Low resource availability causes extremely male-biased investment ratios in the European beewolf, *Philanthus triangulum* F. (Hymenoptera, Sphecidae)

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SUMMARY

Conditional sex allocation theory predicts that under poor conditions parents should produce more of the cheaper sex. Alternatively, females could provide less food for the single progeny or store resources (and thus decrease their rate of reproduction) when food is scarce. These non exclusive options were experimentally tested in the European beewolf where females provision brood cells with paralysed honey bees. Depending on the severity of the food restriction (number of available prey bees per day) females made use of one or more of the different options. In accordance with conditional sex allocation theory the investment ratio was biased towards the cheaper sex (sons) under poor conditions. Females also decreased the amount of food per progeny at very low food availability and stored food under one condition.

1. INTRODUCTION

Organisms should allocate resources in a way that maximizes their fitness returns. Trade-offs between size and number of offspring, and between numbers of sons and daughters are to be expected. Fisher (1930) proposed that due to frequency-dependent selection parents should devote equal amounts of investment to sons and daughters. This theory, however, applies only to the population wide investment ratio. Individual parents might profit from biasing sex ratios depending on ecological, social, or physiological conditions (Charnov 1982). The idea of conditional sex allocation was first proposed by Willson & Pianka (1963) but became widely known as the Trivers–Willard theory (Trivers & Willard 1973). Trivers & Willard developed it for polygynous mammals but it can be applied much more generally (Bull 1981; Charnov 1982; Frank & Swingland 1988). It has been discussed with regard to host size influences on the sex ratio in parasitoid wasps (Charnov 1982; King 1987, 1993), sex ratio biases of some mammals that correlate with the social status of the mother (Clutton-Brock *et al.* 1986), and for the timing of sex change in sequential hermaphrodites (Charnov & Bull 1989).

The prerequisite for conditional sex allocation is that under certain ecological or social conditions progeny of one sex gain more fitness than the other sex. Frank & Swingland (1988) derived two predictions: first, under poor conditions the investment ratio should be biased towards the sex with higher relative fitness under poor conditions (often called the ‘cheaper sex’), but under good conditions the optimal equilibrium investment ratio should be produced and, second, depending on the abundance of poor conditions or patch types, the investment ratio of the population might become biased towards the cheaper sex. It is

often assumed that in polygynous mammals sons suffer more from bad conditions that cause smaller body size and disadvantages in male–male competition. In invertebrates the situation is reversed because females are assumed to benefit relatively more from large body size (Clutton-Brock 1991). With the exception of parasitoids (Charnov 1982; King 1993; King & King 1994; King & Lee 1994), little experimental support exists for conditional sex allocation theory (Clutton-Brock 1991).

Field investment ratios in the European beewolf are heavily male biased and deviate from a Fisherian investment ratio. Males received $73.3 \pm 8.2\%$ of the food provisions (Strohm & Linsenmair 1997b). Conditional sex allocation could provide an explanation. The aim of this study is an experimental test of the qualitative predictions of this theory: females should bias their offspring sex ratio towards sons under bad conditions, and should produce an equilibrium investment ratio under unrestricted conditions. If the investment sex ratio under good conditions is even (or female biased), it might be concluded that the male bias in field populations is caused by conditional sex allocation because of a predominance of poor conditions. If, however, investment ratios under good conditions in the laboratory and in the field are similar, the male bias can not be assumed to be the result of conditional investment allocation.

Female European beewolves provide paralysed honeybees as larval food (details of the biology of beewolves are presented in Hamm & Richards (1930), Olberg (1953), Rathmayer (1962), Simon-Thomas & Simon-Thomas (1972), Evans & O’Neill (1988) and Strohm (1994)). Males receive from 1 to 5, on average 2.2, and females from 3 to 5, on average 3.8, bees in the field (Strohm & Linsenmair 1997c). Thus, the individual amounts of provisions are relatively variable

and a daughter receives on average 1.74 times more bees than a son. This suggests that daughters gain larger benefits from more bees. Conditional sex allocation theory predicts that more sons should be produced under poor ecological conditions.

We tried to simulate good and poor conditions by limiting the number of bees a female could hunt per day. Females can vary *a priori* three different reproductive parameters in response to the imposed restriction: rate of reproduction, food amount for individual progeny and investment ratio. Specifically, females could (1) interrupt their provisioning at times of low food availability, (2) store food items for some time until they have enough to provision a particular number of bees, (3) decrease the number of food items per single progeny, or (4) according to the conditional sex allocation theory females could bias the sex ratio towards sons. These options do not exclude each other and the females' responses might differ depending on the severity or pattern of the restriction.

