}{2\lambda}. \quad (10)$$

Note that the upper bound is always greater or equal to  $1/2$ .

It would also be very interesting to know if the critical sex ratio  $r^*$  is a *continuously stable strategy* (CSS), which means that not only  $r^*$  is an ESS sex ratio, but it also satisfies the following condition: if the population is fixed on any value, sufficiently close to  $r^*$ , then there is selective advantage to those mutations that render the individual's strategy at least slightly closer to it and selective disadvantage to those that render the individual's strategy further apart from it. This condition is also known

as the *convergence-stability* condition (see Christiansen (1991) and Eshel (1996) for details).

A sufficient condition for an ESS sex ratio to be a CSS sex ratio is given by (Eshel, 1996)

$$\frac{\partial^2 V}{\partial r \partial \hat{r}} + \frac{\partial^2 V}{\partial \hat{r}^2} \Big|_{r=\hat{r}=r^*} < 0,$$

where  $V$  is a payoff function. Using  $E[W]$  as our payoff function, the CSS condition becomes

$$\begin{aligned} & \frac{\partial^2}{\partial r \partial \hat{r}} E[W] + \frac{\partial^2}{\partial \hat{r}^2} E[W] \Big|_{r=\hat{r}=r^*} \\ &= -\frac{\lambda}{r^{*2}} E \left[ \frac{e^{-\lambda r^{*(K+1)}}}{K+1} (2\lambda r^{*2}(2+\lambda-\lambda r^*) \right. \\ & \quad + \lambda r^* K^2(-1+2r^*(1+\lambda)-2\lambda r^{*2}) \\ & \quad + K(-1+e^{\lambda r^{*(K+1)}}+4\lambda^2 r^{*2}(1-r^*) \\ & \quad \left. + \lambda r^*(-1+6r^*)) \right] < 0. \end{aligned}$$

TABLE 1

ESS Sex Ratio Obtained by Solving Eq. (8)

