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Oviposition behavior and substrate utilization by *Lestes congener* (Odonata: Lestidae)

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Abstract

Here we describe tandem oviposition (contact guarding) in *Lestes congener* and the use of dry stems of the sedge *Eleocharis obtusa* as oviposition substrates at a pond in New York State. Pairs formed away from the pond, then flew to *Eleocharis* patches on dry land 0.5-3 m from the water's edge. Some copulations occurred at or near oviposition sites; these pairs began ovipositing immediately afterwards. Eggs were placed singly in a line of incisions down the length of the plant stem, and several to many different pairs might utilize a single stem over a period of time. However, less than 1% of the surface area of such stems possessed incision scars, although, in regions of stems with a high density of incisions, some eggs were close enough to be touching. Lone males were present in small numbers at the pond, but male harassment of tandems was minimal and we observed no female take-overs. Some females remained to complete oviposition alone after being deserted by their mates. Lone females were most common in late afternoon, when few lone males remained at the pond and take-over risks were small.

Introduction

Lestes congener Hagen is a late-season zygopteran that is widely distributed throughout North America (Walker 1953). Females oviposit in tandem within the stems of sedges and other plants, and as is typical of temperate-zone lestids, the species overwinters in the egg stage (Montgomery 1925; Harwood 1960; Sawchyn & Gillott 1974a). In this paper we extend earlier observations of oviposition in *L. congener* and discuss the utilization of dry *Eleocharis obtusa* stems as oviposition sites at a small pond in New York State.

Material and methods

Field data were collected during 77 h of observations between the approximate start of the flight period of *Lestes congener* on 18 August and its approximate end on 6 October 2002 at an artificial pond 4 km east of Hamilton, Madison County, New York. The pond measured ca 16 m x 14 m during most of the study period.

Its muddy, rocky shoreline was covered with sparse vegetation, including scattered patches of *Eleocharis obtusa*. This low-growing sedge, whose stems served as oviposition sites for *L. congener*, is described by Fernald (1970) as an annual (rarely perennial) species growing to a height of 3-70 cm. *L. congener* was the only lestid common at the pond during the study period. We saw only 3-4 individuals of other lestid species for brief periods of time; these were not identified to species. The pond had been stocked with fathead minnows, *Pimephales promelas* (Pisces).

The study site consisted of six patches of *Eleocharis* ranging from 1.4 m^2 - 4.8 m^2 in size (total area = 14.1 m^2) and located within a 16-m length of the shoreline. One much smaller patch at the pond was excluded from observation because it was isolated from the others and attracted few *L. congener*. At the start of the study period, all six patches occupied dry ground 0.5-3 m from the water's edge. In late September, heavy rains raised the water level of the pond such that approximately 10% of each of three patches stood in shallow water, and a few plants were completely submerged. By mid-November, additional rainfall drowned all study sites; later, ice and snow covered the pond throughout the period from December to mid-March.

Most observations were made between 12:30 - 17:30 h Eastern Daylight Time (11:30 - 16:30 h Eastern Standard Time). On 11 days, we conducted 4-11 censuses at 30-min intervals, recording the number and behavior of pairs and unpaired individuals at all six patches. Most observations were of unmarked insects. In addition, 86 ♂ and 62 ♀ were uniquely marked on the wings and/or body with enamel paint, and subsequent behavior of marked individuals was recorded during censuses as well as opportunistically. Sustained observations of mating and oviposition were facilitated by the ease with which individuals and pairs could be approached as close as 30-40 cm and monitored for long periods. Focal observations were also conducted on eight tandem pairs, each of which was observed from the time it was first sighted until the pair separated or was lost from view.

Table 1. Details of tandem oviposition in *Lestes congener* from focal observations of eight pairs. Oviposition durations are partial times.

# Pair	1	2	3	4	5	6	7	8
# minutes observed in tandem oviposition								
	66.0	92.9	127.2	63.7	19.6	50.5	3.9	4.9
# stems used or investigated								
	43	34	46	20	13	28	7	7
# time approached by lone males								
	19	3	5	5	1	1	1	0
# stem changes following approach by males								
	3	1	1	0	2	1	1	0

To study substrate utilization, we collected *Eleocharis* stems and examined them at 10x magnification using a dissecting microscope equipped with a previously calibrated ocular micrometer, which provided a precision of measurement of ± 0.01 mm. Records were made of the number and size of incision scars, as well as the spacing between scars. A scalpel was used to slit stems lengthwise to search for eggs in the interior pith and vascular tissues. Since we saw other lestid species only rarely during the entire breeding season, as described above, we assumed that the eggs we observed in stems were laid by *L. congener*. Eggs were classified as recently laid or older according to descriptions by Sawchyn & Gillott (1974a).

