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# Local mate competition and transmission bottlenecks: A new model for understanding malaria parasite and other sex ratios

Allison T. Neal<sup>a,\*</sup>, Peter D. Taylor<sup>b</sup><sup>a</sup> Department of Biology, University of Vermont, Burlington, VT 05405, USA<sup>b</sup> Department of Mathematics and Statistics, Queen's University, Kingston, ON, Canada K7L 3N6

## HIGHLIGHTS

- Local mate competition assumes females increase transmission to the next generation.
- Malaria female production and transmission success may not be linearly related.
- We model the effect of a non-linear female-transmission relationship on sex ratio.
- Decreasing fitness returns on female production favors less investment in females.
- More offspring per patch also favors more equal investment in males and females.

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## ABSTRACT

The local mate competition model from sex ratio theory predicts female-biased sex ratios in populations that are highly subdivided during mating, and is thought to accord well with the population structure of malaria parasites. However, the selective advantage of female-biased sex ratios comes from the resulting increase in total reproductive output, an advantage the transmission biology of malaria parasite likely reduces. We develop a mathematical model to determine how bottlenecks in transmission that cause diminishing fitness returns from female production affect sex ratio evolution. We develop four variations of this model that incorporate whether or not parasite clones have the ability to detect others that occupy the same host and whether or not the number of clones affects the total mating population size. Our model indicates that transmission bottlenecks favor less female-biased sex ratios than those predicted under LMC. This effect is particularly pronounced if clones have no information about the presence of coexisting clones and the number of mating individuals per patch is fixed. The model could extend our understanding of malaria parasite sex ratios in three main ways. First, it identifies inconsistencies between the theoretical predictions and the data presented in a previous study, and proposes revised predictions that are more consistent with underlying biology of the parasite. Second, it may account for the positive association between parasite density and sex ratio observed within and between some species. Third, it predicts a relationship between mortality rates in the vector and sex ratios, which appears to be supported by the little existing data we have. While the inspiration for this model came from malaria parasites, it should apply to any system in which per capita dispersal success diminishes with increasing numbers of females in a patch.

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## 1. Introduction

Evolutionary models rest on their underlying assumptions, with some models more robust than others to deviations from those assumptions. Stressing a model by altering its assumptions is often very informative, and can lead to intriguing and unexpected

insights. We focus on one example from sex ratio theory, a prominent focus in evolutionary biology that makes quantitative predictions about how natural selection will shape the ratio of males to females in populations (West, 2009). The early models in sex ratio theory, which were conceived by Düsing (1884, translation in Edwards (2000)) and popularized by Fisher (1930), considered large, randomly mating populations. They concluded that equal investment in males and females would be favored because parents producing the less common sex would receive a fitness advantage due to the greater mating success of their offspring. The first major extension of the theory came from Hamilton (1967),

\* Correspondence to: University of Vermont, Department of Biology, 120 Marsh Life Science, Burlington, VT 05405, USA. Tel.: +1 802 656 0702, 802 922 4820.

E-mail addresses: [aneal@uvm.edu](mailto:aneal@uvm.edu) (A.T. Neal), [peter.taylor@queensu.ca](mailto:peter.taylor@queensu.ca) (P.D. Taylor).

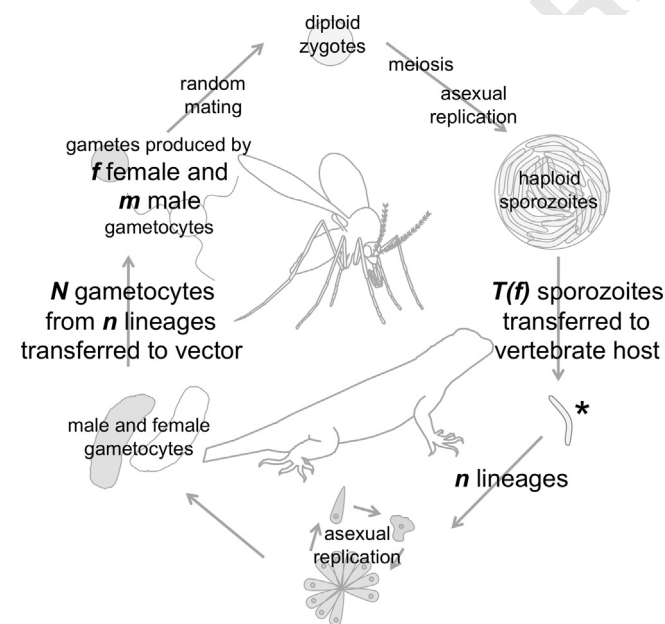
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who showed that modifying certain key assumptions of the Fisherian model could favor strongly biased sex ratios. For example, if, during mating, a population is highly subdivided into patches containing the offspring of one or a few mothers and these offspring compete with one another for breeding opportunities, then female-biased sex ratios can be favored by the resulting increase in the reproductive value of the offspring or, equivalently, in the total number of grand-offspring produced.