Mean and variance of $K$	Distribution of $K$	$\lambda = 1$	$\lambda = 2$	$\lambda = 3$	$\lambda = 4$	$\lambda = 5$	$\lambda = 10$	$\lambda = \infty$	Nishimura
$\mu_K = 0, \sigma_K^2 = 0$	Fixed	0.443	0.396	0.358	0.327	0.301	0.218	0.000	0.000
$\mu_K = 1, \sigma_K^2 = 0$	Fixed	0.430	0.381	0.347	0.322	0.303	0.261	0.250	0.250
$\mu_K = 1, \sigma_K^2 = 0.9$	$B(10, 1/10)$	0.433	0.388	0.356	0.331	0.311	0.253	0.188	0.194
$\mu_K = 1, \sigma_K^2 = 1$	$P(1)$	0.433	0.389	0.356	0.331	0.312	0.251	0.184	0.188
$\mu_K = 1, \sigma_K^2 = 1.5$	$BN_m(2, 2/3)$	0.435	0.391	0.358	0.333	0.312	0.249	0.167	0.156
$\mu_K = 1, \sigma_K^2 = 2$	$G_m(1/2)$	0.436	0.392	0.359	0.334	0.313	0.246	0.153	0.125
$\mu_K = 2, \sigma_K^2 = 0$	Fixed	0.427	0.385	0.361	0.348	0.340	0.333	0.333	0.333
$\mu_K = 2, \sigma_K^2 = 1.8$	$B(20, 1/10)$	0.431	0.391	0.365	0.348	0.335	0.304	0.288	0.300
$\mu_K = 2, \sigma_K^2 = 2$	$P(2)$	0.431	0.391	0.365	0.348	0.334	0.301	0.284	0.296
$\mu_K = 2, \sigma_K^2 = 4$	$BN_m(2, 1/2)$	0.433	0.394	0.367	0.347	0.331	0.285	0.250	0.259
$\mu_K = 2, \sigma_K^2 = 6$	$G_m(1/3)$	0.435	0.396	0.368	0.346	0.329	0.275	0.225	0.222
$\mu_K = 3, \sigma_K^2 = 0$	Fixed	0.429	0.396	0.382	0.377	0.376	0.375	0.375	0.375
$\mu_K = 3, \sigma_K^2 = 2.7$	$B(30, 1/10)$	0.431	0.398	0.380	0.369	0.362	0.349	0.345	0.354
$\mu_K = 3, \sigma_K^2 = 3$	$P(3)$	0.432	0.398	0.379	0.368	0.361	0.346	0.342	0.351
$\mu_K = 3, \sigma_K^2 = 7.5$	$BN_m(2, 2/5)$	0.435	0.400	0.378	0.362	0.350	0.317	0.300	0.316
$\mu_K = 3, \sigma_K^2 = 12$	$G_m(1/4)$	0.437	0.402	0.377	0.358	0.343	0.300	0.269	0.281
$\mu_K = 4, \sigma_K^2 = 0$	Fixed	0.432	0.408	0.402	0.400	0.400	0.400	0.400	0.400
$\mu_K = 4, \sigma_K^2 = 3.6$	$B(40, 1/10)$	0.434	0.407	0.395	0.389	0.386	0.381	0.380	0.386
$\mu_K = 4, \sigma_K^2 = 4$	$P(4)$	0.434	0.407	0.394	0.388	0.384	0.379	0.377	0.384
$\mu_K = 4, \sigma_K^2 = 12$	$BN_m(2, 1/3)$	0.437	0.407	0.388	0.376	0.366	0.343	0.333	0.352
$\mu_K = 4, \sigma_K^2 = 20$	$G_m(1/5)$	0.439	0.407	0.385	0.369	0.356	0.320	0.300	0.320
$\mu_K = 5, \sigma_K^2 = 0$	Fixed	0.436	0.420	0.417	0.417	0.417	0.417	0.417	0.417
$\mu_K = 5, \sigma_K^2 = 4.5$	$B(50, 1/10)$	0.437	0.417	0.409	0.406	0.404	0.403	0.402	0.407
$\mu_K = 5, \sigma_K^2 = 5$	$P(5)$	0.437	0.416	0.408	0.405	0.403	0.401	0.401	0.405
$\mu_K = 5, \sigma_K^2 = 17.5$	$BN_m(2, 2/7)$	0.439	0.413	0.398	0.387	0.380	0.363	0.357	0.376
$\mu_K = 5, \sigma_K^2 = 30$	$G_m(1/6)$	0.441	0.412	0.392	0.378	0.367	0.336	0.321	0.348
$\mu_K = 10, \sigma_K^2 = 0$	Fixed	0.456	0.455	0.455	0.455	0.455	0.455	0.455	0.455
$\mu_K = 10, \sigma_K^2 = 9$	$B(100, 1/10)$	0.455	0.451	0.451	0.451	0.451	0.450	0.450	0.452
$\mu_K = 10, \sigma_K^2 = 10$	$P(10)$	0.455	0.451	0.450	0.450	0.450	0.450	0.450	0.451
$\mu_K = 10, \sigma_K^2 = 60$	$BN_m(2, 1/6)$	0.451	0.437	0.430	0.426	0.423	0.418	0.417	0.432
$\mu_K = 10, \sigma_K^2 = 110$	$G_m(1/11)$	0.451	0.431	0.418	0.409	0.402	0.386	0.380	0.414

Note. The number of offspring per foundress,  $T$ , is supposed to be a Poisson variable with mean  $\lambda$ . ( $B$  for binomial,  $P$  for Poisson,  $BN_m$  for modified binomial negative, and  $G_m$  for modified geometric.)

After rearrangement, we get

$$\begin{aligned} & \left. \frac{\partial^2 E[W]}{\partial r \partial \hat{r}} + \frac{\partial^2 E[W]}{\partial \hat{r}^2} \right|_{r=\hat{r}=r^*} \\ &= \frac{-\lambda}{r^{*2}} \left[ E \left[ \frac{K}{K+1} (1 - e^{-\lambda r^*(K+1)}) \right] \right. \\ & \quad + 2\lambda r^{*2} (2 + \lambda(1 - r^*)) E[e^{-\lambda r^*(K+1)}] \\ & \quad \left. + \lambda r^* (2r^*(1 + \lambda - \lambda r^*) - 1) E[Ke^{-\lambda r^*(K+1)}] \right] < 0. \end{aligned}$$