Results

Diel densities of pairs and unpaired individuals

Tandem pairs began appearing at *Eleocharis obtusa* patches in early afternoon; the earliest pair was recorded at 13:00 h. The density of tandems reached a peak by 14:00 h, then declined throughout the rest of the day (Fig. 1A). The latest pair was observed at 17:00 h.

Lone males were also present in small numbers at the pond, sometimes as early as 12:00 h. The number of lone males was highest between 14:30 - 15:30 h, after the daily peak in tandem pairs (Fig. 1A). Hence, many of these males may have recently been in tandem with ovipositing females. Data on marked males confirmed that this was in fact the case for four individuals.

Unpaired females, though not common at the pond, were most numerous later in the day (16:00 - 16:30 h), after the peak densities of tandem pairs and lone males (Fig. 1B). The earliest female was recorded at 14:40 h, ovipositing alone; the latest at 16:50 h.

Return visits to the pond

Of 86 marked males, 34 (40%) re-visited the pond on one or more subsequent days, and 31 of these were seen in one or more tandem ovipositions ($\bar{x}$ per male = 1.8; s.d. = 1.03; range = 1-4). One male, captured in tandem and released after marking, was seen paired with a different female 25 min later, but for all other males, no more than one tandem oviposition was recorded per day. Males returned to the pond an average of 2.2 additional days after marking (s.d. = 1.27; range = 1-5).

Of 62 marked females, 21 (34%) were observed on one or more subsequent days, and 17 of these were seen in tandem oviposition ($\bar{x}$ per female = 1.9; s.d. = 1.45; range = 1-5). We recorded no more than one oviposition for an individual female per day. Females returned to the pond an average of 2.1 additional days after marking (s.d. = 1.70; range = 1-6). A log-likelihood ratio (G) test showed that there was no significant difference in the percentages of marked males and females that revisited the pond on one or more subsequent days ($G = 0.49$, $df = 1$, $p > 0.1$).

Pair formation and copulation

The vast majority of *L. congener* appearing at the pond were already in tandem, either perching or flying slowly along the shoreline between *Eleocharis* patches. Searches of the pond bank and adjacent field prior to the start of the daily oviposition period revealed neither unpaired individuals nor pairs; hence, we could not determine where tandems were forming before arriving at oviposition areas. We induced one pairing by capturing a female during tandem oviposition, marking her, then releasing her near a perched unpaired male. The male grasped the female without prior courtship display and the pair assumed the wheel position after 1-2 min, while perched. After mating, the pair flew directly to an *Eleocharis* stem and began ovipositing. Two other females that were released after marking were clasped by lone males, but when they did not assume the wheel position, they were released.