Additionally, we tried to get information about the period of time that is used by females to assess food availability. If females base their decisions regarding the allocation of provisions on short time periods, a high discontinuous short-term availability (x bees every n th day) should result in an allocation pattern that is similar to a high continuous availability (x bees every day). However, if females average over a longer time period, the allocation under high discontinuous availability (x bees every n th day) should be similar to a lower continuous food rate (x/n bees every day). Therefore in one experimental condition prey items were supplied in a temporally clumped pattern.

2. METHODS

Females were caught at a colony near Würzburg (Germany) and housed singly in nest boxes in the laboratory. The cages consisted of a lower part ($60 \times 30 \times 25$ cm³) that was filled with sand. Moisture was regulated by watering the sand through holes in the bottom of the boxes. The upper part consisted of a flight cage ($60 \times 60 \times 25$ cm³). Cages were illuminated by neon lamps (that lie on the flight cage) for 10 h a day; this is the maximum activity period in the field (Strohm 1994). Maximum daily temperature in the room varied from 25 to 30 °C.

Field observations of Simon-Thomas & Simon-Thomas (1972) showed that in southwest France, beewolf females brought in, on average, four bees per day in a supposedly good year and two per day in a year with unfavourable weather conditions. We chose the following food conditions: one bee every second day (1 b/2d), one bee each day (1 b/d, low continuous pattern), two bees each day (2 b/d), four bees each day (4 b/d, high continuous pattern), four bees every fourth day (4 b/4d, high discontinuous pattern), and *ad libitum*.

In solitary Hymenoptera most of the parental investment consists of food that the mother provides for her progeny. The often used fresh or dry weights of emerged progeny (e.g. Trivers & Hare (1976); Danforth (1990)) might be prone to several confounding factors (Boomsma & Isaacs 1985; Boomsma 1989) especially in beewolves (Strohm & Linsenmair 1997b) and are thus less reliable as investment measures (but see Danforth 1990). In beewolves, amounts of provisions can be easily quantified by counting the number of

bees in a brood cell (Strohm 1994), since honeybees are of very similar size (Ruttner 1992). In this study parental investment was quantified as the number of bees in a brood cell.

Prey bees were caught from the same hive throughout the experimental period and released into the flight cages, where they could be easily detected by the beewolf females. Cages were controlled daily (in the morning prior to the female's activity period) and bees that had died or had been brought into the nest were replaced by live bees in order to keep the number of available prey items constant for each day. The fate of each bee could thus be determined. Under *ad libitum* conditions, there was always at least one bee available in the flight cage. The food condition remained unchanged for the whole life span of a female. Females were provided with honey *ad libitum*. Four weeks after the female's death the nests were excavated and the number of bees in brood cells was determined by counting the cuticular remains of the thoraces or abdomens (Strohm 1994; see also Stubblefield *et al.* (1993)). Cocoons with larvae were measured, put into small plastic containers with moist sand, and hibernated at 8 °C. After six months the temperature was raised to 20 °C to induce pupation and emergence. Adults were sexed.

Additional data for 1 b/d ($N = 6$ females) and *ad libitum* ($N = 6$ females) were available from exploratory experiments and for 4 b/d ($N = 28$) from breeding beewolves in the laboratory. The principal methods and abiotic conditions were the same as for the main experiment, however, females came from different colonies.

Statistical analysis was based on means of individual females. Investment ratios were calculated for individual females as the proportion of bees for emerged sons from the total of bees for all emerged progeny of a female. Statistical procedures were chosen after Bortz *et al.* (1990) and Sachs (1984).

3. RESULTS

All females hunted bees and laid eggs, even under the very restrictive condition of 1 b/2d. The mean ($\pm$ s.d.) number of brood cells that were finished per day was for 1 b/2d = 0.33 ± 0.034 , 1 b/d = 0.38 ± 0.03 , 2 b/d = 0.68 ± 0.07 , 4 b/d = 0.61 ± 0.08 , 4 b/4d = 0.34 ± 0.016 , *ad lib.* = 0.81 ± 0.046 ($N = 5-6$ females per group and ≥ 8 brood cells for each female) and differed significantly between groups (Kruskal-Wallis ANOVA by ranks: $H = 24$, d.f. = 5, $p < 0.001$).

The frequency distributions of brood cells with different numbers of bees show high variation contingent on treatment (figure 1). With 1 b/2d most bees were provisioned in brood cells with only one bee. With one and two bees per day brood cells were predominantly provisioned with two bees. Under the feeding regimes of 4 b/d and 4 b/4d brood cells with four bees were the most common type, whereas under *ad libitum* feeding, cells containing two bees were the most frequent type. The mean number of bees per brood cell (figure 1) varied significantly between food regimes (Kruskal-Wallis ANOVA by ranks: $H = 25.2$, d.f. = 5, $p < 0.001$).

