ARTICLE

Male mating behaviour reduces the risk of sexual cannibalism in an Australian praying mantid

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Abstract In cases where sexual cannibalism represents a sexual conflict, we should expect to find male traits that reduce the risk of cannibalism. In fact, a wide variety of such traits have been proposed, including elaborate courtship displays, cautious approach behaviours, and opportunistic mating whilst a female is feeding. However, there is very little direct evidence that these behaviours actually reduce the risk of sexual cannibalism for males, and the evidence that does exist comes mainly from spider studies. In this study of *Pseudomantis albofimbriata* praying mantids we found evidence of various male behaviours that reduced the risk of sexual cannibalism. Most males attempted to avoid detection entirely and others moved in a slow and stealthy manner. We also observed five cases of opportunistic mating, but saw no evidence of any male courtship routine. It seems that mounting from the rear of a female or slowly approaching her from the front, allows many males to go unnoticed and, therefore, substantially reduces the risk of sexual cannibalism in this mating system. Interestingly, we could not identify any female traits that males use to assess the risk of sexual cannibalism. It may be that *P. albofimbriata* males use alternative means to assess these risks. The presence of these behavioural strategies by males suggests a net cost of being consumed, and that sexual cannibalism is likely to be a female strategy in this system.

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Introduction

Mating systems rarely represent a totally harmonious venture to produce offspring, but are instead the result of a relationship in which individuals from each sex attempt to maximise their own reproductive fitness (Trivers 1972; Parker 1979). Asymmetric selection pressures on males and females may cause a conflict of interest, whereby behaviours that increase the lifetime reproductive success of individuals from one sex may decrease the success of individuals from the other (Arnqvist and Rowe 2005; Tregenza et al. 2006). Sexual cannibalism, where females attack and consume approaching and/or courting males before, during, or immediately after mating, may represent the ultimate conflict of interest between the sexes (Darwin 1871; Elgar 1992). Females may gain nutritional benefits from male consumption that consequently translate into increased fecundity (Birkhead et al. 1988; Newman and Elgar 1991; Barry et al. 2008), or they might use cannibalism as an extreme form of mate choice where only males of preferred phenotypes are allowed to copulate and sire offspring (Elgar and Nash 1988; reviewed in Prenter et al. 2006).

The fitness consequences for cannibalised males are often less obvious than one might expect, and largely depend on the timing of cannibalism in relation to insemination (Elgar and Schneider 2004). If cannibalism occurs during or after mating, a male's loss of future reproductive output may be at least partially outweighed by associated benefits. For example, males of many spider species

prolong copulation by being cannibalised, thereby increasing sperm transfer and their share of paternity (Andrade 1996; Schneider et al. 2000). However, non-copulatory cannibalism presents a substantial fitness cost to males because all present and future reproductive successes are forfeited (Buskirk et al. 1984).

In cases where sexual cannibalism represents such a sexual conflict, we should expect to find male traits that reduce the risk of cannibalism (Darwin 1871; Elgar 1992). In fact, a wide variety of such traits have been proposed, including elaborate courtship displays (Polis and Farley 1979; Liske and Davis 1987; Elgar and Nash 1988; Lelito and Brown 2006), cautious approach behaviours (Roeder 1935; Liske and Davis 1987; Maxwell 1999b; Lelito and Brown 2006), and opportunistic mating whilst a female is feeding (Prenter et al. 1994; Elgar and Fahey 1996; Moya-Larano et al. 2004; Fromhage and Schneider 2005; Gemeno and Claramunt 2006). However, there is very little direct evidence that these behaviours actually reduce the risk of sexual cannibalism for males, and the evidence that does exist comes mainly from studies of spiders (Moya-Larano et al. 2004; Fromhage and Schneider 2005). For example, Fromhage and Schneider (2005) found that opportunistic mating with feeding females greatly reduced the risk of cannibalism and injury for male *Nephila fenestrata*.