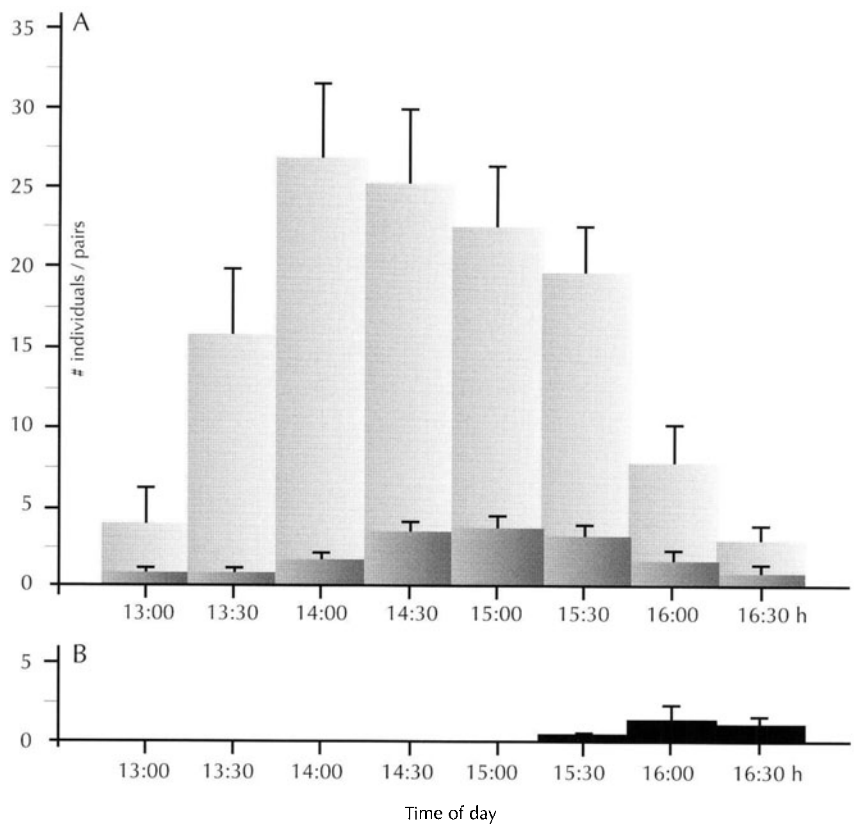

Figure 1: Number of individuals of *Lestes congener* at *Eleocharis* patches (total area = 14.1 m^2). Data are from a total of 74 censuses taken every 30 min on 11 different days, from 31 August - 20 September, 2002. Vertical bars are +1 s.e.

A. Mean number of tandem pairs (light grey) and lone males (dark grey).

B. Mean number of lone females (black).

We observed 21 copulating pairs at the pond. For one pair, timed continuously from the onset of the wheel position to disengagement from the wheel, copulation duration was 5.0 min. For 10 other pairs we missed a portion of each copulation; here, durations ranged from 2.2-12.1 min. While in copula, pairs perched in *Eleocharis* patches or on other vegetation within 2 m of patches. Occasionally they changed perch sites, either on their own initiative or after being approached by unpaired males. No copulations were ever terminated by male interference. After copulation, pairs remained in tandem and joined other pairs at *Eleocharis* patches.

Oviposition behavior and substrate utilization

Female *L. congener* inserted eggs within the pith of *Eleocharis* stems (Fig. 2). Such stems possessed one or more oval incision scars that were visible externally. The mean length of 30 scars was 0.34 mm (s.d. = 0.066 mm); the mean width (at the widest point) was 0.22 mm (s.d. = 0.033 mm). Examination of 1,437 incision scars on 76 stems indicated that 84% of incisions contained an egg (s.d. = 2.0%). No incision site ever held more than a single egg. Recently laid eggs were glistening white; these turned opaque grayish white within 3-4 hours and eventually, during maturation, became dark purplish-brown to almost black. The mean length of 15 eggs was 1.20 mm (s.d. = 0.11 mm); the mean width was 0.18 mm (s.d. = 0.025 mm). In all cases, eggs were oriented parallel to the long axis of the stem.

We collected 37 *Eleocharis* stems at random on 1 October at 14:20 h, at a time of day when no pairs were ovipositing. The mean length of these stems was 26.4 cm (s.d. = 3.22 cm). Each stem contained at least one egg (range = 1-75). The mean number of eggs per stem was 28.2 (s.d. = 22.38). The largest number of incision scars found on a single stem was 78; however, collectively these occupied only ca 0.2% of the total surface area of the stem, approximated as a cylinder. At the start of the reproductive season, pairs oviposited in vertical or nearly vertical stems; however, as autumn progressed, an increasing number of stems became broken or bent over at various angles. These were also used for oviposition. Examination of 492 scars on 26 stems revealed that oviposition was restricted to the upper 65% of the stem. Most stems used by pairs possessed withered inflorescences at their tips and had become dry, brittle, and yellow-brown to brown. However, when we examined nine stems that were still partly or completely green, we also found one or more newly deposited eggs (eight stems), or older eggs (one stem), in addition to empty incision sites. All eggs and scars were still in the upper 65% of the stem.

We never observed females descending underwater to oviposit, even when heavy rains in late September raised the water level of the pond and submerged small portions of three patches. Pairs continued to use only the upper portions of stems and did not visit plants that were more than half submerged in the water. During tandem oviposition, the male appeared to take the initiative in flight and in perching. The male first alighted on a stem; then the female clasped the stem with all three pairs of legs. Sometimes the male seemed to swing the female's body forward as if assisting her in establishing contact. Occasionally, in tangled clumps of *Eleocharis*, the male might land on one stem and the female on an adjacent one. The pair eventually moved to another site once coordinated movement between partners could no longer be sustained.

