

PARENTAL INVESTMENT AND SEXUAL DIMORPHISM
IN DIGGER WASPS
(HYMENOPTERA: SPHECIDAE)

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Objectives

While investigating the mating strategy of wasps in the genus Philanthus we have discovered that the major determinant of mating success in males is body size (i.e., larger males are more successful at obtaining matings; this will be summarized further at the end of this report). In vertebrates that display sexual dimorphism and where there is male-male combat involved in the mating strategy, males are usually the larger sex. This is not the case in the Sphecidae where, in the vast majority of species (including Philanthus), the males are smaller, on the average, than females. This is puzzling, given the superiority of larger males in intrasexual competition. Even though larger males show a higher reproductive success than smaller males, there must be stronger selection pressures acting on female body size which promotes larger size in most species of digger wasps.

Our studies this past summer were aimed at more fully elucidating those parameters which relate to sexual size dimorphism and variation in body size in both males and females. They included both an extension of our work with Philanthus and an investigation of females of Bembix americana obtained information on the form of the mating strategy of Philanthus bicinctus, P. crabroniformis, P. pacificus and P. zebratus. We also extended our knowledge of the nesting biology of several species of Philanthus.

Methods

Philanthus pulcher was studied at 6.5 km WNW of the Moran P.O., Teton Co., Wyoming. P. zebratus was studied at 14 km SW of the Moran P.O., Teton Co., Wyoming and at Huckleberry Hot Springs. P. crabroniformis and Bembix americana were studied at Huckleberry Hot Springs.

In the lab, head width was used as an indication of body size and was measured to the nearest 0.05 mm with a VWR Scientific Products Micro-meter. In the field, head width was measured to the nearest 0.1 mm. After the ovaries were removed from the females, the length of the terminal oocytes (developing eggs) on all six ovarioles was measured,

when possible. Deteriorated eggs and those disrupted during dissection were not included in the analysis. In the first species dissected (P. zebratus), all six terminal eggs were not always measured since smaller eggs were often hidden between larger ones. In subsequent dissections, the ovarioles were teased apart so that all of the terminal oocytes were visible. The eggs were measured along their major axis under a dissecting microscope equipped with an ocular micrometer. For ease of analysis and to reduce rounding error, the units of egg length are presented as micrometer units (MU), each of which equals 0.4 mm. For egg size analysis, live females were placed in 70% ethanol immediately after collection and transferred to Kahle's solution within several hours. All females were dissected within several weeks of collecting.

The prey used in the analysis were taken from females at their nest entrances as they returned from foraging flights. After drying prey in an oven to a stable weight, mass of each insect was determined to the nearest 0.01 mg on a Mettler H51AR analytical balance. Statistical methods were derived from Zar (1974).

Results

Degree and Direction of Sexual Dimorphism. In all three species for which egg size was analysed, although the size ranges of the sexes overlap, females were significantly larger than males on average. Females of Philanthus zebratus, P. pulcher, and Bembix americana had mean head widths of 3.81 mm (S.D.=0.18; N=120), 2.73 mm (S.D.=0.18; N=98) and 4.5 mm (S.D.=0.30; N=54), respectively. The mean head widths for males were 3.24 mm (S.D.=0.21; N=179), 2.33 mm (S.D.=0.22; N=262), and 4.38 mm (S.D.=0.16; N=57), respectively. All intraspecific comparisons showed significant differences between size of the sexes (t-test; $P < 0.01$).

Head width is a convenient and reliable measure of body size in the field and is itself highly significantly correlated with two other body size parameters which are biologically important to the questions asked here. In P. zebratus, dry mass and head width are highly significantly correlated in both males ($r=0.93$; N=30; $P < 0.001$) and females ($r=0.97$; N=23; $P < 0.001$). Linear regression analysis indicates that females of mean size of this species weigh 74% more than males of mean size. In addition, female head width is highly significantly correlated with abdomen width across the 2nd tergite in P. zebratus ($r=0.97$; N=27; $P < 0.001$), P. pulcher ($r=0.97$; N=23; $P < 0.001$). The size of the abdomen of females should place spatial constraints upon the size of eggs she can carry. Abdomen size varies considerably within females of a given species.