Here we describe all aspects of male mating behaviour in the sexually cannibalistic praying mantid *Pseudomantis albofimbriata*, paying particular attention to those behaviours previously implicated in risk avoidance for mantids (Liske and Davis 1987; Lawrence 1992; Maxwell 1999a, b; Barry 2004; Lelito and Brown 2006). The direction of male mount, rate of male approach, presence/frequency of male courtship display, and opportunistic mating were recorded, and the effect of each on the risk of cannibalism was determined. Although the onset of cannibalism occurs prior to copulation in this species, males are able to initiate copulation and transfer sperm while being consumed. There is also some evidence that male mantids can increase their reproductive output as a result of being consumed (Birkhead et al. 1988; Barry et al. 2008), however, mantids are capable of multiple matings and fertilisations during their lifetime (Lawrence 1992; Hurd et al. 1994; Holwell et al. 2007). Thus, cannibalism is likely to be a sexual conflict in this species, and we predict that *P. albofimbriata* males will employ one or more of the aforementioned risk-avoidance behaviours, and that these behaviours will reduce the risk of being attacked and consumed by a female conspecific. We further investigated the relationship between these male risk-avoidance behaviours and various measures of female body size, as an increase in body condition has a significant negative effect on the propensity of a female to cannibalise in this (Barry et al. 2008) and other mantid species (Buskirk et al. 1984; Liske and Davis 1984; Maxwell 2000).

Materials and methods

Collection and housing

Individual *P. albofimbriata* were collected from various sites around Sydney and Canberra, Australia, from 15 December 2005 to 6 February 2006. Most of the individuals were found in *Lomandra longifolia* bushes in Kuringai Bicentennial Park, West Pymble, and on the Australian National University campus, Canberra. Juvenile animals (usually in their antepenultimate or penultimate instar) were collected from the study sites and maintained on a diet of two small crickets *Acheta domestica* (mean cricket body mass $\pm$ SE = 0.037 $\pm$ 0.003 g, $N = 50$) three times a week and sprayed with water daily. Animals were housed individually within well-ventilated 425-mL transparent cups in the laboratory, at a temperature of 24–26°C and with a diurnal period of 10–12 light hours per day. Experiments were carried out from 15 February to 16 March 2006, each beginning at around 8 a.m. and continuing until copulation/cannibalism was complete.

Measuring and sexing mantids

The pronotum length of mantids was recorded after the final moult (mean male fixed size $\pm$ SE = 13.150 $\pm$ 0.146 mm, $N = 38$; mean female fixed size $\pm$ SE = 15.582 $\pm$ 0.187 mm, $N = 38$) and body mass was measured immediately preceding each individual's mating trial (mean male body mass $\pm$ SE = 0.265 $\pm$ 0.006 g, $N = 38$; mean female body mass $\pm$ SE = 0.665 $\pm$ 0.030 g, $N = 38$). Because pronotum length remains constant throughout adulthood and can only be influenced by feeding during the juvenile stages, it is used as a measure of fixed size. Body mass is, instead, variable and depends upon size and feeding levels during adulthood. We used the residuals of a regression of body mass over fixed size as an index of body condition (see Jakob et al. 1996 for discussion of this and other indices). The sex of *P. albofimbriata* individuals was determined from differences in adult abdomen and wing morphology (males $N = 77$, females $N = 74$).

Mating behaviour

We carried out 75 unmanipulated mating trials that allowed a description of general male mating behaviour for this species. Particular attention was paid to previously described risk-avoidance behaviours such as courtship displays, mounting from the rear of a female, increased latency to approach a female, and/or approaching and mounting whilst a female is feeding or grooming. The frequency of these behaviours, and their effect on the

occurrence of sexual cannibalism, is described. We further tested whether males use female fixed size, body mass, or body condition to assess the risk of being attacked and alter their behaviour accordingly.

Virgin males and females were randomly chosen from the laboratory population the day after feeding had occurred, so that females were neither hungry nor satiated during mating trials. On the basis of previous work with mantids, individuals become sexually mature and are receptive to mating approximately 2–3 weeks after adult emergence (Roeder 1935; Liske and Davis 1987; Birkhead et al. 1988; Lawrence 1992; Kynaston et al. 1994). We therefore chose males that were 24.95 ± 1.52 days (mean $\pm$ SE) post-adult emergence and females that were 24.25 ± 1.38 days (mean $\pm$ SE) post-adult emergence for experimentation. Because most of the mantids were collected from *Lomandra* sp. bushes in the field, we placed each experimental pair on to one of five *Lomandra longifolia* plants (approximately 1 m tall in 40-cm-diameter pots, with 2 m between each plant). Females were placed vertically on the upper portion of a plant frond and then males were placed on the plant approximately 10 min after the female and at least 20 cm behind her (to reduce the likelihood of immediate visual detection by the female). It has been suggested that the enclosed conditions created by captivity may increase the natural frequency of cannibalism because there is nothing to distract females and to hide the movements of males (Lawrence 1992; Roeder 1935). We, therefore, carried out all experiments in an open outdoor environment so as to better simulate natural conditions, while also giving males the means to escape. If an interaction did not occur within 3 h, the trial was terminated. The two males that failed to mate during their first trial were given at least five days before being paired with another female.