This model, termed local mate competition (LMC), has received support from studies of a wide range of arthropods whose population structure matches this model well (reviewed by West, 2009). LMC has also been tested for malaria parasites (*Plasmodium* and related genera sensu Martinsen et al., 2008) with more limited success (reviewed by Schall, 2009). Deviations from the predictions of LMC have often been attributed to adaptive sex ratio adjustments to compensate for limited male fecundity or mating group size within a patch (Fertility Insurance, Shutler and Read, 1998; West et al., 2001, 2002). Here we consider another possibility – that the life cycle of malaria parasites deviates from the standard assumptions of LMC in a way that may alter sex ratio predictions – and we determine what sex ratios would be favored if such deviations were accounted for.

Malaria parasites have a two-host life cycle (Fig. 1). Asexual replication in a vertebrate host culminates in the production of male and female sexual cells, the gametocytes, which are the only parasite stage to survive transmission to the second host, a blood-feeding insect vector. Mating takes place within minutes of entering the vector, with female gametocytes producing one female gamete and males producing up to 8 flagellated male gametes. Following mating, zygotes undergo further asexual replication and become oocysts, with each oocyst containing 1000s of transmission stage parasites, the sporozoites (Rosenberg and Rungsiwongse, 1991).



**Fig. 1.** Starting at the asterisk (bottom right), a vertebrate host harbors  $n$  clonal parasite lineages one of which is mutant. These lineages each reproduce asexually and ultimately produce male and female sexual cells, termed gametocytes. Transmission through a blood meal provides  $f$  female and  $m$  male gametocytes to the vector, where  $N=f+m$  is regarded as a function of  $n$ . Gamete production and random mating produce diploid zygotes in numbers proportional to  $f$  and these eventually produce a large number of haploid sporozoites. These are transmitted to a new vertebrate host in numbers  $T(f)$  written as function of  $f$  but with diminishing returns (Fig. 2). These start the cycle again. This life cycle is common to all malaria parasites, though the specific hosts pictured are those of the lizard malaria parasite *Plasmodium mexicanum*.

The sporozoites travel to the insect's salivary glands from whence they will be transmitted the next time the insect feeds.

The division of malaria parasites in separate insect vectors during mating coupled with the presence of many parasites deriving from only one or a few clonal lines (we refer to these as clones or lineages; they are the result of asexual replication in both insect and vertebrate host; Paul and Day, 1998; Read and Day, 1992) apparently match the population structure assumed by LMC well (Read et al., 1992). However, despite the similarities of the malaria life cycle to the standard LMC model, the advantage of producing a female-biased sex ratio could be reduced if the number of female gametocytes ingested isn't linearly related to ultimate transmission success. If increased female production does not increase patch productivity at all, no female bias is favored (Colwell, 1981). Intermediate situations in which producing more female gametocytes increases transmission somewhat, but not proportionally, are also possible and are explored here (Table 1). For malaria parasites, having a linear relationship between female production and transmission success would require the number of female gametocytes ingested to be directly proportional to the number of zygotes, oocysts and sporozoites produced and for the number of sporozoites produced to be directly proportional to the probability of initiating a new infection.

Several characteristics of malaria parasite transmission biology make it possible that increased female production does not linearly increase transmission success. For example, there is evidence of density-dependent mortality during zygote development (Zollner et al., 2006); even if more zygotes are formed when sex ratios are female-biased, higher mortality rates may prevent a proportional increase in oocyst and sporozoite production. Furthermore, increased sporozoite production itself may not greatly affect transmission success. Sporozoites are passed to a new vertebrate host from the salivary glands of the insect vector, which may become saturated. Also, transmission is relatively efficient even with very few sporozoites (Klein et al., 1987; Ungureanu et al., 1976). One study found that doses of 10 to 10,000 sporozoites were all equally capable of inducing infection, with only a slight reduction in time to patency between the highest and lowest dose (12 days for 10,000, 16–17 days for 10; Ungureanu et al., 1976). These traits almost certainly complicate the relationship between the number of females present in the mating population and transmission success, a relationship on which the selective advantage of female-biased sex ratios depends.

Here we develop a mathematical model to explore the consequences of a non-linear female-transmission relationship on the evolutionarily stable sex ratio. We compare four variations of this model that incorporate differences in the information available to the clones and the effects of multiple co-occurring lineages on the total number of offspring in the patch. These variations are: (1) plastic/additive—clones are able to detect and respond to the presence of other lineages occupying the same patch (i.e. sex ratios display phenotypic plasticity sensu Schall, 2009) and each additional clone increases the total mating population by a set amount

**Table 1**  
The strength of the  $T(f)$  bottleneck.

	Fitness $w(n)$ (Eq. (5))	ES sex ratio ( $n=4$ )
No bottleneck pure LMC on males	$w(n)=pf$	$r^* = \frac{n-1}{2n} = 0.375$
Partial bottleneck (Fig. 1) LMC on males, partial LRC on females	$w(n)=pT(f)$	$r^* = 0.440$
Complete bottleneck Male LMC and female LRC balanced	$w(n)=p$	$r^* = 0.500$

Tabulated values of  $r^*$  belong to the plastic additive model.

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