A sufficient condition for this to occur is

$$2r^*(1 + \lambda - \lambda r^*) - 1 \geq 0,$$

which is true if and only if

$$\frac{(1 + \lambda) - \sqrt{1 + \lambda^2}}{2\lambda} \leq r^* \leq \frac{(1 + \lambda) + \sqrt{1 + \lambda^2}}{2\lambda}. \quad (11)$$

## NUMERICAL RESULTS WITH SOME PARTICULAR DISTRIBUTIONS FOR COLONY SIZE

Equation (8) can be solved numerically, with a software as Mathematica, for a variety of distributions for the variable  $K$ . We have done this (see Appendix 2) for  $K$  fixed and for the following distributions: Poisson, binomial, modified geometric (that is to say  $K + 1$  is a geometric random variable), modified negative binomial (that is to say  $K + 2$  is a negative binomial random variable). The results are summarized in Table 1. All critical sex ratios are less than  $1/2$ . Then the upper limit of condition (10) is never reached. On the other hand, the lower limit of condition (10) is given by 0.382 for  $\lambda = 1$ , 0.293 for  $\lambda = 2$ , 0.232 for  $\lambda = 3$ , 0.191 for  $\lambda = 4$ , 0.161 for  $\lambda = 5$ , and finally 0.090 for  $\lambda = 10$ . The respective critical sex ratios are always greater than these values and consequently all critical sex ratios in Table 1 are ESS sex ratios. Moreover, condition (11) is always satisfied for these values and therefore all ESS sex ratios in Table 1 are CSS sex ratios.

## CASE OF A LARGE BROOD SIZE

We are interested in the special case where  $T = \infty$ , which corresponds to the case of a very large number of offspring by each foundress, because the ESS sex ratio

has already been found in this case by Karlin and Lessard (1986) and by Nunney and Luck (1988). These authors have obtained as ESS sex ratio

$$r^* = \frac{v-1}{2v},$$

where  $v$  is the mean size of non-void colonies. On the other hand, if we take the limit as  $\lambda$  goes to infinity in Eq. (8), we get

$$r^* = \frac{1 - I(0)}{2} = \frac{1}{2} E \left[ \frac{K}{K+1} \right].$$

These two results do not seem to agree unless  $K$  is fixed. But actually, they agree. To show this, let us recall the definition of the random variable  $K$ :  $K$  is the number of co-foundresses of a foundress chosen at random in the population at large. The relation between the variable  $K$  and the variable  $N$ , representing the colony size, is given by the equation

$$\begin{aligned} P(K = n) &= P(\text{a foundress chosen at random in the} \\ & \quad \text{population comes from a colony of size } n + 1) \\ &= \frac{(n + 1) P(N = n + 1)}{\sum_{k \geq 0} (k + 1) P(N = k + 1)}. \end{aligned} \quad (12)$$

Note that in general,  $N \neq K + 1$ . Therefore, we have

$$\begin{aligned} E \left[ \frac{1}{K+1} \right] &= \frac{\sum_{n \geq 0} P(N = n + 1)}{\sum_{k \geq 0} (k + 1) P(N = k + 1)} \\ &= \frac{P(N \geq 1)}{\sum_{k \geq 0} (k + 1) P(N = k + 1)} \\ &= \frac{1}{\sum_{k \geq 0} (k + 1) P(N = k + 1 | N \geq 1)} \\ &= \frac{1}{E[N | N \geq 1]} \\ &= \frac{1}{v}. \end{aligned}$$

Thus, we get

$$r^* = \frac{1 - E[1/(K+1)]}{2} = \frac{v-1}{2v},$$

and our results coincide with previous results in the special case where the number of offspring per foundress is very large.