Data analysis

Data were analysed using SPSS 15.0 for Windows and were visually and statistically checked (Kolmogorov–Smirnov test) for normal distribution before further statistical analysis. Unless otherwise stated, all values are mean $\pm$ SE and all statistical tests are two-tailed.

Results

Although there was an interaction between the male and female in 38 out of 75 mating trials, five of these cases were excluded from the data set because the male did not visually detect the female and was attacked within a few minutes of the start time. The remaining 33 interactions consisted of: 22 copulations without cannibalism, five copulations with cannibalism (pre-copulatory cannibalism), and six cases of cannibalism with no copulation (non-copulatory cannibalism). There was no interaction between the male and female in the remaining 37 out of 75 trials. Most of these males (35/37) were still interested in the female, and slowly approached her throughout the experimentation period, but did not reach the female within the 3 h timeframe, so were excluded from the data set.

General mating behaviour

During mating trials, male mantids performed a series of pre-copulatory and copulatory behaviours. Components of male sexual behaviour typically included; oscillation of antennae in the general direction of a female; visual fixation on the female; cessation of movement; slow lateral swaying (commonly associated with depth perception in praying mantids; Kral 1999); slow rate of approach; rapid lateral swaying; a flying leap on to the female's back from 3 to 5 cm away; touching and stroking the female with antennae; bending of the terminal abdominal segments and searching movements of the cerci; and intromission of male genitalia. There was no obvious courtship routine/display exhibited by any of the males during the approach phase. Males that mounted from the front landed head-to-tail on the female, and repositioned themselves before copulation began. All matings without cannibalism ($N = 22$) occurred in the "copulatory posture", where the male forelegs grip the female pronotum, the back legs grip the female abdomen and the tip of the male abdomen is curved to the left so the genitalia are directed forward into the female genital opening. Males appeared to be safe from attack once they had mounted the female and attained the copulatory posture. At the cessation of copulation males flew away from the female to an adjacent leaf/flower, leaving a white spherical spermatophore between the female sternum and ovipositor.

Sexual cannibalism

Cannibalistic females typically attacked the head region of an approaching male, and consumed in an anterior–posterior direction. Once a male was in the female grasp, he seemed to have little chance of escape, and feeding began almost immediately. All males that were attacked and captured ($N = 11$) struggled to get away (some males tried to bite and/or grasp at the female) and subsequently attempted to copulate with their female attacker: the male back legs reached out and the same bending and searching of the abdomen seen during copulation without cannibalism began. Forty-six percent of males being cannibalised (5/11) were positioned sufficiently close to the female, gripping her abdomen with the back legs and pulling her

closer so that intromission of the male genitalia was possible (pre-copulatory cannibalism). Copulation did not seem to affect female consumption of the male—consumption of most males continued to the posterior section of the thorax, leaving the decapitated male to mate in the copulatory posture. In all but one case ($N = 4$), what remained of the male was consumed by the female after copulation had ceased. The remaining 54% of captured males were unable to initiate copulation (non-copulatory cannibalism).

Risk-avoidance behaviour and sexual cannibalism

Direction of approach

Sixty-four percent of males that interacted with a female, encountered and began their approach from the rear of that female (Fig. 1). However, during many of these rear approaches, the female turned to face the advancing male, forcing him to approach and mount from the front. The other 36% of males encountered the female from a frontal position, and none of these switched to a rear mounting during any stage of their advance.

The difference between the number of males that were cannibalised while mounting from the front (11, $N = 25$; shown in grey in Fig. 1) and those cannibalised while mounting from the rear (0, $N = 8$) was significant (Fischer's exact: $P = 0.031$; Fig. 1).

