



Sex ratio variation as a function of host size in *Pseudacteon* flies (Diptera: Phoridae), parasitoids of *Solenopsis* fire ants (Hymenoptera: Formicidae)

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Some *Pseudacteon* (Diptera: Phoridae) flies are parasitoids of *Solenopsis* (Hymenoptera: Formicidae) ant workers in North and South America. Laboratory studies of sex allocation revealed a pattern of sex ratio variation as a function of host size, with more females arising from larger hosts. Environmental sex determination is a possible mechanism for the observed pattern, and examination of *Pseudacteon* life history reveals several traits assumed to be important in models predicting conditions under which environmental sex determination is favoured. Sex allocation patterns of *Pseudacteon* are compared with theoretical predictions and empirical data from better-studied hymenopteran parasitoids that have haplodiploid sex determination. The pattern of sex ratio variation observed has important implications for biocontrol efforts of imported *Solenopsis* fire ants by the introduction of *Pseudacteon* parasitoids.

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ADDITIONAL KEY WORDS: biocontrol Brazil environmental sex determination parasite sex allocation Texas.

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INTRODUCTION

The ability of an organism to pass its genes on to future generations is affected to a significant degree by the sex ratio of its offspring, which accordingly, should be under strong selective pressure (Fisher, 1930; Hamilton, 1967; Charnov, 1982). The optimal sex ratio may vary according to environmental conditions, however, so that selection should favour mechanisms which allow the sex ratio to change in response to changing environmental variables (Trivers & Willard, 1973; Charnov *et al.*, 1981).

If the amount of resources available to offspring differentially affects the development of males versus females, and resources are distributed in discrete patches, selection should favour a mechanism which allows the sex of offspring to be matched to the appropriate patch type. Host quality models developed for solitary (one egg per host) hymenopteran parasitoids predict that mothers should produce more daughters in larger hosts (Charnov *et al.*, 1981; Werren, 1984), assuming that females gain more reproductive success than males from being large.

Although these host quality models were developed for parasitoid wasps in which haplodiploid sex determination provides a mechanism for sex ratio manipulation, the general argument that more daughters should be produced in larger hosts can be extended to other solitary parasitoids, and also to other mechanisms of sex determination (Bull, 1981).

We have recently obtained evidence for sex ratio variation as a function of host size in *Pseudacteon* flies (Diptera: Phoridae) that are parasitoids of *Solenopsis* fire ants (Hymenoptera: Formicidae). *Solenopsis* workers are highly polymorphic with the largest workers being almost three times the length of the smallest workers (Porter & Tschinkel, 1985). Adult *Pseudacteon* females oviposit on foraging workers in rapid aerial attacks, injecting a single egg into a worker's thorax with a hypodermic-style ovipositor. The larva migrates to the worker's head where pupariation occurs, resulting in death of the ant (Porter *et al.*, 1995a). Fecundity in *Pseudacteon* is of the order of several hundred eggs (S. D. Porter, unpublished data), and females have been observed to attack at rates of several workers per minute under laboratory conditions (Morrison, Dall'Aglio-Holvorcem & Gilbert, 1997; Gilbert & Morrison, 1997). All *Pseudacteon* species studied to date are solitary parasitoids.

Although an estimated 20% (or 16000 species) of all dipterans are parasitoids (Eggleton & Belshaw, 1992), this is the first documented case, to our knowledge, of sex ratio variation as a function of host size in this group. Although the mechanism producing the observed sex ratios has yet to be conclusively determined, environmental sex determination (ESD) appears to be the most likely possibility. In laboratory cultures of the phorid *Megaselia scalaris* the sex ratio of emerging adults seemed to be influenced by temperature (Disney, 1994). Otherwise, published evidence of ESD in insects appears to be very rare.

METHODS

Two *Pseudacteon* species, *P. tricuspis* and *P. litoralis*, oviposited on *Solenopsis saevissima* complex (*S. invicta* and *S. saevissima*) workers in the field in Brazil, where both the flies and ants are native. Worker ants were placed out in 40 × 26 × 8 cm trays at two sites in Brazil: Rio Claro and Jaguariuna, both in São Paulo State. At each site,

trays with 3000–10000 workers from different colonies were set out at intervals of 10–60 m for periods of several hours over 3–5 days. A small inverted box under which workers tended to congregate was placed in each tray. Moving the box from one side of the tray to the other as soon as most ants had gone under it resulted in a constant movement of workers that were vulnerable to phorid ovipositions.