During egg-laying, the female curled her abdomen so as to position the ovipositor directly between her hind legs. With the male moving along in synchrony, she walked down the length of the stem, probing and penetrating the plant tissues. As she moved slowly away from the terminal inflorescence, she left a line of incision scars along the length of the stem. Examination of four stems, each bearing a single line of seven to nine scars, showed that the average distance between scars was 1.8, 1.5, 1.8, and 2.0 mm (s.d. = 1.06, 0.54, 0.42, 0.58 mm, respectively), and thus greater than the mean length of a single egg. Sometimes, however, we noted scars packed more closely together around all sides of the stem, with some eggs touching others. We assumed that such stems had been used by multiple pairs. One stem, collected on 1 October, possessed 32 scars within a 4.75 cm length; this was the highest density of scars per unit area for the 37 stems collected on that date.

Pairs used multiple sites during the course of oviposition (Table 1), sometimes remaining for 15 min or longer on a single stem. Cessation of oviposition and/or rejection of a particular stem (*Eleocharis* or other vegetation) appeared to be communicated to the male by the orientation of the female's abdomen. Once she ceased curling her abdomen and held it out horizontally, the pair left the stem after 5-10 s. Although pairs sometimes moved from one *Eleocharis* patch to another, many stayed for long periods in a single patch, moving from one stem to another within an area as small as 30 cm^2.

In practice, it was difficult to tell if females whose abdomens were curled and apparently contacting an *Eleocharis* stem were always depositing eggs at that time. We collected 14 stems used by tandem females with curling times ranging from 7-23 s before each pair changed perch sites. Of these stems, only four contained fresh eggs in the region contacted by the female. The 10 remaining stems contained no fresh eggs, although nine contained one or more empty incisions. In the remaining stem (curling time = 14 s), there were neither fresh eggs nor incisions, suggesting that the female had simply probed the surface and then moved on. In practice, we considered the oviposition period to include acts of probing and/or piercing the stem, in addition to egg deposition.

We do not have complete oviposition durations for any pairs; however, we recorded partial times of 60 min or longer for 24 tandems (max. = 127.2 min). Since pairs were either discovered while oviposition was already in progress, or were lost from sight before they separated, tandem oviposition probably took considerably longer than we document here.

Figure 2: Portion of stem of *Eleocharis obtusa* cut open lengthwise to show mature *Lestes congener* egg in pith.

Interactions between pairs were uncommon. Occasionally the male of a tandem fluttered his wings in apparent display when another pair flew within 5-10 cm. However, pairs generally tolerated the close proximity of other perched tandems: often two (sometimes three) pairs oviposited only 1-2 cm apart on the same stem, with no apparent interference. The highest density of tandem pairs was recorded on 14 September at 14:00 h, when 15 pairs simultaneously utilized a 2 m^2 area. We collected three females on *Eleocharis* stems with their abdomens curled in typical oviposition position and embedded within the plant tissue. The females were motionless and appeared to be dead, but all disengaged themselves and flew away while the stems were being handled. A fourth female was discovered dead on the ground within a patch, missing the last few abdominal segments. We witnessed no predation attempts on ovipositing pairs or lone females, nor did we find any dead males.

Pair separation and behavior of lone females

Tandem oviposition ended when the male abruptly disengaged from the female and either perched nearby or flew away from the patch. After pair separation, some females continued perching for several minutes with their abdomens held horizontally or drooping downward; then they rose slowly upwards until they disappeared from sight. Others remained on the same stem and continued egg-laying alone. One female, timed since the departure of her mate, oviposited alone for 9.2 min; another female, for 60.3 min before leaving the pond. Oviposition behavior by unpaired females appeared similar to that of females in tandem. We separated the members of three pairs by gently pulling the male off the female. All females continued to oviposit alone, but each was taken into tandem by a different male than the first after 35.5 min, 15.0 min, and 2.0 min respectively. One pair was lost from sight, but the other two copulated while perched 0.5-1 m away. Under natural conditions, however, we observed few interactions between unpaired males and lone females. On one occasion, a male contacted a lone ovipositing female repeatedly but was unable to clasp her. She performed no apparent rejection displays but continued to oviposit at the same perch site. We also saw two instances in which a lone ovipositing female was clasped, but in both cases the male detached after the female did not assume the wheel position. One female, marked when ovipositing alone, re-visited the pond six days later in tandem; another was seen 6, 7, and 11 days later, each time in tandem oviposition.

