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Whole brood mortality increases the opportunity for female-biased sex ratios under local mate competition

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ABSTRACT

Fisher predicted that sex ratios should be even when the cost of producing each sex is equal, assuming large panmictic populations. Hamilton showed that when individuals breed exclusively in small groups (local mate competition), the sex ratio does not comply with Fisherian theory, but instead favours a female bias. Local mate competition has been suggested to explain female biases most often in haplo-diploids and parasitoids, where a small number of foundresses make up a breeding group. Here I show how pre-reproductive mortality can affect the predicted ESS sex ratio under local mate competition. Specifically, whole brood mortality reduces the number of families in the breeding pool each generation and, therefore, increases the probability that brothers will compete for mating opportunities. This effect is predicted to be strongest when females lay a small number of clutches each generation. These findings suggest that Hamilton's classic model for group-structured sex ratios may be applicable to a much wider range of systems than was previously believed, since the requirements of the model are not always confined to small deme sizes.

Keywords: brood mortality, evolutionarily stable strategy, local mate competition, *Micrathena gracilis*, sex ratio.

INTRODUCTION

Fisher (1930) predicted that sex ratios should be near 1 when the cost of investing in each sex is the same. This prediction stems from the notion that individuals of the rarer sex will always have greater relative fitness than individuals of the predominant sex, driving the sex ratio towards unity. Hamilton (1967) showed how an overproduction of females can be favoured when individuals breed in small patches, a phenomenon termed 'local mate competition'. Local mate competition can be viewed as reducing competition among brothers for mating opportunities. In the extreme case, when one mother founds the deme, the favoured sex ratio is all females and one male, since the production of multiple males only creates mating competition among brothers and reduces the potential number of grand-offspring a mother can produce. A consistent empirical result is found in a mite whose offspring breed inside their mother before they are born; clutches generally consist of all daughters and one son (Newstead and Duvall, 1918). Group structure is not predicted

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to affect sex allocation in large demes, since the probability that brothers will compete for mating opportunities is negligible (Bulmer, 1986).

Selection favouring a female-biased sex ratio results from the fact that groups characterized by a larger proportion of female offspring will have higher productivity and thus will yield a greater number of dispersing individuals than neighbouring demes. Although Fisherian selection within the deme favours mothers producing a 1 : 1 sex ratio, the between-group selection ultimately contributes to a mother's fitness as well and thus favours the groups that yield the most dispersers. The favoured female bias is predicted to dissolve with increasing deme size, since any individual mother's fitness becomes less influenced by the success of the group. The prediction of a female bias is consistent with group selection under the haystack model (Bulmer and Taylor, 1980), since a mother's fitness is influenced by the group's success.

Under local mate competition theory, sex ratios that deviate substantially from unity can only occur when the deme is very small. Specifically, the predicted proportion of male offspring produced is equal to $(n-1)/2n$, where n is the number of females in the breeding group (Hamilton, 1967). Consequently, the theory is commonly used to explain sex ratio biases in parasitoids (reviewed in Hamilton, 1967; Hardy, 1994), but has only rarely been used as an explanation for female biases in non-parasitic insects and other animals that typically exhibit larger breeding groups (Bulmer, 1986; Madsen and Shine, 1992).

Hamilton's model illustrates the effect of competition among brothers on the evolutionarily stable strategy (ESS) sex ratio, but does not account for post-investment, pre-reproductive mortality. Nagelkerke and Hardy (1994) demonstrated that male-specific mortality during development could decrease the favoured female bias under local mate competition in small clutches, due to the possibility of producing maleless clutches when there is one foundress. In nature, it is often the case that mortality can affect entire broods, ultimately influencing the contribution of a mother's progeny to the success of the deme. Here I examine the effect of whole brood mortality on sex allocation in structured demes.