Three different *Solenopsis* colonies were used at Rio Claro: One colony was keyed to *S. invicta* Buren, but the other two colonies were ambiguous between *S. invicta* and *S. saevissima* (F. Smith), according to the morphological characters in Trager's (1991) key. At Jaguariuna, eight different colonies were used: four colonies keyed to *S. invicta* and four colonies were ambiguous between *S. invicta* and *S. saevissima*. Studies were conducted at Rio Claro in May of 1996 and at Jaguariuna in June of 1996. *P. tricuspis* was present at both sites, while *P. litoralis* was present only at Rio Claro.

Solenopsis invicta has been introduced to North America, but *Pseudacteon* species that are parasitic on *S. invicta* are absent. We imported *Pseudacteon* flies from Brazil to Texas to allow them to parasitize North American populations of *S. invicta* in the laboratory. *P. tricuspis* and *P. litoralis* adult females were collected from a residential area near the University of Campinas (UNICAMP), São Paulo State, Brazil and transported to Austin, Texas, where they were placed in flight chambers containing a random selection of approximately 500 *S. invicta* workers collected from Travis County, Texas. All trials were conducted in the containment facility at The University of Texas' Brackenridge Field Laboratory from November 1995 to November 1996.

In the laboratory tests, *Pseudacteon* females were introduced into flight chambers one at a time and allowed to oviposit for 20 to 60 min. Workers that were attacked were immediately removed from the trays and replaced with fresh workers of a similar size range from the same *S. invicta* colony. (See Morrison *et al.*, 1997 for a more detailed description of the laboratory set-up.)

Adult phorids were reared from the parasitized workers as in Porter *et al.* (1995a) and Morrison *et al.* (1997). At both sites in Brazil, flies were subsampled from pupae that were collected over a period of about a week. Parasitized workers from Rio Claro were kept segregated according to colony of origin during phorid development, but parasitized workers from Jaguariuna were not. Head width was used as an indicator of worker ant size; mesonotum width was used as an indicator of phorid size.

RESULTS

P. litoralis is larger than *P. tricuspis* (0.55 ± 0.05 [mean \pm SD] vs. 0.50 ± 0.04 mm, mean adult female thorax width; Morrison *et al.* [1997]), and overall, *P. litoralis* parasitized significantly larger workers than *P. tricuspis* (1.13 ± 0.13 [mean \pm SD] vs. 0.95 ± 0.13 mm; $t = 12.4$, $df = 376$, $P < 0.0001$).

Pseudacteon offspring size was directly related to the size of the worker ant host (Fig. 1). Furthermore, more female offspring were produced from larger workers (Fig. 2, Table 1). This was true for both species of *Pseudacteon*, in Texas and Brazil.

For both *P. tricuspis* and *P. litoralis*, the effect of sex was highly significant but there were no significant differences among sites (Rio Claro, Jaguariuna, and Texas for *P. tricuspis*; Rio Claro and Texas for *P. litoralis*) in a two-way ANOVA (Table 2, top). The interaction terms were not significant. Among the three different colonies used