When differentiated between the sexes (figure 2) the mean number of bees differed significantly between treatment groups for males but not for females (Kruskal-Wallis ANOVA by ranks: males: $H = 17.3$, d.f. = 5, $p < 0.001$; females: $H = 0.6$, d.f. = 2, n.s.). Under heavily restricted conditions, males received

Figure 1. Number of bees in brood cells (y axis) with 1, 2, 3, or 4 bees (x axis) under different food regimes (N = number of females in one treatment).

only about half the food compared to mediocre or good conditions (comparison between 1 b/2d and 4 b/d: Kolmogoroff-Smirnov test: $D = 1$, $N_1 = 5$, $N_2 = 6$, $p < 0.05$).

The sex ratio of investment differed significantly between treatment groups (Kruskal-Wallis ANOVA by ranks: $H = 23.5$, d.f. = 5, $p < 0.001$, figure 3). At low food rates (1 b/2d, 1 b/d, 2 b/d) only males were produced. With 4 b/d the mean investment ratio

($\pm$ s.d.) was 0.48 ± 0.27 (median = 0.39), with 4 b/4d it was 0.41 ± 0.16 (median = 0.37) and under *ad libitum* conditions it was 0.65 ± 0.11 (median = 0.66). Multiple comparisons after Schaich & Hamerle (Bortz *et al.* 1990) revealed that each of the first three treatment groups (1 b/2d, 1 b/d, 2 b/d) differed significantly from each of the other groups (critical rank difference between each of the first three groups and 4 b/d = 16.7, $p < 0.001$; 4 b/4d = 19.25, $p < 0.001$; *ad lib.* =

Figure 2. Mean ($\pm$ s.d.) number of bees per brood cell (mean of means for offspring of individual beewolf females) for male and female progeny under the different food regimes.

Figure 3. Investment ratio (proportion of bees for males, means for individual beewolf females $\pm$ s.d.) as a function of resource availability. The numbers of bees for sons and daughters of individual females were compared (χ^2 test) with an 1:1 expectation, the χ^2 values and degrees of freedom were added (Sachs 1984) and are given for each treatment group (significance levels *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$).

12.25, $p < 0.05$). The observed investment ratios were in concordance with a 1:1 expectation after Fisher (1930) only in the 4 b/d treatment (figure 3). For 4 b/4d, the investment ratio was significantly female biased, the 1 b/2d, 1 b/d, 2 b/d, and *ad libitum* treatment groups were significantly male biased.

A second set of experiments was not performed simultaneously with the experiment above, but the same cages and abiotic conditions were used and prey bees were from the same stock. However, female beewolves came from different colonies. Compared with the main experiment, at a food rate of 1 b/d, more bees were found in cells with one bee (53 bees in one-bee cells and 28 in two-bee cells, $N = 6$ females) but in agreement with the above data only males emerged. The data from breeding beewolves with 4 b/d had the following frequencies of bees in brood cells from 1 to 4 bees: 304, 1172, 1059, 776 ($N = 28$ females). Compared with the main experiment, more bees were allocated to brood cells with two bees. After *ad libitum* feeding the respective values were: 27, 64, 72 and 28 ($N = 6$ females). In contrast to the main experiment,

under the 4 b/d conditions the investment ratio was 0.67 ± 0.12 . Under *ad libitum* conditions the investment ratio in the second data set was 0.72 ± 0.08 . All additional trials were significantly male biased (χ^2 -test: $p < 0.05$).

4. DISCUSSION

In this study on the European beewolf, limited availability of prey caused both a significant decrease in the amount of resources individual progeny received and extremely male-biased investment ratios. Under field conditions availability of provisions for solitary wasps and bees seems to be limited by several factors (e.g. time in the season, temperature, body size, age Torchio & Tepedino (1980); Tepedino & Torchio (1982a, b); Willmer (1985a, b); Stone (1994)). Thus, female bees and wasps should have been selected to respond adaptively and the results of the food limitations in the laboratory are not artifacts of anomalous conditions.

Data from breeding experiments with females taken from another colony revealed differences in investment patterns, in particular for the food rate of 4 b/d. Nonetheless, the most important result, that no daughters were produced when few prey bees were provided, was not affected. The observed variability may have been caused by differences in allocation patterns due to different ecological conditions in the colonies. These differences might either have a genetical basis and represent local adaptations (Begon *et al.* 1996) or might be caused by developmental differences as well as prior experience of the females in the original colonies.