THE MODEL

In Hamilton's model, individuals live and breed in small patches, such as in association with a particular host. When the number of offspring produced by each mother is large, the fitness gain through each daughter is equal to $1 + p$, where p is the probability that the daughter will mate with her brother. Fitness through each son is $((1 - r)/r)(1 - q)$, where r is the proportion of male offspring produced and q is the probability that a son's mating opportunity will displace the mating opportunity of a brother. At equilibrium, fitness through sons and daughters is equal, such that

$$1 + p = \left(\frac{1 - r}{r}\right)(1 - q) \tag{1}$$

When mating is random in the deme, $p = q$, so that r^*, the ESS sex ratio, is

$$r^* = \frac{(1 - p)}{2} \tag{2}$$

When n is equal to the number of females in the deme, $p = 1/n$ and $r^* = (n - 1)/2n$, as in Hamilton's equation.

I consider a population structure identical to that of Hamilton (1967), but include mortality that occurs before individuals leave their broods, such as depredation or environmental factors that result in the loss of entire clutches. This form of mortality has an all-or-none effect on the survival of the clutch. β is defined as the proportion of broods that survive each generation.

Crow and Morton (1955) characterized the distinction between individual and clutch survival, calling the latter 'survival of the family as a unit'. They envisioned a scenario where the fate of individuals in the same clutch was linked to their spatial and temporal proximities. Brood mortality is known from a diverse array of natural systems in circumstances where members of the brood are physically associated with one another. Brood mortality is likely to occur in oviparous species when eggs are laid in masses or when offspring are reared in nests. High levels of brood mortality should be coupled with large brood sizes, since few broods will comprise the recruitment in a given generation. Possible factors causing whole brood attrition are parasites, predators and stochastic events. High brood mortality (>60% of clutches have no survivors) has been observed in various invertebrate systems, including spiders (Bukowski and Christenson, 1997), crabs (Navarrete *et al.*, 1999) and beetles (Ragenovich, 1980), as well as several vertebrates, including amphibians (Stenhouse, 1987), fishes (Lukas and Orth, 1993) and birds (Suarez *et al.*, 1993).

When a proportion of broods die, the probability that a female will mate with one of her brothers is affected. The probability that a daughter will sib-mate will now be

$$p = \frac{1}{(1+m)} \tag{3}$$

where m is the number of unrelated surviving broods in a deme. The ESS sex ratio is now

$$r^* = \frac{m}{2(m+1)} \tag{4}$$

We can expect that m has a mean of $\beta(n-1)$, such that

$$r^* = \frac{\beta(n-1)}{2(1+\beta(n-1))} \tag{5}$$

where β is the proportion of surviving broods. Even when the number of females breeding in a deme (n) is large, the ESS sex ratio is still strongly female-biased if brood mortality is sufficiently high. Note that individual survival will not affect the ESS sex ratio, since it applies to all individuals regardless of clutch and, therefore, does not alter the genetic contribution of one female relative to other females. This analysis does not take into account the effect of individual mortality on the possibility of producing completely maleless broods when clutch size is very small, which has been shown to favour less of a female bias when there is one foundress (Green *et al.*, 1982; Nagelkerke and Hardy, 1994).

Equation (5) shows the ESS sex ratio when a proportion of broods does not survive. One limitation of this analytical equation is the presumption of fixed mortality. In nature, the proportion of broods surviving may remain constant over time, but is expected to show variance. Thus, a more precise prediction of ESS sex ratios can be obtained from incorporating variance in the proportion of broods that survive. Variance in β will cause our expectation of p to be greater than $1/(1 + (\beta n - 1))$, thus increasing the favoured female bias.

Figure 1 compares the ESS sex ratios found using both the analytical equation that lacks variance and a solution incorporating binomial variance (for formulations, see the Appendix). Although the analytical equation provides a close approximation of the predicted sex ratio, the variance solution results in a slightly greater female bias. This result can be explained by the fact that variance in clutch mortality increases the opportunity for a small effective deme size, which disproportionately increases the predicted female bias. This pattern is consistent with other models that show that the ESS sex ratio under local mate competition is slightly more female-biased when the number of families present is variable as opposed to fixed (Herre, 1985; Lively, 1990). When $\beta = 1$, all broods survive and the equation for the ESS sex ratio is identical to that of Hamilton.

