Laboratory assistance provided by Kristen E. Richardson is gratefully acknowledged.

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J. Parasitol., 83(3), 1997 p. 543–544

Adaptive Sex-Ratio Manipulation in *Pediculus humanus capitis*: Possible Interpretations of Buxton's Data

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ABSTRACT: The sex-ratio pattern of an exceptional population of human head lice (collected in the Colombo Prison, Ceylon, in 1934 to 1936) was found to be consistent with a current hypothesis on adaptive sex-ratio manipulation. Data suggest that the louse burdens were isolated and, therefore, small burdens were inbred. Thus, local mate competition favored females that produced offspring with a female bias. This is the first report to suggest that anopluran lice are capable of adaptive sex-ratio manipulation.

The human head louse (*Pediculus humanus capitis*) has not been well studied by evolutionary ecologists, thus its natural history is poorly understood. Here, I use data published half a century ago to show that sex-ratio patterns of an exceptional sample fit a current hypothesis on adaptive sex-ratio manipulation in animal lice (Phthiraptera).

Sex ratio is manipulated to decrease local mate competition (LMC) in a number of arthropod species (Wrensch and Ebbert, 1993). Decreasing LMC is adaptive when a population is divided into a number of small infrapopulations where inbreeding is more pronounced. Under such conditions, a female can maximize her breeding success by producing offspring with an unequal sex ratio. Reducing the production of the sex characterized by higher sexual competition (usually the male) in favor of the noncompetitive sex will result in a decrease of sexual competition among her offspring (Hamilton, 1967). Louse populations are divided into more or less isolated infrapopulations living on different host individuals. In species of avian lice (Phthiraptera: Amblycera, Ischnocera), the female bias was found to be more pronounced in infrapopulations predisposed for inbreeding, i.e., in small infrapopulations compared with large ones and in the lice of territorial birds compared with those of colonial hosts. This pattern suggests that inbreeding and LMC are responsible for the emergence of the bias (Rózsa et al., 1996).

Buxton (1941) published data covering 858 complete crops of hair, collected from louse-infested people in different tropical countries. The sex ratios of 125 infrapopulations from Colombo, Ceylon (now Sri Lanka), correlated with intensity (Buxton, 1941). Infrapopulations were grouped into 5 intensity pools (infrapopulation size 1–2, 3–10, 11–25, 26–100, >100). Sex ratios of the pools correlated with log mean intensity (linear regression, $r = 0.9703$, $F = 48.20$, $P < 0.007$, df = 1).

Buxton (1937) had previously showed experimentally that female mortality increased with repeated copulations. He suggested that in case of high intensity (>100) this effect resulted in a male bias. However, as he pointed out, there was only 1 pool (9 infrapopulations) of this size, and this hypothesis cannot explain why the majority of the infrapopulations belonging to the first 3 pools (103 infrapopulations, 1–25 individuals) tended to be female biased (271 males, 345 females, differs from unity, Fisher's exact test, $P < 0.04$). His experiments to test the influence of starvation and crowding in early larval life on the sex ratio were not conclusive (Buxton, 1940). Interestingly, louse samples from Nigeria (63 samples from 2 sites), Kenya (127

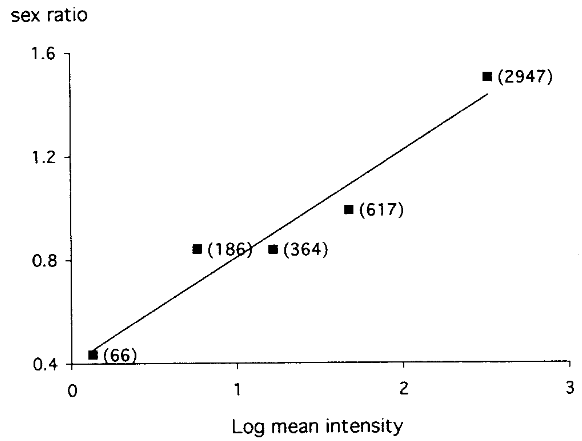

FIGURE 1. Pooled sex ratio (males/females) correlates with log mean intensity of an exceptional population of the human head louse, *Pediculus humanus capitis* (sample size in parentheses).

samples 2 sites), and southwest India (543 samples) exhibited no correlation between intensity and sex ratio, although the ranges of intensity were similar. The alternative hypotheses to interpret the sex-ratio bias are as follows.

Marshall (1981) suggested that the female bias often experienced in louse collections may result from sampling bias; males are smaller and, therefore, easier to overlook. This sampling bias is unlikely to affect the present data set because collection methods were uniform and standardized. This hypothesis predicts a male bias of louse populations with no difference among sites of collection and no correlation between intensity and sex ratio.

Theory predicts that parents allocate resources to produce males and females equally. Thus, in case of unequal costs of production, producing offspring of the cheaper sex is favored (Charnov, 1982). Because males are smaller than females in *P. humanus,* they may be cheaper to produce than females. However, it would be hard to apply this hypothesis to lice because sexual size dimorphism in the egg phase is not known. This hypothesis predicts a male bias of louse populations with no difference among sites of collection and no correlation between intensity and sex ratio.

Presuming a female bias in the lice departing from large infrapopulations to colonize on new hosts could explain the female bias of the small infrapopulations and perhaps even the male bias of the large ones. However, transmission is not known to be biased toward females in this species. The sex ratio of lice collected as single specimens from their hosts in Kakamenga, Kenya, did not differ from the sex ratio of the whole population (9:9 and 528:703, Fisher's exact test, $P > 0.63$), giving no support to the hypothesis that colonizing individuals in this species tend to be females. On the other hand, single specimens tended to be females in Ceylon (1:25 and 2346:1834, χ^2 test: $\chi^2 = 26.55$, df = 1, $P < 0.0001$).

Finally, presuming that lice are capable of an adaptive manipulation of the sex ratio of their offspring if inbred may provide a hypothesis to interpret the correlation between intensity and sex ratio experienced in Ceylon. Because no similar correlation was found at any other site, this hypothesis is acceptable only if isolation among infrapopulations was more pronounced in Ceylon than at other sites. Indeed, this particular sample was taken from men in jail (Buxton, 1938). There are 2 arguments to suggest that the prison environment could increase inbreeding in lice. First, transmission rate was likely to be low simply because the prison host population consisted of adult males only. Second, once infested, a prisoner could not get rid of lice quickly; rather, he had to harbor lice continuously throughout the year (prisoners used coconut oil to decrease intensity but could not eliminate infestations in this manner). Thus, these infrapopulations could subsist through several generations. This situation was likely to increase inbreeding and to favor females that decrease the ratio of males within their offspring. On the other hand, this hypothesis cannot explain the male bias in the pool of highest intensity (>100), a phenomenon explained as a result of an increase in female mortality (Buxton, 1937).

Though there is an increasing body of evidence indicating that lice are capable of adaptive sex ratio manipulation, their genetic or cytological mechanism of sex determination is still unexplored.

This work was supported by grant OTKA F016792.

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