## DISCUSSION

Hamilton (1967) assumed a fixed colony size and a fixed very large brood size to show that the unbeatable sex ratio should be female-biased in the LMC model. Nagelkerke (1996) pointed out that a small brood size diminishes the bias in favor of females in the ESS sex ratio. This is presumably to diminish the probability of extinction of colonies due to the absence of male offspring to inseminate the female offspring. These results were obtained assuming a fixed brood size and a fixed colony size. Our results in the case of a fixed number of foundresses producing a random number of offspring that follows a Poisson distribution suggest that randomness of  $T$  reduces the diminution of the bias in favor of females. For a colony size  $N = 1, 2, 3, 4$ , Table 2 shows the ESS sex ratio obtained by solving Eq. (8) with a brood size  $T$  that follows a Poisson distribution with mean  $\lambda = 1, 2, 3, 4, 5, 10, \infty$  and the one obtained by Nagelkerke (1996) with a fixed brood size  $T = 1, 2, 3, 4, 5, 10, \infty$ . The ESS sex ratio is always lower in the former case with a random  $T$  than in the latter case with a fixed  $T$ . Of course, in both cases, as the mean brood size increases to  $\infty$ , the ESS sex ratio approaches Hamilton's (1967) prediction. Note that it actually decreases to that prediction in both cases. This is surprising since the probability of extinction of a colony is larger for a random  $T$  than for a fixed  $T$  due to Jensen's inequality, that is,

$$E[(1-r)^{\sum_{i=1}^N T_i}] \geq (1-r)^{\lambda N}.$$

It seems that the advantageous possibility of producing more female offspring with a random  $T$  outweighs the disadvantageous possibility of producing no male offspring.

TABLE 2

Comparison of Our Results for a Poisson  $T$  of Mean  $\lambda$  with Nagelkerke's (1996) Results for a Corresponding Fixed  $T$

	$\lambda = 1$ ( $T = 1$ )	$\lambda = 2$ ( $T = 2$ )	$\lambda = 3$ ( $T = 3$ )	$\lambda = 4$ ( $T = 4$ )	$\lambda = 5$ ( $T = 5$ )	$\lambda = 10$ ( $T = 10$ )	$\lambda = \infty$ ( $T = \infty$ )
$N = 1$	0.443 —	0.396 (0.50)	0.358 (0.43)	0.327 (0.37)	0.301 (0.34)	0.218 (0.22)	0 (0)
$N = 2$	0.430 (0.50)	0.381 (0.43)	0.347 (0.38)	0.322 (0.35)	0.303 (0.33)	0.261 (0.26)	0.250 (0.250)
$N = 3$	0.427 (0.50)	0.385 (0.44)	0.361 (0.39)	0.348 (0.37)	0.340 (0.36)	0.333 (0.35)	0.333 (0.333)
$N = 4$	0.429 (0.50)	0.396 (0.44)	0.382 (0.42)	0.377 (0.41)	0.376 (0.40)	0.375 (0.40)	0.375 (0.375)

The effect of a random colony size coupled with a random brood size is also interesting. When the mean brood size and the mean of  $K$ , the number of co-foundresses of a foundress chosen at random, are both small, an increase in the variance of  $K$  causes an increase of the ESS sex ratio (see Table 1). The relation is reversed when either the mean brood size or the mean of  $K$  is large.

It is instructive to compare Nishimura's (1993) approximation for the ESS sex ratio with our exact results. Nishimura (1993) has obtained the ESS sex ratio

$$r^* = \frac{\mu_K}{2(1 + \mu_K)} + \frac{\mu_K}{2\mu_T(1 + \mu_K)^2} \left(1 - \frac{\sigma_T^2}{\mu_T}\right) - \frac{\sigma_K^2}{2(1 + \mu_K)^3}, \quad (13)$$

where  $\mu_K, \mu_T, \sigma_K^2$ , and  $\sigma_T^2$  are the means and variances of  $K$  and  $T$ ,  $K$  being the number of co-foundresses of a foundress chosen at random and  $T$  being the progeny size of a foundress. Since  $T$  is supposed to be a Poisson random variable with mean  $\lambda$ , then  $\sigma_T^2 = \mu_T = \lambda$  and the second term in the right side of Eq. (13) disappears. Then, in this special case, Nishimura's approximation becomes

$$r^* = \frac{\mu_K}{2(1 + \mu_K)} - \frac{\sigma_K^2}{2(1 + \mu_K)^3}, \quad (14)$$

which does not depend on the parameter  $\lambda$ . Because Nishimura did not take into account the possibility that a colony producing no male disappears, his approximation cannot be good, underestimating the exact ESS sex ratio, when  $\lambda$  and  $\mu_K$  are both small. For very large values of  $\lambda$ , corresponding to the case  $\lambda = \infty$ , Nishimura's predictions slightly overestimates the exact ESS sex ratio except for small  $\mu_K$  and large  $\sigma_K^2$  as illustrated in Table 1.