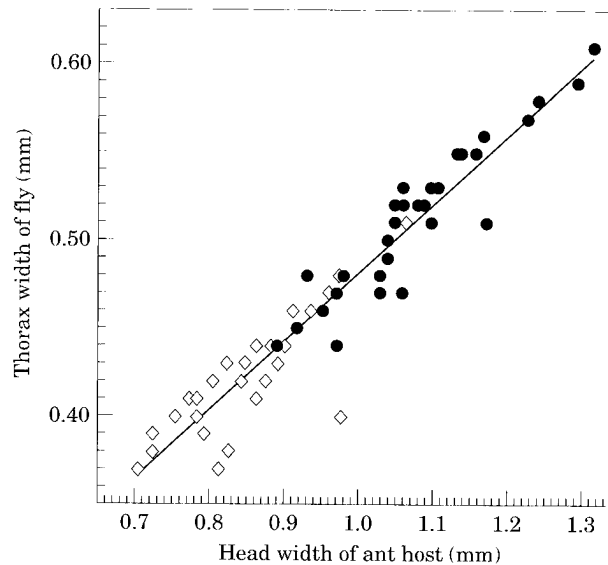


Figure 1. Correlation between host worker ant size and size of emerging phorid parasitoids for *Pseudacteon tricuspis* on *S. saevissima* complex workers from Brazil. Note that males (\diamond) and females (\bullet) both fall on the same regression line ($y=0.390x+0.0917$, $r^2=0.91$). Patterns for *P. tricuspis* and *P. litoralis* on North American *S. invicta* workers are similar (Morrison & Gilbert, 1998).

at Rio Claro, the effect of sex was significant, but there were no significant differences among the three colonies in a two-way ANOVA, for both *Pseudacteon* species (Table 2, bottom). Again, there was no significant interaction.

Given that the different sites encompass two different continents, two different host ant species, and a number of different ant colonies, the observed patterns of sex ratio variation as a function of host size appear to be a very robust feature of this parasite-host relationship.

Sex ratios of emergent phorids when a wide size range of hosts were available approached 50:50 for both *Pseudacteon* species in Brazil and Texas. Proportions of male offspring produced were 0.52 (*P. tricuspis*, Brazil), 0.53 (*P. tricuspis*, Texas), 0.48 (*P. litoralis*, Brazil), and 0.56 (*P. litoralis*, Texas). In laboratory tests in Texas we have found that providing *P. tricuspis* with a limited range of relatively small workers resulted in male-biased sex ratios, while providing a limited range of relatively large workers produced female-biased sex ratios (L. W. Morrison, unpublished data).

Although wild-caught females were used to infect worker ants in the experiments described above, we also reared females from infected workers in the lab and exposed these virgin females to worker ants. Fifteen unmated females were observed to attack >100 worker ants in the usual fashion in an attempt to oviposit, but no larval development was observed in any of the attacked workers.

DISCUSSION

Host quality models

Although parasitoids occur in five orders of holometabolous insects (Hymenoptera, Diptera, Coleoptera, Lepidoptera and Neuroptera) (Eggleton & Belshaw, 1992), the