Investigation of Egg Size. Females of Philanthus and Bembix have ovaries of three ovarioles each. The ovarioles are polytrophic, with alternating trophocytes (nurse cells) and oocytes (developing eggs). The latter become larger towards the terminal (posterior) segments of the ovarioles. Sphecids generally have no more than two mature oocytes in the abdomen at any one time. Preliminary dissections of females suggested that there

may be limitations on egg size, simply because of limitations of available space in the abdomen. All females dissected, except those that had recently emerged, showed the same crowding of organs in the abdomen. The posterior half of the abdomen is completely filled with the digestive tract (exclusive of the crop), the large poison sac, fat bodies, and the Malpighian tubules. The latter occupy most of the space amidst the convoluted gut. The ventral, anterior portion of the abdomen is dominated by the crop, which when inflated with nectar (as it was in all females dissected), pushes the ovaries against the dorsal abdominal wall. The large terminal oocytes press against the material in the posterior portion of the abdomen. Given these observations, it was hypothesized that limitations on egg size that result from packing of organs in the abdomen might be a major selective pressure affecting female size. One major implication of this is that there should be a positive correlation between egg size and female size within the species of Philanthus and Bembix.

Forty-one females of P. zebratus were dissected for egg size analysis. The largest egg carried by a female ranged in size from 5.2 M.U. to 10.5 M.U. and had a mean of 8.10 M.U. ($=3.24$ mm; S.D.=0.97). For each of the five largest eggs of females dissected, there was a significant correlation between female size and total length of the six terminal oocytes (table 1). Two eggs layed on prey and extracted from nests by H. E. Evans measured 10.0 M.U. and 11.0 M.U. The eggs of three of the four smallest nesting females dissected were packed together and misshapen (i.e. were not generally cylindrical with hemispherical ends). On the other hand, eggs of larger females were often well-separated and symmetrical in form.

Eighteen females of P. pulcher that were carrying prey were dissected for egg size analysis. The size of the largest oocyte carried by females ranged from 5.2 M.U. to 7.2 M.U. with a mean of 6.05 M.U. ($=2.42$ mm; S.D.=1.03 M.U.). There were significant correlations between the size of the largest, third largest, and fourth largest oocytes and female size, but not for the other eggs or for the total length of the six terminal oocytes (table 1).

Thirty females of Bembix americana were dissected for egg size analysis, none of which were carrying prey. The size of the largest oocyte ranged from 6.5 M.U. to 12.1 M.U. with a mean of 10.1 M.U. ($=4.04$ mm; S.D.=1.27 M.U.). Female size-egg size correlations were significant for each of the four largest oocytes and for total oocyte length (table 1).

Investigation of prey size. Alternative to or in conjunction with the advantage accrued by large females due to the size of their eggs, they may be able to provision their nests with larger prey. In Jackson Hole, both P. zebratus and P. pulcher are generalists, preying on a wide variety of Hymenoptera. The prey vary considerably not only in size, but in shape (from long slender parasitic wasps to shorter, but stouter bees). For P. zebratus there was a low but significant correlation between female size and prey size ($r=0.23$; $N=98$; $P<0.05$).

Table 1. Female size-egg size correlations for the three species studies.

Species	Terminal Oocyte (Size Rank ^b)						Total Length
	1	2	3	4	5	6	
<u>P. zebratus</u>	r^a	0.87	0.54	0.64	0.64	0.48	0.78
	N	41	41	41	39	28	28
	Prob. ^c	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.05$	$P < 0.001$
<u>P. pulcher</u>	r^a	0.62	0.23	0.49	0.54	0.29	0.46
	N	18	18	18	18	18	18
	Prob. ^c	$P < 0.01$	N.S.	$P < 0.05$	$P < 0.05$	N.S.	N.S.
<u>B. americana</u>	r^a	0.63	0.62	0.37	0.39	0.28	0.66
	N	30	30	30	30	30	27
	Prob. ^c	$P < 0.001$	$P < 0.001$	$P < 0.05$	$P < 0.05$	N.S.	$P < 0.001$

^a Pearson's r for relationship between female head width and terminal oocyte length.