Additionally, we can examine the case for iteroparous populations, where females lay

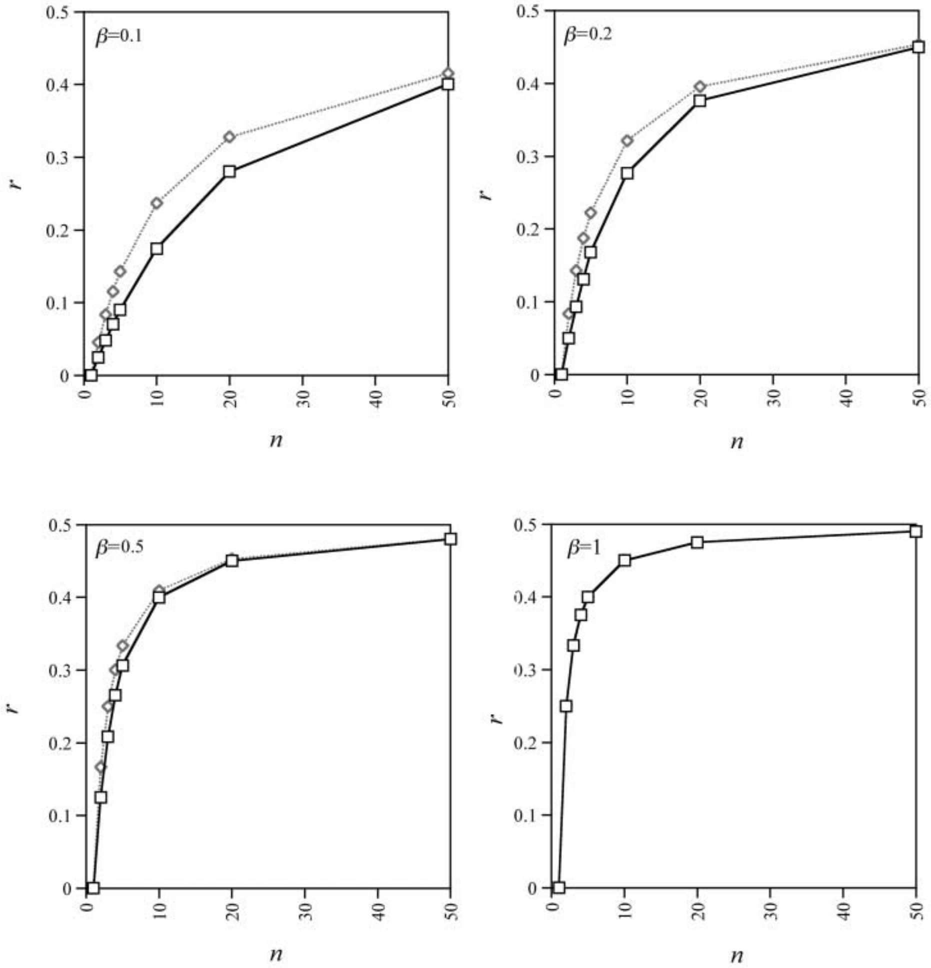

Fig. 1. Comparison of predicted sex ratios (r) for various population sizes (n = number of breeding females) with variable brood survival (β) using the analytical equation (A4) and variance solution (A7). □, variance solution; ◇, analytical equation.

multiple broods each generation. The probability that daughters will sib-mate can now be defined as

$$p = \frac{b}{b + m} \tag{6}$$

where m is again the number of surviving unrelated broods and b is the number of surviving broods from the focal female. The ESS sex ratio is thus:

$$r^* = \frac{m}{2(b + m)} \tag{7}$$

Although high clutch mortality can increase the probability that a mother's sons will compete for mating opportunities, the favoured female bias resulting from clutch-specific mortality disappears as the number of broods in each generation increases. Specifically, as the number of broods becomes large, p becomes $1/n$ and the ESS sex ratio becomes $(n - 1)/2n$ as in Hamilton's equation (2). This results from the fact that given enough reproductive opportunities, every mother will contribute relatively equal numbers of offspring into the breeding pool, as every female will have the same number of surviving broods (assuming clutches have an equal probability of survival, regardless of maternal identity). Thus, clutch mortality will most often increase the opportunity for local mate competition in semelparous populations, or populations in which each female produces a small number of clutches each generation. Brood mortality does not increase the opportunity for local mate competition in long-lived species, since individuals surviving from separate breeding seasons will reduce the impact of a single mother's progeny on the group's success.