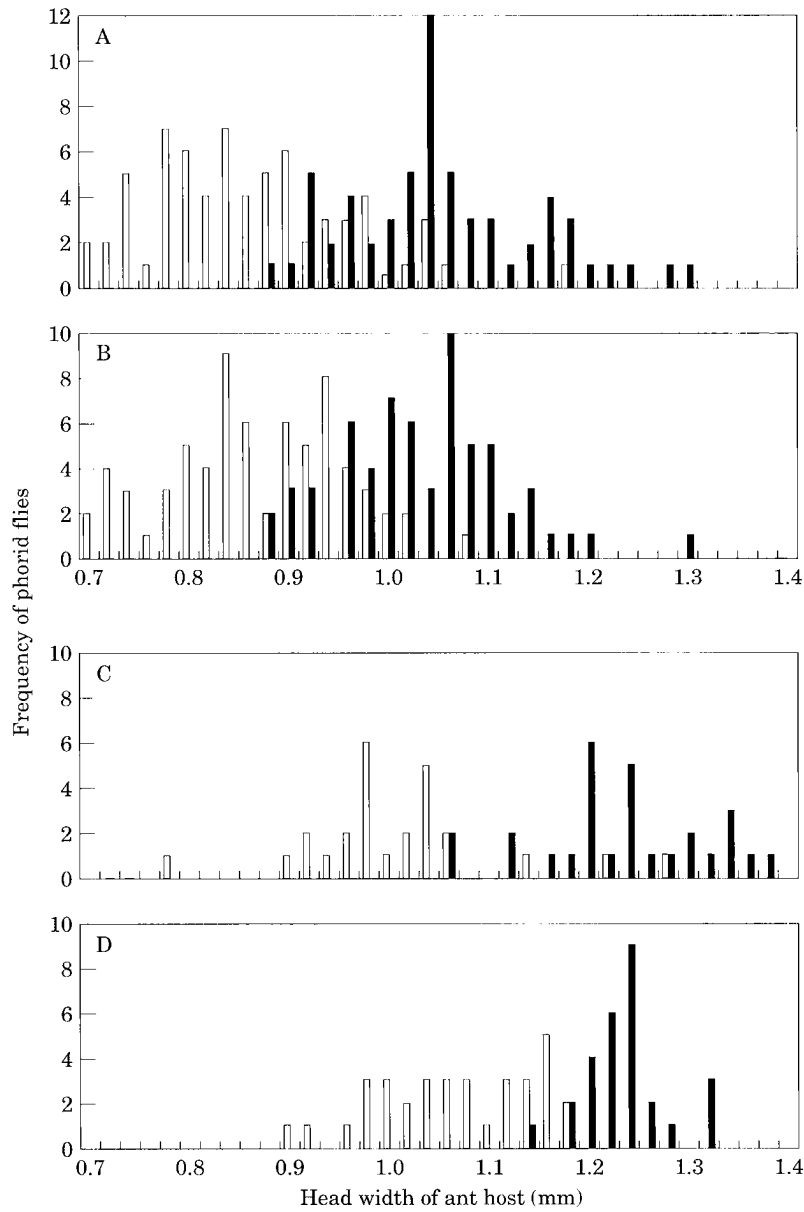


Figure 2. Distribution of male (\square) and female (\blacksquare) *Pseudacteon* flies as a function of host worker ant head width in *P. tricuspis* (top) and *P. littoralis* (bottom). A & C, Brazil; B & D, Texas.

majority of estimated parasitoid species are hymenopterans. Hymenopterans have also been the subject of almost all recent research on insect parasitoids (Feener & Brown, 1997). Yet hymenopterans possess a number of unique characteristics (i.e. haplodiploidy) (reviewed in Feener & Brown, 1997) that necessitate the study of other taxonomic groups before we obtain a general understanding of the parasitoid life-style. At this point, it is of interest to compare the predictions of theoretical

TABLE 1. Head widths of *Solenopsis* worker ants from which *Pseudacteon* phorids emerged. Numbers represent mean \pm SD

Location	Females	Males
<i>P. tricuspis</i>		
SE Brazil	1.06 \pm 0.10	0.87 \pm 0.10
Texas, U.S.A.	1.03 \pm 0.08	0.87 \pm 0.09
<i>P. littoralis</i>		
SE Brazil	1.21 \pm 0.13	1.01 \pm 0.10
Texas, U.S.A.	1.22 \pm 0.05	1.07 \pm 0.09

TABLE 2. Two-way ANOVAs of all data (Texas, Jaguariuma, and Rio Claro) and data from Rio Claro only

Effect	<i>F</i>	df	<i>P</i>
All data:			
<i>P. tricuspis</i>			
Sex	222.22	1	0.0001
Site	1.30	2	0.2754
Sex X Site	1.22	2	0.2961
<i>P. littoralis</i>			
Sex	97.00	1	0.0001
Site	2.79	1	0.0974
Sex X Site	2.10	1	0.1497
Rio Claro (Brazil) only:			
<i>P. tricuspis</i>			
Sex	20.76	1	0.0001
Colony	0.14	2	0.8733
Sex X Colony	0.16	2	0.8508
<i>P. littoralis</i>			
Sex	6.94	1	0.0115
Colony	1.40	2	0.2582
Sex X Colony	0.49	2	0.6144

models and accumulated empirical data generated from studies of hymenopteran parasitoids to what we know about *Pseudacteon* parasitoids.

Host quality models developed for solitary hymenopteran parasitoids explain how maternal control of offspring sex ratio may be an adaptive response to host characteristics such as size. Such models predict that more daughters should be produced in larger hosts, based on the assumption that larger hosts confer more to the ultimate reproductive success of females than males relative to smaller hosts (Charnov *et al.*, 1981; Werren, 1984). This may happen if host size is positively correlated with parasitoid offspring size, and if parasitoid size increases the reproductive success of females more than the reproductive success of males (Charnov *et al.*, 1981).

Many empirical studies of solitary parasitic Hymenoptera have demonstrated that more daughters do, in fact, arise from larger hosts (Charnov, 1982; Clausen, 1939; King, 1987). In most parasitic Hymenoptera species studied, females are larger than males (Hurlbutt, 1987), and a positive relationship between host size and parasitoid

offspring size has been documented for a number of solitary species (King, 1987). While it is very difficult to prove that females suffer more than males from being small, limited laboratory studies have found that females gained more fitness than males with increasing wasp size (Jones, 1982; van den Assem, van Iersel & Losden Hartogh, 1989; Heinz, 1991).