(a) Do females reduce the rate of reproduction?

Under poor conditions females might have kept the investment ratio and the amount of provisions per individual progeny constant by pausing and waiting for better conditions. This did not happen. Females hunted for bees and provisioned brood cells even under the most restrictive conditions. The life of a female might be too short to wait for better conditions. Alternatively, females could store bees until the preferred number (two for males and at least three for females) is attained. The distribution of bees in cells (figure 1) and the data on the number of brood cells per day suggest that females stored single bees for one day at most, when they received one bee per day. However, this reduction in the rate of cell provisioning was not sufficient to keep the number of bees per individual progeny constant. Females very rarely stored bees when they received two food items per day and produced mostly sons with two bees. Bees are stored in the main burrow prior to construction of the brood cell (Olberg 1953; Strohm 1994) and this might increase the risk of parasitism or microbial infestation. Parasitoid chrysidids, for example, are very capable of finding nest burrows (Rosenheim 1987; Strohm, unpublished observations) and one species is known to be an important cause of larval mortality in the European beewolf (Simon-Thomas & Simon-Thomas 1972; Veenendaal 1987).

(b) Do females reduce the food amount for individual progeny?

With lowered food availability females could decrease the amount of food for an individual progeny but keep the investment ratio unchanged. Sons received only half as much food under poor than under good conditions (figure 2). Because of significant correlations both between the number of bees and cocoon length (Spearman correlation: $r_s = 0.64$, $n = 161$, $p < 0.001$) and cocoon length and weight of adults ($r_s = 0.79$, $n = 40$, $p < 0.001$; Strohm & Linsenmair (1997c)), the lower food amounts result in smaller body sizes of the progeny.

The food quantity for daughters did not differ between the *ad libitum*, 4 b/d, and 4 b/4d conditions. In beewolves, the number of bees that a daughter requires to become a successful reproductive might be invariably high since females must attain a body size large enough to take off and fly with a paralysed bee. Because European beewolves prey exclusively on honeybees the minimum load (80–160 mg) is rather high compared with the weight of the wasp (60–160 mg; Strohm & Linsenmair (1997a)). Producing a daughter with only two bees would result in a female that is too small and would thus be a complete loss of investment. Though male beewolves are territorial, selection pressures on body size seem to be much weaker and sons can be produced with the lowest possible food amount, i.e. one bee (Strohm & Linsenmair 1997c). Females of other aculeate species behave differently under food limitation. In the monoleptic bee, *Hoplitis anthocopoides*, females are specialized to a single type of flower and females need a certain minimum size to exploit these flowers most effectively (Strickler 1982). Males are territorial and of similar size to females. Thus neither reduction of individual food amounts nor a sex ratio bias would be profitable in this species, and consequently, females reduced their rate of finishing brood cells under low resource availability late in the year. Contrary to beewolves, in *Osmia lignaria* mainly daughters receive less food under poor conditions (Torchio & Tepedino 1980). It is likely that the different allocation patterns under food limitation in these different species are due to differences in the investment-dependent fitness returns of sons and daughters (see Torchio & Tepedino (1980) for a graphical model).

(c) Do females bias the investment ratio to the cheaper sex under poor conditions?

One important confounding effect when investigating investment ratios is differential mortality between the sexes. However, the extreme differences between the three most restricted conditions and the other food regimes in this study are very unlikely to be caused by differential mortality. Because survival of a progeny is correlated with the number of bees it has as larval food (Strohm & Linsenmair 1997c), mortality can be assumed to be somewhat higher for sons. Thus, the primary sex ratios for the less restricted food regimes (4 b/d, 4 b/4d, *ad lib.*) are most probably

somewhat more male biased than is apparent from the emerged progeny.

In the field daughters received at least three bees as larval food (Strohm & Linsenmair 1997c). Under the most limited conditions very few brood cells with three or more bees were produced (figure 1). The extreme assumption, that female eggs were laid also in brood cells with one and two bees but died during development due to insufficient food resources, though very unlikely, cannot be definitely ruled out and waits for further testing.