As with the case for semelparity, a more precise prediction of the ESS sex ratio can be determined by a solution incorporating variance in both the survival of non-related broods and the survival of additional broods produced by the focal female. A comparison of a non-variable analytical equation and a solution incorporating binomial variance is shown in Fig. 2 (for formulations, see the Appendix). As expected, the analytical equation provides a close approximation of the predicted sex ratio, but is slightly less female-biased than the variance solution. As the number of broods becomes large, the contribution of all females is relatively equal and the effect of brood mortality on local mate competition disappears.

The results from the analytical equations and variance solutions under both semelparity and iteroparity suggest that, under certain conditions of brood mortality and clutch number, female-biased sex ratios can result from local mate competition despite large population sizes. Thus, local mate competition may operate in a much larger range of natural systems than was previously thought. One example may be seen in orbweaving spiders, where egg mass mortality occurs frequently due to predation. Bukowski and Christenson (1997) reported 97% brood mortality in *Micrathena gracilis*, the spiny orbweaving spider. The high brood mortality, coupled with a relatively small number of broods produced per female each generation (1.6 ± 0.8; mean $\pm s$), suggests that local mate competition may operate despite a population size exceeding 200 individuals. Although difficulty in censusing wandering males may affect the observed sex ratio, the strong female bias found (2.4 : 1, $P = 0.02$) in the final censusing period is consistent with the occurrence of local mate competition in this population. Additional data on population size and structure can further confirm the presence of local mate competition in this population, as well as other species characterized by high levels of brood mortality.