Rate of approach

Most males attempted to avoid female detection entirely—they became motionless upon sight of a female, altered their posture so that the thorax and abdomen were pressed against the substrate, and made a gradual and deliberate (sometimes imperceptible) advance in the female's direction. Generally, a male's approach took an average of 55.13 ± 7.793 min ($N = 33$) from the time of visual fixation on the female until the start of copulation or sexual cannibalism. There was no significant difference in the rate of approach by rear-mounting (48.92 ± 7.398, $N = 8$) and front-mounting males (68.63 ± 22.045, $N = 25$; t test: $T_{31} = -1.102$, $P = 0.279$). Since front-mounting males are more likely to be detected by females, we took an additional measure of approach rate for front-mounting males only (termed "latency to approach"). This was taken from the time of visual fixation on the male (by the female) until the start of copulation or sexual cannibalism.

When males mounted from the front of a female ($N = 25$), there was a general trend for the faster-moving males to be attacked and cannibalised (logistic regression: $F_{1,25} = 3.535$, $P = 0.060$; Fig. 2). Twenty-four of these females (96%) remained in the same position while males
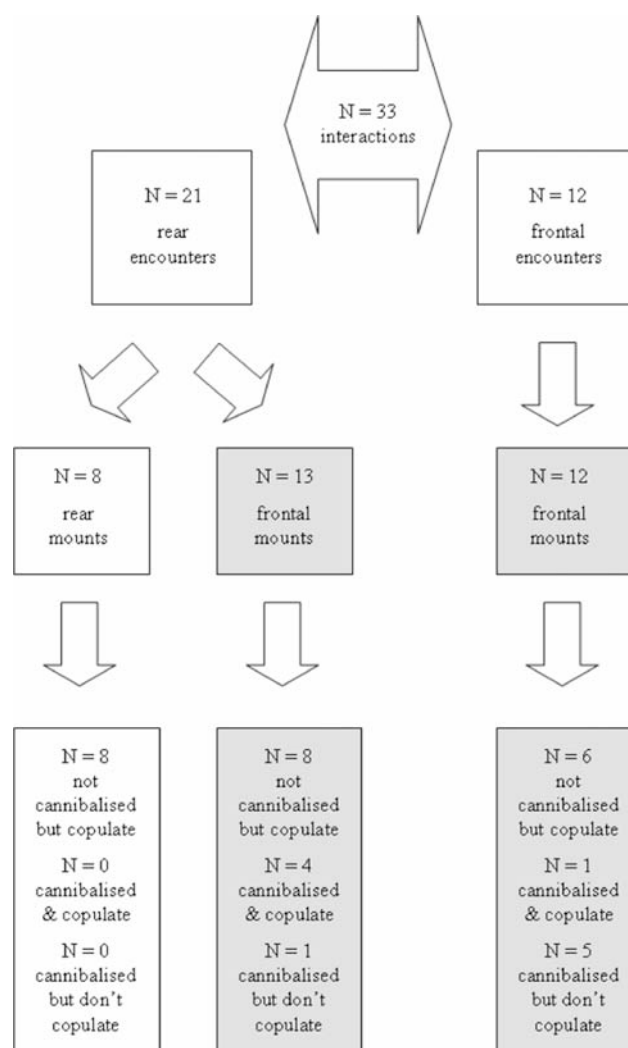

Fig. 1 Box flow chart showing the fate of males from female encounter through to cannibalism and/or copulation. Males that mount from a frontal position, regardless of the direction of encounter, are shaded in *grey*

approached from the front: they attained the usual attack posture and were often seen to sway laterally (a behaviour associated with depth perception in praying mantids; Kral 1999). The body condition of females was also a significant predictor of sexual cannibalism for males that mounted from a frontal position ($F_{1,25} = 4.882$, $P = 0.027$)—females in poorer condition were more likely to attack and cannibalise a male—however, female fixed size (pronotum length) was not ($F_{1,25} = 0.887$, $P = 0.346$).

