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Heritability of sex ratio manipulation in response  
to host size in the parasitoid wasp  
Muscidifurax raptor

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by

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## Abstract

Natural selection is the process by which organisms accumulate favorable traits that increase reproductive success. One factor that may influence reproductive success is the ability to manipulate one's offspring sex ratio. Sex ratio manipulation has been especially well-examined in parasitoid wasps, in which manipulation may be quite common.

The host-quality model proposes that females will lay a greater proportion of daughters on large hosts than on small hosts because the large host will provide greater resources for the daughters and subsequently will increase their fitness or their ability to pass on their genes by increasing their egg production (Charnov et al., 1981). The parasitoid wasp Muscidifurax raptor exhibits this sex ratio pattern (Seidl and King, in press). However, in M. raptor no evidence was found to support the model's assumption that sex ratio manipulation gives a female a selective advantage over females that do not manipulate their offspring (Seidl and King, in press).

In response to Seidl and King, I attempt to offer an explanation for sex ratio manipulation in the absence of selection for the behavior. This study shows no detectable genetic variation in maternal sex ratio manipulation in response to host size in M. raptor. This suggests an alternative hypothesis to the host quality model--that offspring sex ratio manipulation persists only because there is a lack of genetic variation to do otherwise.

## Introduction

Parental manipulation of offspring sex ratio has been examined in many types of organisms--vertebrates and invertebrates alike (Clutton-Brock and Iason 1986; Charnov 1982). Sex ratio manipulation has been especially well-examined in the case of parasitoid wasps, in which manipulation may be quite common (King 1993). Parasitoid wasps have the ability to manipulate offspring sex ratio by controlling fertilization. A female usually lays one egg on a fly pupae after drilling through the fly case. If a female releases stored sperm, she fertilizes an egg and it develops into a daughter; if she withholds sperm, she lays an unfertilized egg which develops into a son. The offspring then consumes the host until it develops and emerges as an adult wasp. Here, sex ratio manipulation is examined in the parasitoid wasp Muscidifurax raptor.

One factor to which females may respond in manipulating sex ratio is host size. The manipulation of offspring sex ratio in response to host size can allow a female to maximize the perpetuation of her genes as described in the host-quality model. The host-quality model is a model of how animal behavior will be affected by natural selection. In attempting to explain the adaptations of a species to its environment, Charles Darwin developed the theory of evolution by natural selection. Natural selection explains that competition between organisms over limited resources will lead to evolution in a population, i.e. to a change in the relative frequency of different genetic traits. Natural selection occurs when beneficial genetic traits that give

an organism a reproductive advantage over other members of its species allow the organism to pass on its genes to offspring at a greater success rate than others without the advantageous trait (Krebs and Davies, 1987). The host-quality model attempts to explain how sex-ratio manipulation behavior may have evolved by natural selection due to the behavior's effect on the reproductive success of the wasp.

The host-quality model proposes that females will lay a greater proportion of daughters on large hosts than on small hosts. The reasoning behind the model is that 1) a large host may provide more resources and so wasps from them may be bigger and 2) being big may increase the reproductive ability of a daughter more than the reproductive ability of a son (Charnov et al., 1981). In other words, the model assumes that a lack of abundant resources and hence small size will not negatively affect a male's ability to inseminate females; however, the same conditions would negatively affect a female's egg production.

Because the host quality model is a natural selection model, it assumes that the trait of manipulation is heritable, i.e. exhibits genetic variation. This assumption has not previously been examined. Here, the genetic variation in maternal sex ratio manipulation in response to host size is examined in M. raptor.

Aspects of the host-size model have been examined in over 75 species (King 1993, table 12.1). Previous studies have shown that in about 50 of 75 species of parasitoid wasps,

including M. raptor (Seidl and King, in press), females produce a greater proportion of daughters in large versus small hosts (King 1993, table 12.1). However, in M. raptor the model's assumption that wasps will be bigger when they develop on bigger hosts is not supported (Seidl and King, in press). Also, females from larger hosts did not produce more offspring. Thus, no evidence has been found for M. raptor to support the model's assumption that sex ratio manipulation gives a female a selective advantage over females that do not manipulate their offspring. In response to the study by Seidl and King (in press), this study attempts to offer an explanation for sex ratio manipulation in the absence of selection for the behavior. In other words, an alternative hypothesis is tested--that offspring sex ratio manipulation persists only because there is a lack of genetic variation to do otherwise.

### **Materials and Methods**

The M. raptor that were used in this experiment are from a colony established in 1990. The colony originated from wasps that emerged from parasitized Musca domestica pupae from a poultry and sheep farm in DeKalb, Illinois. The colony has been maintained on M. domestica, M. raptor's natural host species, and the maintenance of the wasps and hosts is described in King 1988.

In order to estimate the heritability of sex ratio response to host size, offspring sex ratio data were collected

from over 30 females and one daughter of each of the females. All experimental females were given hosts of approximately the same size. Small hosts (2.24cm) were produced using approximately one third the water and one half the media used to produce the large hosts (2.75cm) (King 1988). Wasps used in experiments were developed on large hosts, and were similar in size.

Each of the females had been isolated prior to emergence and was observed to mate with a virgin male. Both wasps were used less than 24 hrs. from emergence. After mating, each female was placed in a 2.2 cm diameter x 5.4 cm tall or 1.9 cm diameter x 7.0 cm tall vial containing eight large and eight small hosts and a drop of honey. She was allowed to parasitize the hosts for 24h. The hosts were then removed, and she was given 16 more hosts--eight large and eight small. This treatment was repeated for a total of three days for each female.