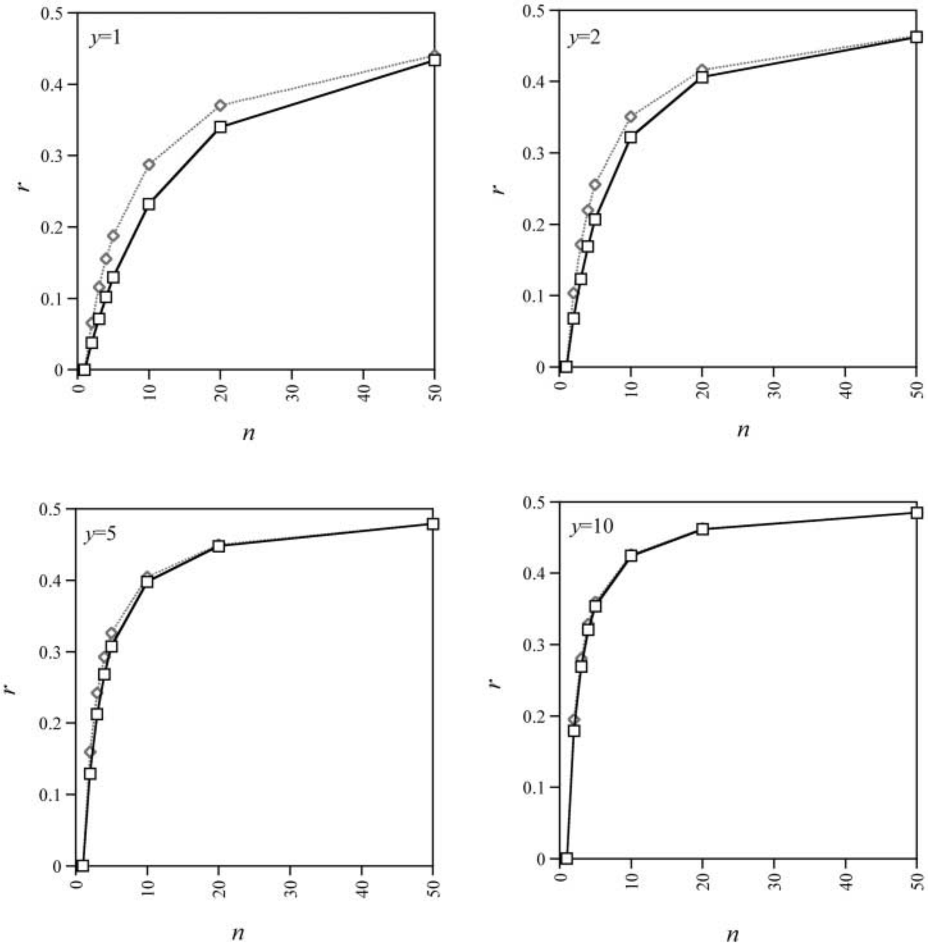

Fig. 2. Comparison of predicted sex ratios (r) for various population sizes (n = number of breeding females) with variable number of broods per female (y) using the analytical equation (A6) and variance solution (A8). Brood survival (β) is 0.15. □, variance solution; ◇, analytical equation.

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REFERENCES

Bukowski, T.C. and Christenson, T.E. 1997. Natural history and copulatory behavior of the spiny orbweaving spider *Micrathena gracilis* (Araneae, Araneidae). *J. Arachnol.*, **25**: 307–320.

Bulmer, M.G. 1986. Sex ratios in geographically structured populations. *Trends Ecol. Evol.*, **1**: 35–38.

Bulmer, M.G. and Taylor, P.D. 1980. Sex ratio under the haystack model. *J. Theor. Biol.*, **86**: 83–89.

Crow, J.F. and Morton, N.E. 1955. Measurement of gene frequency drift in small populations. *Evolution*, **9**: 202–214.

Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Oxford: Oxford University Press.

Green, R.F., Gordh, G. and Hawkins, B.A. 1982. Precise sex ratios in highly inbred parasitic wasps. *Am. Nat.*, **120**: 653–665.

Hamilton, W.D. 1967. Extraordinary sex ratios. *Science*, **156**: 477–488.

Hardy, I.C.W. 1994. Sex ratio and mating structure in the parasitoid Hymenoptera. *Oikos*, **69**: 3–20.

Herre, E.A. 1985. Sex ratio adjustment in fig wasps. *Science*, **228**: 896–898.

Lively, C.M. 1990. Male allocation and the cost of biparental sex in a parasitic worm. *Lect. Math. Life Sci.*, **22**: 93–107.

Lukas, J.A. and Orth, D.J. 1993. Reproductive ecology of redbreast sunfish *Lepomis auritus* in a Virginia stream. *J. Freshwater Ecol.*, **8**: 235–244.

Madsen, T. and Shine, R. 1992. Sexual competition among brothers may influence offspring sex ratio in snakes. *Evolution*, **46**: 1549–1552.

Nagelkerke, C.J. and Hardy, I.C.W. 1994. The influence of developmental mortality on optimal sex allocation under local mate competition. *Behav. Ecol.*, **5**: 401–411.

Navarrete, N., Soto, R., Quiroga, E., Vargas, M. and Wehrtmann, I.S. 1999. Egg production in *Eurypodius latreillii* Guerin, 1828 (Decapoda: Majidae) in the Straits of Magellan, southern Chile. *Scientia-Marina*, **63**: 333–337.

Newstead, R. and Duvall, H.M. 1918. Bionomic, morphological, and economic report on the acarids of stored grain and flour. *R. Soc. Rep. Grain Pests* (*War*) *Comm.*, **2**: 1–59.

Ragenovich, I. 1980. Effects of subzero Fahrenheit temperatures on southern pine beetle (*Dendroctonus frontalis*) populations in the southern Appalachians, USA. *Southern J. Appl. Forestry*, **4**: 201–203.

Stenhouse, S.L. 1987. Embryo mortality and recruitment of juveniles of *Ambystoma maculatum* and *Ambystoma opacum* in North Carolina (USA). *Herpetologica*, **43**: 496–501.

Suarez, F., Yanes, M., Herranz, J. and Manrique, J. 1993. Nature reserves and the conservation of Iberian shrubsteppe passerines: the paradox of nest predation. *Biol. Cons.*, **64**: 77–81.