Opportunistic mating

Opportunistic mating by an approaching male was observed in five trials: these males moved quickly towards the female and mounted while she was grooming (3/5) or feeding on a passing prey item (2/5). Three of these mounts
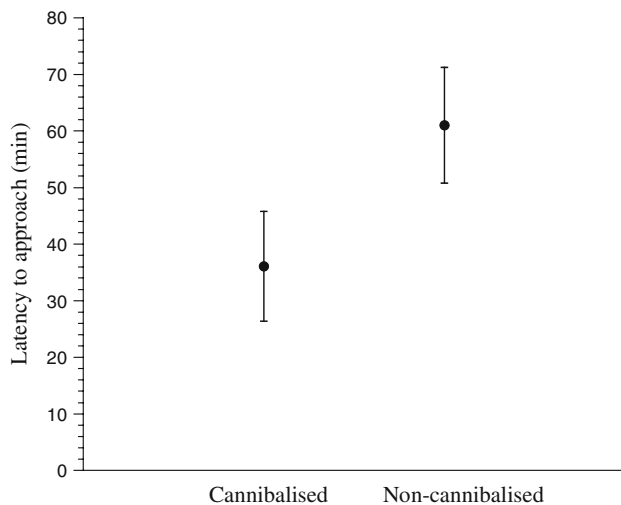
Fig. 2 Males that mounted from the front and were cannibalised ($N = 11$) took less time to approach than males that mounted from the front and survived the encounter ($N = 14$; $P = 0.060$)

occurred from a frontal position and two from a rear position. All five males copulated and survived the encounter.

Risk-avoidance behaviour and female condition

There was no significant difference in the fixed size (t test: $T_{31} = 0.550$, $P = 0.586$), body mass (t test: $T_{31} = -0.174$, $P = 0.896$), or body condition (t test: $T_{31} = -0.627$, $P = 0.535$) of females that were mounted by males from the front (fixed size $= 15.704 \pm 0.242$ mm; mass $= 0.672 \pm 0.032$ g; condition $= -0.036 \pm 0.199$; $N = 25$) or the rear (fixed size $= 15.440 \pm 0.379$ mm; mass $= 0.685 \pm 0.0493$ g; condition $= 0.237 \pm 0.460$; $N = 8$). Latency to approach a female from the front was not related to any measure of her body size (Pearson's (fixed size): $R = -0.217$, $N = 25$, $P = 0.296$; Pearson's (mass): $R = -0.158$, $N = 25$, $P = 0.450$; Pearson's (condition): $R = 0.000$, $N = 25$, $P = 0.999$).

Discussion

Male *P. albofimbriata* employ many of the behavioural traits previously implicated in risk-avoidance for mantids (see Maxwell 1999a for review), and many of these traits significantly reduce the risk of being attacked and consumed by female conspecifics. Risk-avoidance behaviours were most obvious during the approach phase, where males attempted to avoid detection entirely—they ceased movement upon sight of a female, made a slow (sometimes imperceptible) advance in her direction, and typically began their approach from the rear. Those that mounted from behind the female were significantly less likely to be attacked than those that mounted from in front of her. Most other previously studied mantid species show a similar tendency for males to approach from the rear (Roeder 1935; Birkhead et al. 1988; Maxwell 1995, 1998, 1999b, 2000), however, the Chinese praying mantis *Tenodera aridifolia* preferentially approaches a female from the front (Liske and Davis 1987). It may be that the elaborate courtship ritual described for this species (including shuffling, foot stamping and abdominal bending; see also Lelito and Brown 2006) enables quick recognition of a potential mate and subsequently reduces female aggression. The lack of such a display in *P. albofimbriata* may, instead, increase the success of stealthy males in the wild, aided by the dense vegetation that is typical of their environment (Holwell et al. 2007).

For those males that, instead, mounted from a frontal position during the current study, a slow rate of approach was the most important risk-reducing behaviour: the latency to approach a female from the front was substantially less for cannibalised males than for males that were not attacked. Because all but one female remained stationary while the male made his frontal approach, this reduced latency to approach is most likely to be because of faster movement by males rather than attack behaviour by females. Similarly, when males of other mantid species approach females, they cease movement when she looks in their direction (Roeder 1935; Lawrence 1992), creating a longer approach time while in full view of the female. It seems that mounting from the rear or slowly approaching from the front allows many males to go unnoticed by females and, therefore, substantially reduces the risk of sexual cannibalism in *P. albofimbriata*.