## APPENDIX 1

Let us determine the moment-generating function of the random variable  $\hat{m}$ . We have

$$\begin{aligned} E[e^{t\hat{m}}] &= E[e^{t\sum_{i=1}^T X_i}] = E[E[e^{t\sum_{i=1}^T X_i} | T]] \\ &= E[\Pi_{i=1}^T E[e^{tX_i} | T]] = E[(E[e^{tX_i}])^T] \\ &= E[((1 - \hat{r}) + \hat{r}e^t)^T] = \sum_{T=0}^{\infty} ((1 - \hat{r}) + \hat{r}e^t)^T \frac{\lambda^T e^{-\lambda}}{T!} \end{aligned}$$

$$\begin{aligned}
&= e^{-\lambda} \sum_{T=0}^{\infty} \frac{[\lambda((1-\hat{r}) + \hat{r}e^t)]^T}{T!} = e^{-\lambda} e^{\lambda[(1-\hat{r}) + \hat{r}e^t]} \\
&= e^{\lambda\hat{r}(e^t-1)},
\end{aligned}$$

which is the moment-generating function of a Poisson random variable with mean  $\lambda\hat{r}$ . Thus,  $\hat{m}$  is a Poisson random variable with mean  $\lambda\hat{r}$ . The same argument also holds if we substitute  $\hat{m}$  by  $\hat{f}$  and  $\hat{r}$  by  $1-\hat{r}$ . Then,  $\hat{f}$  is a Poisson random variable with mean  $\lambda(1-\hat{r})$ . Moreover, we have

$$\begin{aligned}
P(\hat{m}=k, \hat{f}=n) &= E[P(\hat{m}=k, \hat{f}=n | T)] \\
&= E[P(\hat{m}=k, T-\hat{m}=n | T)] \\
&= \sum_{t=0}^{\infty} P(\hat{m}=k, \hat{m}=T-n | T=t) \frac{\lambda^t e^{-\lambda}}{t!} \\
&= \sum_{t=0}^{\infty} P(\hat{m}=k, t=k+n | T=t) \frac{\lambda^t e^{-\lambda}}{t!} \\
&= P(\hat{m}=k | T=k+n) \frac{\lambda^{k+n} e^{-\lambda}}{(k+n)!} \\
&= \binom{k+n}{k} \hat{r}^k (1-\hat{r})^n \frac{\lambda^{k+n} e^{-\lambda}}{(k+n)!} \\
&= \frac{(\lambda\hat{r})^k e^{-\lambda\hat{r}}}{k!} \times \frac{(\lambda(1-\hat{r}))^n e^{-\lambda(1-\hat{r})}}{n!} \\
&= P(\hat{m}=k) \times P(\hat{f}=n).
\end{aligned}$$

Therefore the random variables  $\hat{m}$  and  $\hat{f}$  are independent.

The variables  $M$  and  $F$  can be written as

$$M = \sum_{i=1}^K m_i \quad \text{and} \quad F = \sum_{i=1}^K f_i = \sum_{i=1}^K (T_i - m_i),$$

where the  $m_1, m_2, \dots$  are independent Poisson random variables with mean  $\lambda r$  and  $f_1, f_2, \dots$  independent Poisson random variables with mean  $\lambda(1-r)$ . Then by the additivity of independent Poisson variables,  $M$  and  $F$  are, given  $K$ , Poisson variables with means  $K\lambda r$  and  $K\lambda(1-r)$ , respectively. Moreover, the preceding proof shows that the variables  $m_i$  and  $f_i$  are independent. Actually  $m_i$  is independent of all  $f_j$ , and  $M$  is independent of  $F$ , conditionally on  $K$ .