APPENDIX

Analytical equations

In Hamilton's (1967) model, individuals live and breed in small patches, such as in association with a particular host. Each patch consists of n females. The proportion of male offspring produced by most females is denoted by (r), while $(1 - r)$ is the proportion of female offspring. A rare mutant produces a fraction (s) of male offspring and $(1 - s)$ of female offspring. The overall genetic contribution (w) of the rare mutant female is:

$$w = (1 - s) + \left(\frac{(n - 1)(1 - r) + (1 - s)}{(n - 1)r + s}\right)s \tag{A1}$$

where the bracketed term is the average number of matings each male gets. The evolutionary equilibrium proportion of males is found by $(\partial w/\partial s = 0)$ evaluated at $s = r$; this is shown to be evolutionarily stable, since there is no mutant sex ratio that beats the evolutionarily stable population sex ratio. The ESS sex ratio, r^*, is thus:

$$r^* = \frac{(n - 1)}{2n} \tag{A2}$$

Taking into account brood survival (β), the genetic contribution of the rare mutant is now

$$w = (1-\beta)0 + \beta\left((1-s) + \left(\frac{(1-r)(n-1)\beta + (1-s)}{r(n-1)\beta + s}\right)s\right) \tag{A3}$$

$(1-\beta)0$ represents fitness when the mutant's broods die and $\beta(\ldots)$ represents fitness gained through surviving broods. Thus, within the bracketed term, the mutant female's broods $[(1-s), s]$ are not affected by the brood survival term (β), since this term represents the fraction of time they have survived brood selection.

Once again, there is no sex ratio that the mutant can produce that beats the ESS sex ratio, and thus w is maximized when $s = r$. To determine the ESS sex ratio, r^*, we find the solution for $(\partial w/\partial s = 0 \mid s = r)$:

$$r^* = \frac{\beta(n-1)}{2(1+\beta(n-1))} \tag{A4}$$

Under iteroparity, the effect of brood mortality on the sex ratio is influenced by the number of clutches produced. Here, y is the number of clutches that each female produces. The genetic contribution of the mutant mother will then be

$$w = (1-\beta)0 + \beta\left((1-s) + \left(\frac{(1-r)(n-1)\beta y + (1-s)(1+\beta(y-1))}{r(n-1)\beta y + s(1+\beta(y-1))}\right)s\right) \tag{A5}$$

where $(n-1)\beta y$ represents the total number of individuals from additional sets of clutches among which the mutant's offspring may breed and $\beta(y-1)$ represents the number of additional clutches that the mutant female will produce.

To determine the ESS sex ratio, I again set the derivative equal to zero ($\partial w/\partial s = 0$ when $s = r$):

$$r^* = \frac{\beta y(n-1)}{2(1+\beta(ny-1))} \tag{A6}$$

Variance solutions

The solution for brood mortality with semelparity that incorporates variance in the number of surviving broods is

$$w = (1-\beta)0 + \beta\left(\sum_{i=0}^{i=n-1} p_i w_i\right) \tag{A7}$$

where p_i is the probability that i non-related broods survive:

$$p_i = \binom{n-1}{i}\beta^i(1-\beta)^{n-1-i}$$

and w_i is the fitness when in a deme with i non-related surviving clutches:

$$w_i = (1 - s) = \left(\frac{(1 - r)i + (1 - s)}{ri + s} \right) s$$

Under iteroparity, there will be variance in both the number of surviving clutches from the focal female and in the number of surviving, non-related clutches. The solution can be found using:

$$w = \sum_{j=1}^{j=y} q_j \left(\sum_{i=0}^{i=(n-1)y} v_i w^*_{ij} \right) \tag{A8}$$

where q_j is the probability that j clutches survive from the focal female:

$$q_j = \left(\frac{y}{j} \right) \beta^j (1 - \beta)^{y-j}$$

v_i is the probability that i non-related clutches survive:

$$v_i = \left(\frac{(n-1)y}{i} \right) \beta^i \beta^{(n-1)y-i}$$

and w^*_{ij} is the fitness when in a deme with i non-related surviving clutches and j surviving clutches from the focal female:

$$w^*_{ij} = (1 - s)j + \left(\frac{(1 - r)i + (1 - s)j}{ri + sj} \right) sj$$