In the *Pseudacteon* species studied, females are larger than males and parasitoid size is positively correlated with host ant worker size (Fig. 1; Morrison & Gilbert, 1998). Although relative fitness gains of each sex with increasing size have not been measured, it is not unlikely that females benefit more than males from large size. For example, larger females may have more eggs, a longer life span, and be able to sustain longer periods of flight and longer oviposition bouts on worker ants. Whereas larger males may benefit from a longer life span and a size advantage in competition for mates, it is certainly plausible that the relative benefit of large size may not be as great to males as to females.

Sex determination mechanisms

Genetic sex determination with differential mortality

Differential mortality during larval development could produce the observed results if mortality was relatively higher for males in larger hosts and for females in smaller hosts. This possibility does not appear likely, however, because only 15–20% of mature larvae fail to pupate; this mortality rate is much less than the 40–50% mortality rates that would be required to achieve the observed size frequency distributions. Differential mortality could also occur in very young larvae, but it is unclear why they would die before food became limited. If food is a limiting factor, female offspring might experience higher mortality rates in smaller hosts, which provide relatively less nutrition, but there is no obvious reason why males should suffer greater mortality in larger hosts.

Maternal control

In most parasitoid hymenopteran species, females control the sex of their offspring by storing sperm after mating and regulating the access of sperm to eggs (i.e. haplodiploidy). Fertilized eggs become females and unfertilized eggs become males (Werren, 1987). This mechanism of maternal sex determination allows females to match the sex of their offspring to the size of a resource patch.

In insects, haplodiploidy is common among the Hymenoptera and Thysanoptera, but is rare among other orders. It is not known from any Diptera with the exception of the Cecidomyiidae, in which it is limited to a few species and embedded in a complex life history with paedogenesis (Bull, 1983). Information on chromosome number is available for only two species of Phoridae: *Megaselia scalaris* and *M. spiracularis*. In *M. scalaris*, females are larger than males, which are both diploid ($n=3$), and sex is determined by a transposable epistatic male determining factor (Mainx, 1964; Traut, Khuong & Schneider, 1990; Traut & Willhoeft, 1990). *M. spiracularis* also has three regular chromosome pairs, of a similar structure to those of *M. scalaris* (Wolf, Mitchell & Liu, 1996). Transposable elements, including such maleness factors, are not unusual among dipterans (Green, 1980).

Virgin females of a large number of haplodiploid species are known to readily reproduce in the laboratory, producing only male progeny (Godfray & Hardy, 1993). The fact that virgin *Pseudacteon* females were observed attempting to oviposit on worker ants but no larval development followed is evidence against haplodiploidy as the mechanism responsible for the observed phenomenon.

Other, apparently less common, mechanisms of maternal control of offspring sex ratio have been documented in various animal groups, such as the XX/XO system of sex determination in aphids (Morgan, 1909; Blackman, 1987), and the effect of territory quality and number of 'helpers' in the Seychelles warbler (Komdeur *et al.*, 1997).

Environmental sex determination

Environmental sex determination (ESD) differs from genotypic sex determination (GSD) in the degree to which an environmental factor overwhelms genetic differences in the ontogeny of sex. Clear cases of ESD are rare, and operative environmental factors are diverse. These include larval-settling substrate in marine echinurid worms, host crowding and nutritional status in parasitic Mermithid nematodes, photoperiod in brackish-water amphipods, and temperature in reptiles (Bull, 1983).

It has been proposed that ESD is favoured when: (a) offspring enter a patchy environment that has a lasting effect on fitness, some patches conferring a greater advantage on one sex than the other, and vice versa; and (b) neither parents nor offspring exercise much control over which patch type the offspring enters (Charnov & Bull, 1977). ESD is favoured under these conditions because GSD would result in a large number of offspring entering a patch that is more favourable for development of the opposite sex.