## APPENDIX 2

### *K Fixed*

In this case, we can use Eq. (5) directly, giving

$$\begin{aligned}
\frac{\partial}{\partial \hat{r}} E[W] \Big|_{r=\hat{r}=r^*} &= -2\lambda(1-e^{-\lambda r^*(K+1)}) \\
&\quad + 2\lambda^2(1-r^*) e^{-\lambda r^*(K+1)} + \frac{\lambda}{r^*} \\
&\quad \times \left( \frac{K}{K+1} - \frac{K e^{-\lambda r^*(K+1)}}{K+1} \right).
\end{aligned}$$

After a few simplifications, we obtain the following criterion for  $r^*$  to be a critical sex ratio:

$$\begin{aligned}
-2r^* + e^{-\lambda r^*(K+1)} \left( 2r^* + 2\lambda(1-r^*) - \frac{K}{K+1} \right) \\
+ \frac{K}{K+1} = 0.
\end{aligned} \tag{15}$$

### *K Poisson P(a)*

If we assume that  $K$  is a Poisson random variable with mean  $\alpha$ , the moment-generating function of  $K$  is given by

$$\varphi(t) = E[e^{tK}] = e^{\alpha(e^t-1)}.$$

Furthermore, we have

$$\begin{aligned}
I(x) &= \int_{-\infty}^x e^t \varphi(t) dt = \int_{-\infty}^x e^t e^{\alpha(e^t-1)} dt \\
&= \left[ \frac{e^{\alpha(e^t-1)}}{\alpha} \right]_{-\infty}^x = \frac{e^{\alpha(e^x-1)} - e^{-\alpha}}{\alpha},
\end{aligned}$$

so that

$$I(0) = \frac{1-e^{-\alpha}}{\alpha} \quad \text{and} \quad I(-\lambda r) = \frac{e^{\alpha(e^{-\lambda r}-1)} - e^{-\alpha}}{\alpha}.$$

Substituting into Eq. (8), the critical sex ratio  $r^*$  must then be a solution of the equation

$$\begin{aligned}
(2r^* - 1 + 2\lambda r^*(1-r^*)) e^{\alpha(e^{-\lambda r^*}-1)-\lambda r^*} &= 2r^* - 1 \\
+ \frac{(1-e^{\alpha(e^{-\lambda r^*}-1)})}{\alpha}.
\end{aligned} \tag{16}$$



**K Binomial B(n, p)**

If  $K$  is a binomial random variable with parameters  $n$  and  $p$ , then we have

$$\varphi(t) = (q + pe^t)^n$$

and

$$\begin{aligned} I(x) &= \int_{-\infty}^x e^t (q + pe^t)^n dt \\ &= \frac{(q + pe^t)^{n+1}}{p(n+1)} \Big|_{-\infty}^x = \frac{(q + pe^x)^{n+1} - q^{n+1}}{p(n+1)}, \end{aligned}$$

where  $q = 1 - p$ . Equation (8) now becomes

$$\begin{aligned} -2r^* + e^{-\lambda r^*} (q + pe^{-\lambda r^*})^n (2r^* + 2\lambda r^* (1 - r^*) - 1) + 1 \\ - \frac{(1 - (q + pe^{-\lambda r^*})^{n+1})}{p(n+1)} = 0. \end{aligned} \tag{17}$$

**K Modified Geometric G\_m(p)**

If we assume that  $K + 1$  is a geometric random variable with parameter  $p$ , then

$$\varphi(t) = E[e^{t(K+1)-t}] = \frac{p}{1 - qe^t}$$

and

$$\begin{aligned} I(x) &= \int_{-\infty}^x e^t \varphi(t) dt = \int_{-\infty}^x \frac{pe^t}{1 - qe^t} dt = \int_0^{e^x} \frac{p}{1 - qu} du \\ &= -\frac{p}{q} \ln(1 - qe^x), \end{aligned}$$

giving

$$\varphi(-\lambda r^*) = \frac{p}{1 - qe^{-\lambda r^*}}, \quad I(0) = -\frac{p}{q} \ln p$$

and

$$I(-\lambda r^*) = -\frac{p}{q} \ln(1 - qe^{-\lambda r^*}),$$

where  $q = 1 - p$ . Equation (8) becomes

$$\begin{aligned} -2r^* + \frac{pe^{-\lambda r^*}}{1 - qe^{-\lambda r^*}} (2r^* + 2\lambda r^* (1 - r^*) - 1) + 1 \\ + \frac{p}{q} \ln p - \frac{p}{q} \ln(1 - qe^{-\lambda r^*}) = 0. \end{aligned} \tag{18}$$