Females shifted the investment ratio to male progeny under very restrictive food conditions (1 b/2d, 1 b/d, 2 b/d). In the main experiment, more daughters are produced with 4 b/d than in the breeding experiments with females from other locations. However, the results of all *ad libitum* conditions and the additional data for 4 b/d suggest that the average proportion of bees for daughters does not exceed about 40%. This result supports the prediction of Frank & Swingland (1988), that the investment ratio under poor conditions should be biased towards the cheaper sex, but that under good conditions an equilibrium investment ratio should be produced. The proportion of 35–40% of bees used to produce females under good conditions in the laboratory is similar to investment ratios from field populations (mean $\pm$ s.d. = $36.7 \pm 8.2\%$, $n = 7$ years; Strohm & Linsenmair 1997b). Thus, unlimited food availability in the laboratory does not result in less male-biased broods compared with the field and the prediction that conditional sex allocation is responsible for the population wide male bias in the field is not supported.

Field sex ratio and/or investment ratio data are available for some sphecids (e.g. Krombein 1967; Danks 1970; Trivers & Hare 1976; Brockmann & Grafen 1992) and they show a high variation within and between species that might correlate with special features of the species or population. Experimental limitation of food availability has very rarely been conducted with other solitary aculeate Hymenoptera (Rosenheim *et al.* 1996). There are, however, some correlative hints that resource limitation influences investment ratios. Torchio & Tepedino (1980) observed a sex bias in the investment ratio of *Osmia lignaria* that correlated with pollen availability (caused by ageing of the bees; Tepedino & Torchio (1982b)). Early in the season when much pollen was available, mainly expensive females were produced and later cheaper sons. In *Trypoxylon politum*, food availability might also influence investment allocation (Brockmann & Grafen 1992).

Nonacs (1986) provided evidence that in ants the investment ratio is influenced by food availability. By experimental food limitation, Backus & Herbers (1992) could not confirm this in *Leptothorax longispinosus*. King & King (1994) limited food availability by providing only small hosts for a parasitoid wasp. Those females produced either more sons or the same sex ratio as non-restricted females.

In some vertebrates experimental limitation of food availability caused different allocation patterns (McClure 1981; Dobson & Kjelgaard 1984; Austad &

Sunquist 1986; Perrigo 1987). Conditional sex allocation would mostly predict a female bias under poor conditions in mammals. House mice fed on a poor diet biased the sex ratio towards females (Rivers & Crawford 1974). Correlative hints for conditional sex allocation in mammals have been reported for some species (Austad & Sunquist 1986; Gosling 1986; Rutberg 1986; Kent 1992) but not for others (Verme 1969; Guinness *et al.* 1978; Armitage 1987; LeBoeuf 1989). In birds, the situation is similarly equivocal (Leonard & Weatherhead 1996). In mammals, the most convincing results are reported for red deer (Clutton-Brock *et al.* 1986) and baboons (Altmann 1980) where the status of the mother correlates with the proportion of males. In red deer, males are the more expensive sex and are preferably produced by high ranking mothers, whereas for baboons, males are cheaper and the relationship is reversed.

The best evidence for conditional sex allocation, however, comes from parasitoid Hymenoptera. In large hosts female progeny are assumed to have higher fitness gains than males. Thus, it would be profitable to have daughters in large hosts and sons in small ones (Charnov 1982; Werren 1984). From 75 parasitoid wasp species that have been investigated, 53 species show a male bias in small hosts relative to large hosts (King 1993). For six species, not only the predictions but also the assumptions of the conditional sex allocation theory have been analysed. In four species, a host size effect on the fitness of daughters is assumed, whereas in the other two species no such effect could be demonstrated (King & King 1994; King & Lee 1994).

(d) *On what time periods do females base their allocation 'decisions'?*

The distribution of bees and the investment ratio of the high discontinuous food rate (4 b/4d) resembled the data of the high continuous rate (4 b/d) but differed from the low continuous rate (1 b/d). This shows that females allocated the bees opportunistically on a daily basis instead of averaging over longer periods of time. This seems highly adaptive, because a female should take advantage of a high short term food availability and produce female progeny in order to compensate for the prevalent male bias in investment ratio.

(e) *Conclusion*

Female beewolves clearly showed conditional sex allocation. They biased the sex ratio to exclusively male progeny under the most restrictive conditions and an investment ratio similar to field populations under less restricted conditions. However, females also reduced the amount of resources for individual progeny under very restrictive conditions. Thus, sex ratio of parental investment cannot be regarded as an isolated parameter of the reproduction of beewolves. Other factors, in particular investment per individual progeny, might interfere with sex allocation (see Rosenheim *et al.* (1996) for an alternative investment allocation model). Complex interactions of the sex ratio with other characters of reproduction might

occur in birds and mammals (Krackow 1994, 1995). Thus, investment sex ratios have to be analysed in the light of the organism's reproductive biology and the selective forces that underlie the allocation of parental investment in order to judge the adaptiveness of sex ratio shifts.

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