Pseudacteon life history fits most of the conditions of this model: (a) Resources (in the form of individual ants) are patchily distributed and may have differential value to males and females because of large differences in size. An offspring in a small host ant, for example, could become an average male or a below average female, so selection should favour it becoming a male. (b) Offspring cannot choose their patch, nor escape during development. Adult females, however, do have some control over patch choice. In laboratory experiments, when adult females were provided with hundreds of potential hosts of various sizes (with no refuges from parasitism), different *Pseudacteon* species exhibited significantly different host size preferences (Morrison *et al.*, 1997), indicating *Pseudacteon* females are able to discriminate host size (see also Feener, 1987). In general, if parents are able to discriminate patch quality and control which patch their offspring enters, selection may favour a mechanism of maternal control of sex determination (Charnov & Bull, 1977). In nature, however, an abundance of prospective hosts may be the exception rather than the rule. *Solenopsis* species exhibit defensive behaviours in the presence of *Pseudacteon* species such as absconding and a curled body posture which are apparently effective in avoiding parasitism (Feener, 1987; Feener & Brown, 1992; Orr *et al.*, 1995; Porter *et al.*, 1995b). Thus, it may be that much of the time prospective hosts are limited, and *Pseudacteon* females have few options regarding host choice.

The relatively sharp transition between the sexes as a function of host size as plotted in Figure 2 may also be interpreted as providing support for ESD. Charnov *et al.*'s (1981) model of sex allocation for Hymenoptera with maternal control predicts

a critical threshold should exist, below which size all eggs laid should be male and above which all eggs laid should be female, creating a step function. Yet it is relative, rather than absolute host size which is important, and the critical size threshold will change spatially and temporally, depending upon the range of host sizes available in the environment. Even different individuals parasitizing the same population of hosts may differ in their estimation of host distribution. Thus, almost all data sets from hymenopteran parasitoids reveal a gradual, rather than abrupt transition when offspring sex is plotted as a function of host size (Godfray, 1994). In theory, the broader the spatiotemporal dimensions over which the data are collected, the more overlap would be expected. In the present case, if ESD is the operative mechanism, one may still expect to find a region along the host size continuum where both males and females could arise. The width of this region would depend upon the exact nature of the mechanism, but would not change with variation in relative host size. The relative stability of offspring sex as a function of host size documented in this study compared to the broad spatiotemporal dimensions over which the data were gathered suggests that it is absolute, rather than relative host size that is important.

Implications

Pseudacteon spp. native to North and South America may be important in regulating populations of *Solenopsis* fire ants, and *Pseudacteon* spp. from South America have been proposed as biological control agents for imported fire ants in the southeastern U.S. (Fecner & Brown, 1992; Orr *et al.*, 1995; Porter *et al.*, 1995b). The results of this study have important implications for biological control efforts: specifically, it should be possible to control the sex ratio of laboratory-reared flies by manipulating the size distribution of worker ants available for oviposition. Another consideration is that introducing multiple *Pseudacteon* species should put more parasitism pressure on pest *Solenopsis* species than introducing a single *Pseudacteon* species, because variation exists in the size range of workers attacked by different *Pseudacteon* species (Morrison *et al.*, 1997). Additionally, because worker size is usually larger in monogyne (single queen) than polygyne (multiple queen) colonies (Greenberg *et al.*, 1985; Porter, 1992), *Pseudacteon* species such as *P. litoralis* that parasitize larger workers would be better suited to monogyne forms of *S. invicta* (Morrison & Gilbert, 1998).

Finally, if ESD is the operative mechanism, it would reinforce the high species-specificity of this parasitoid. In this case, *Pseudacteon* species could not easily 'switch over' to other ant species which are monomorphic, or even polymorphic but with a larger or smaller worker size range than that found in *S. invicta*, because such hosts may not allow the production of both sexes.

Providing conclusive evidence for the mechanism of sex determination in *Pseudacteon* may be difficult. Karyotyping could reveal the presence or absence of haplodiploidy or other mechanisms of sex determination involving variation in chromosome number. Yet the existence of other mechanisms of maternal control (perhaps previously unknown) would remain as distinct, however unlikely, possibilities. Experimentally transplanting *Pseudacteon* eggs or early instars between different size ant hosts would provide an experimental test of ESD. Such experimental manipulations present an interesting challenge, however, because of the small size of eggs and first instars, and the difficulty of transferring them from one living host to another.

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