In addition to these risk-avoidance behaviours, we saw five cases of opportunistic mating by males whilst females were either feeding or grooming. This behaviour has also been observed in many other cannibalistic spider and mantid species (Robinson and Robinson 1979; Prenter et al. 1994; Moya-Larano et al. 2004; Fromhage and Schneider 2005; Gemeno and Claramunt 2006). For example, male *Mantis religiosa* move towards feeding or grooming females more rapidly than they approach inactive females (Gemeno and Claramunt 2006), and male orb-web spiders *Nephila plumipes* typically initiate courtship and mating after the female has captured a prey item (Elgar and Fahey 1996). During the current study, all five males that mounted while the female was feeding or grooming survived, suggesting a "distracted" female is generally safer to approach than an unoccupied one. Furthermore, a well-fed female is unlikely to attack an approaching male (Liske and Davis 1984; Birkhead et al. 1988; Andrade 1996; Maxwell 2000; Schneider and Elgar 2001; Barry et al. 2008), particularly if her raptorial legs are occupied with prey. It should also be noted that two of the

five opportunistic matings observed during the current study occurred during rear mountings, which could have affected the very low (0/8) percentage of sexual cannibalism seen during these encounters. Finally, the struggle to get away from females once captured, the posture attained during copulation, and the rapid dismounting observed in all mating trials may also occur as a result of selection to avoid sexual cannibalism (Roeder 1935; Lawrence 1992; Maxwell 1998).

The presence and frequency of these risk-avoidance behaviours indicates a net cost to *Pseudomantis* males, and it is, therefore, likely that sexual cannibalism has evolved as a female strategy in this mating system. Female *P. albofimbriata* significantly improve their body condition as a result of male consumption (Barry et al. 2008), which translates into a fecundity benefit for the female (Birkhead et al. 1988; Barry et al. 2008) and also possibly for the male. Even so, the most important factor in determining whether sexual cannibalism is an advantageous male strategy is the expected number of matings in a male's lifetime (Buskirk et al. 1984), and male mantids (including *P. albofimbriata*) have the ability to mate multiple times (Lawrence 1992; Hurd et al. 1994; Holwell et al. 2007). Furthermore, males of this species have particularly good mate-location abilities and high dispersal capabilities, and typically inhabit dense foliage that presumably aids their stealthy approach (Holwell et al. 2007). It, therefore, seems likely that males in this system mate more than once in the wild, which explains the lack of facilitation of cannibalism during our mating trials. Complacent behaviour is, however, seen more frequently in mating systems in which males can expect relatively few matings (Sasaki and Iwahashi 1995; Andrade 1996; Schneider and Elgar 2001; Andrade 2003; Foellmer and Fairbairn 2003; Gaskett et al. 2004; Kasumovic et al. 2007). For example, many male orb-web spiders are morphologically restricted to two matings (Elgar et al. 2000; Herberstein et al. 2005; Nessler et al. 2006), and although they struggle to escape from cannibalism during the first mating, all males are complacent and are cannibalised during the second mating (Sasaki and Iwahashi 1995; Foellmer and Fairbairn 2003; Gaskett et al. 2004; Herberstein et al. 2005).

Interestingly, we found no evidence that males assessed the risk of being attacked on the basis of the size, mass, or body condition of the female they approached, even though these aspects of female phenotype are highly significant predictors of sexual cannibalism in many praying mantid systems (Buskirk et al. 1984; Liske and Davis 1984; Maxwell 2000), including *P. albofimbriata* (Barry et al. 2008). Our study relied on the natural variation in female size characteristics, and it may, instead, be necessary to manipulate these features in order to find a significant effect on male risk avoidance behaviour. Alternatively, males may assess the likelihood of

cannibalism using some other aspect of female phenotype or behaviour, for example female mating history (controlled for in this experiment), which is known to have a significant effect on the propensity to cannibalise in other systems (Newman and Elgar 1991; Herberstein et al. 2002; Prokop and Vaclav 2007).

In conclusion, *P. albofimbriata* males employ various behavioural tactics to avoid the risk of being attacked and consumed by female conspecifics. Mounting from the rear, slowly approaching from the front and/or mounting whilst a female is feeding/grooming allows many males to go unnoticed by females and, therefore, substantially reduces the risk of sexual cannibalism in this mating system.

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