^b Number 1 indicate largest egg.

^c (Zar, 1974).

Considering only the three largest prey taken by females the correlation coefficient is higher ($r=0.47$; $N=24$; $P<0.05$). The data for P. pulcher show a more significant trend for all prey ($r=0.44$; $N=142$; $P<0.001$) and for the three largest prey taken by each size class ($r=0.95$; $N=21$; $P<0.001$).

Studies on Male Body Size and Mating Strategies. We continued our investigation of the mating strategy of P. zebratus, by examining a newly discovered population of this species at Huckleberry Hot Springs. The mating strategy of males in this population was similar to that in the Deadman's Bar population in both form and the role of male body size variability. The latter population was also studied this year, in a continuation of our previous work. Interestingly, we failed to find territorial males in this population although large numbers of males were present in the nesting area. We also expanded our studies of male Philanthus to include P. crabroniformis. Males of this species defend territories in a manner similar to what we have discovered in other species of this genus: they scent-mark territories for the purpose of attracting females and defend the territories from conspecific males via intense physical aggression. The investigation of male body size - territorial success correlations indicate, as we have seen in other Philanthus, that larger males are more successful than smaller males. For example, in 27 observed aggressive interactions between males of known size, the larger male always won and expelled the smaller male. Unlike the situation in territorial birds, there was no resident advantage during aggressive interactions. Small males readily occupied territories from which large residents have been removed. All males which replaced males we had removed from territories were smaller than the original resident ($N=31$).

Miscellaneous Observations. We confirmed that males of P. pacificus and P. bicinctus in Jackson Hole are also territorial and scent-mark territories. Nest structure and prey records were obtained for P. zebratus, P. pulcher and P. crabroniformis females. Steniolia obliqua behavior was not investigated, as we had proposed, since the nesting area which we had previously studied was flooded in June of this year. An extensive search for other nesting areas and clusters of males proved fruitless.

Dr. Brian Freeman, of the University of the West Indies at Kingston, Jamaica, was a guest of Howard Evans for two weeks. He observed and assisted in the field work on Philanthus and Bembix and also conducted a study of an aggregation of wasps (chiefly Crabro latipes) which occurred each sunny day in the bushes around the laboratory building. A short paper on this has been submitted for publication.

Conclusions

There may be no other "trait" of a metazoan animal that is influenced by a larger number of parameters (developmental, genetic, and environmental),

than its body size. Therefore, concentrating upon single selection pressures may have the effect of overly narrowing one's outlook on the evolution of such a trait. However, if we keep this in mind, as well as, the fact that we may be dealing with spurious correlations at times, investigation of selective pressures which seem particularly important ultimate determinants of body size can be very useful.

Most of the adult lifetime of a female sphecid wasp is involved in building a nest and provisioning it with paralyzed insects to be used as food by the developing larvae. Nutritional investment in offspring is in the form of this prey and an egg, which is relatively larger in those Hymenoptera (such as Sphecids) which exhibit advance parental care (Itô, 1978). Offspring size and, presumably, survivability is dependent upon the amount of nutritional investment. It can thus be hypothesized that if large females can supply greater amounts of this investment than do small conspecific females, then the ability to lay larger eggs and provide larger prey may be an important selective pressure favoring large size in female sphecids. The above data on the relationship of female size to prey and egg size generally support this hypothesis.

Sexual size dimorphism is a common phenomenon in insects but has not been treated much in the literature except in terms of a basic description of its extent in various species. We are treating sexual dimorphism as an epiphenomenon, a result of differential selective pressures on the two sexes. Our studies on P. zebratus, P. pulcher, and P. crabroniformis in Jackson Hole and on P. basilaris in southern Colorado (O'Neill, unpublished) show that large males compete more successfully for mates than small males. However, females of these species are larger than males, probably because of selective pressures on body size that are related to parental investments. In both P. pulcher and P. zebratus the smallest females seen to nest were larger than the mean male size, but still at a disadvantage compared to larger females, in terms of egg and prey size.

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