**K Modified Negative Binomial BN\_m(2, p)**

In this case we assume that  $K + 2$  has a negative binomial distribution with parameters 2 and  $p$ . We thus obtain

$$\varphi(t) = E[e^{t(K+2)-2t}] = \frac{p^2}{(1 - qe^t)^2}$$

and

$$I(x) = \int_0^{e^x} \frac{p^2}{(1 - qu)^2} du = \frac{p^2}{q} \left[ \frac{1}{1 - qu} \right]_0^{e^x} = \frac{p^2 e^x}{1 - qe^x}.$$

Then, we have

$$I(0) = \frac{p^2}{1 - q} = p$$

and

$$I(-\lambda r^*) = \frac{p^2 e^{-\lambda r^*}}{1 - qe^{-\lambda r^*}},$$

where  $q = 1 - p$ . In this particular situation, Eq. (8) becomes

$$\begin{aligned} -2r^* + \frac{p^2 e^{-\lambda r^*}}{(1 - qe^{-\lambda r^*})^2} (2r^* + 2\lambda r^* (1 - r^*) - 1) + 1 - p \\ + \frac{p^2 e^{-\lambda r^*}}{1 - qe^{-\lambda r^*}} = 0. \end{aligned} \tag{19}$$

Equations (15), (16), (17), (18), and (19) were solved numerically (with Mathematica) to obtain the results of Table 1.

**ACKNOWLEDGMENT**

We thank two anonymous referees for very useful comments.

**REFERENCES**

Bulmer, M. G. 1986. Sex ratio theory in geographically structured populations, *Heredity* **56**, 69–73.  
 Christiansen, F. B. 1991. Conditions for evolutionary stability for a continuously varying character, *Am. Nat.* **138**, 37–50.  
 Colwell, R. K. 1981. Group selection is implicated in the evolution of female-biased sex ratios, *Nature* **290**, 401–404.  
 Eshel, I. 1996. On the changing concept of evolutionary population stability as a reflection of a changing point of view in the quantitative theory of evolution, *J. Math. Biol.* **34**, 485–510.

- Hamilton, W. D. 1967. Extraordinary sex ratios, *Science* **156**, 477–488.
- Hamilton, W. D. 1979. Wingless and fighting males in fig wasps and other insects, in “Reproductive Competition and Sexual Selection in Insects,” Academic Press, New York.
- Herre, E. A. 1985. Sex ratio adjustment in fig wasps, *Science* **228**, 896–898.
- Karlin, S., and Lessard, S. 1986. “Theoretical Studies on Sex Ratio Evolution,” Princeton Univ. Press, Princeton.
- Lemire, M., and Lessard, S. 1997. On the non-existence of an optimal migration rate, *J. Math. Biol.* **35**, 657–682.
- Maynard Smith, J., and Price, G. R. 1973. The logic of animal conflict, *Nature* **246**, 15–18.
- Nagelkerke, C. J. 1996. Discrete clutch sizes, local mate competition and the evolution of sex allocation, *Theor. Popul. Biol.* **49**, 314–343.
- Nishimura, K. 1993. Local mate competition in a stochastic environment, *Theor. Popul. Biol.* **44**, 189–202.
- Nunney, L., and Luck, R. F. 1988. Factors influencing the optimum sex ratio in a structured population, *Theor. Popul. Biol.* **33**, 1–30.
- Taylor, P. D. 1994. Sex ratio in a stepping-stone population with sex-specific dispersal, *Theor. Popul. Biol.* **45**, 203–218.
- Taylor, P. D., and Bulmer, M. G. 1980. Local mate competition and the sex ratio, *J. Theor. Biol.* **86**, 409–419.
- Wilson, D. S., and Colwell, R. K. 1981. The evolution of sex ratio in structured demes, *Evolution* **35**, 882–897.