Because females alter the sex ratio of their offspring in response to changing environmental conditions (Antolin, 1992), temperature and humidity were kept constant during the three day treatment. The females' vials were placed in 1L jars with humidity maintained at 75% RH with 130 ml of supersaturated sodium chloride solution made from reagent grade sodium chloride (Winston and Bates, 1960). The jars were kept in an environmental chamber at 28°c.

After exposure to a female, the hosts were removed from the glass vial and separated into 1 oz. plastic vials by size. Thus, each day of parasitism yielded two plastic vials,

one containing eight large hosts and one containing eight small hosts. Any hosts from which a fly subsequently emerged were then removed. The remaining hosts, some of which contained wasp larvae, were isolated to ensure that emerging daughters were virgins.

One virgin daughter of each female was allowed to mate with a virgin male from the wasp colony and then was subjected to the same three day host exposure as her mother. For both mothers and their daughters, offspring sex ratio was determined at the adult stage.

For 28 replicates, hosts of both mothers and daughters were isolated in gelatin capsules. For six replicates, mother's hosts were isolated in test tubes but the daughter's hosts were only separated by size into plastic vials. The sex ratio difference of small and large hosts did not differ between the two sets of replicates for mothers ( $t=0.61$ ,  $df=32$ ,  $p=0.54$ ) or daughters ( $t=0.34$ ,  $df=31$ ,  $p=0.74$ ). The number of offspring produced in small minus large hosts also did not differ between the two sets of replicates for either mothers or daughters ( $u=66.5$ ,  $n_1=28$ ,  $n_2=6$ ,  $p=0.44$ ;  $t=0.91$ ,  $df=32$ ,  $p=0.37$ ). The two sets of replicates were, therefore, pooled.

The heritability of sex ratio response to host size was determined using a parent--offspring regression. Two tailed p values are reported throughout.

Heritability is the proportion of variation in a trait that can cause evolution by natural selection and is equal to the slope of the parent--offspring regression times two (Falconer 1981). If heritability is greater than zero, then there is

genetic variation. If offspring sex ratio is not heritable and hence does not exhibit genetic variation, this would support the hypothesis that the manipulation behavior is the result of a lack of variation to do otherwise.

### Results

There was no significant relationship between mothers and daughters in their sex ratios from small minus from large hosts, and the relationship was not even in the predicted positive direction ( $R^2=0.037$ ,  $n=33$ ,  $p=0.29$ ; daughter's sex ratio difference =  $-0.25(\text{mother's sex ratio difference}) + 0.12$ ). Thus, sex ratio response to host size was not significantly heritable.

There was a negative significant relationship between mothers and daughters in the number of offspring produced in small minus large hosts in mothers versus daughters ( $R^2=0.14$ ,  $n=34$ ,  $p=0.03$ ; daughter's offspring number in small minus large hosts =  $-0.28(\text{mother's offspring number in small minus large hosts}) + 3.10$ ).

The sex ratio difference between small versus large hosts was significant for both mothers and daughters (mean  $\pm$  s.e., mothers:  $0.19 \pm 0.02$  versus  $0.11 \pm 0.02$ ,  $t=3.36$ ,  $df=33$ ,  $p=0.002$ ; daughters:  $0.26 \pm 0.04$  versus  $0.16 \pm 0.04$ ,  $t=2.87$ ,  $df=32$ ,  $p=0.007$ ). There was also a significant difference in the number of offspring produced in small and large hosts (mean  $\pm$  s.e., mothers:  $11.27 \pm 0.63$  s.e. versus  $7.09 \pm 0.60$ ,  $t=5.04$ ,  $df=33$ ,  $p<0.001$ ; daughters:  $9.32 \pm 0.56$  versus  $7.41 \pm 0.47$ ,  $t=3.02$ ,



df=33, p=0.005).

At alpha = 0.05, the power, or probability of finding a significant effect, for the sex ratio manipulation correlation is less than 20%. A sample size of about 200 would have been necessary for a power of 80%. For the clutch size correlation, the power was about 60% and a sample size of about 45 would have been needed to get a power of 80% (Cohen, 1977).

### Discussion

In accordance with Seidl and King (in press), the results indicated that M. raptor females were manipulating the sex ratio of their offspring as well as producing more offspring from small hosts. The results also indicate a significant negative relationship between a mother's and daughter's number of offspring produced in small minus large hosts. So a mother who produced a greater number of offspring in small hosts had a daughter who produced a greater number of offspring in large hosts. Why this occurred is not clear.

Numerous studies have suggested genetic variation in traits including some oviposition behaviors (Wajnberg et. al., 1989), body size and development time (Sequeira and Mackauer, 1992), sex patterns in egg laying (Wajnberg, 1993), and the relationship between sex ratio and other traits (Antolin, 1992b).

Because the heritability of sex ratio manipulation in response to host size was not significant, genetic variation is absent or small. This seems to support the hypothesis that sex ratio manipulation in M. raptor is present because there is a

lack of variation to do otherwise. In relation to the host quality model, mothers may be laying a greater proportion of sons on small hosts not to increase the reproductive ability of daughters but because there is no other behavioral option.

Alternatively, the lack of detectable heritability of sex ratio manipulation in response to host size may be due to the inability of the test to detect small heritability. That is, heritability of sex ratio manipulation may be present but small.

Antolin (1992) suggests that some traits not under direct genetic control may be indirectly affected if there are "genetically correlated with other traits." In other words, sex ratio manipulation may be associated with other traits that are under powerful genetic control and, therefore, sex ratio manipulation may have been selected for in that fashion.

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