Behavior of lone males

Unpaired males were present in small numbers at the pond, perching at or near oviposition sites (one to three males per patch) or flying along the shoreline between patches. Occasionally they chased other conspecific males or approached ovipositing pairs, and frequently they made abrupt flights from perch sites for reasons we could not determine. Lone males appeared to exhibit little site tenacity, and most were difficult to keep in sight for longer than 10-15 min at a time. Some males were present sporadically at a particular oviposition area; for example, each of three marked males were recorded at Patch 6 on three to five occasions over a period of 60 min.When a lone male flew near an ovipositing pair, the male of the tandem fluttered his wings and the pair usually retained its perch site (Table 1). On two different occasions a lone male contacted the female of a tandem pair with his legs, and once a male contacted the male of a pair, but in all three cases the tandems continued ovipositing without interruption. On no occasion was a lone male successful in separating a tandem pair and clasping the female. Four lone males were seen 25-110 min later in tandem; however, we did not observe preceding reproductive events.

Discussion

Tandem oviposition, or contact guarding, is widespread among zygopterans and tends to be associated with the absence of courtship behavior, poorly developed or absent male territoriality, and one to only several matings per day or lifetime (Waage 1984). Tandem oviposition has been described in many species of lestids, e.g., *Lestes barbarus* (Fabricius) and *L. virens vestalis* (Rambur) (Utzeri et al. 1987), *L. disjunctus australis* Walker (Bick & Bick 1961), *L. eurinus* Say (Lutz & Pittman 1968), *L. sponsa* (Hansemann) (Stoks et al. 1997), *L. unguiculatus* Hagen (Bick & Hornuff 1965), and previously in *L. congener* (Montgomery 1925; Harwood 1960; Sawchyn & Gillott 1974a). *L. rectangularis* Say appears to be unusual in this respect, since females typically oviposit unattended by males (Gower & Kormondy 1963).

Our observations of *L. congener* suggest that pairs apparently formed some distance away from the water, as also occurs in *L. sponsa* (Watanabe & Matsunami 1990; Stoks 1995), *L. viridis* (Vander Linden) (Dreyer 1978, 1981) or *L. virens vestalis* (Jödicke 1997: 216). Tandems then flew to communally-used oviposition areas (*Eleocharis* patches) along the bank of the pond. Copulation could occur within or near patches, and oviposition followed immediately afterward. Our single record of uninterrupted copulation duration in *L. congener* was 5.0 min (compared with 12 min, as reported by Sawchyn & Gillott 1974a), although partial durations for other pairs were as long as 12 min, suggesting longer total durations, as have been reported for other lestids (see Jödicke 1997: 225).

Lone male *L. congener*, present but not numerous at *Eleocharis* patches, were not territorial, although they occasionally chased one another and also attempted to clasp females held in tandem. However, male harassment never separated the members of a pair. Contact guarding in odonates is generally regarded as more effective than non-contact guarding in preventing female take-overs and thus avoiding possible sperm displacement by rival males (Uéda 1979; Waage 1984; Stoks et al. 1997). Under natural conditions we observed no more than a single mating per male (and per female) per day, although members of artificially separated tandems were receptive to re-mating.

Some *L. congener* males failed to guard for the duration of oviposition, actively disengaging from tandem and leaving the female to continue egg-laying alone. Lone ovipositing females were most common (though still not abundant) in late afternoon, after the peak density of unpaired males. Thus, guarders who deserted mates at this time faced lower risks of female take-over and hence sperm displacement by rival males (Waage 1982, 1986). Ovipositions by unattended females have also been reported for other tandem-ovipositing lestids, such as *L. sponsa* (Stoks et al. 1997), *Archilestes grandis* (Rambur) (Bick & Bick 1970), and *L. disjunctus australis* (Bick & Bick 1961); see also review in Jödicke (1997: 237) and Corbet (1999: 28). Utzeri et al. (1987) found that, in *L. barbarus* and *L. virens vestalis*, unguarded ovipositions were more common when male densities were low. From the female's perspective, selection should favor minimizing delays in completing oviposition (Moore 1989). In *L. congener*, females remaining after mate desertion stayed in the same small area (often on the same stem) as they had been occupying when in tandem. They were not receptive to re-mating and retained their perches despite clasping attempts by the few males that occasionally flew by. The vegetation may have provided some concealment from males, in addition to their tendency (also seen while in tandem) to remain nearly motionless while egg-laying.

Our discovery of three females whose ovipositors had become stuck in *Eleocharis* stems raise the question as to whether endophytic oviposition in *L. congener* may carry some risk, albeit small, of becoming trapped in the substrate. It remains to be determined whether this is more likely to happen to unaccompanied females, whose mates, if still present, might have freed them during tandem flight. However, our observations suggest that, unless disturbed, the tandem male does not initiate flight from a stem until the female ceases curling her abdomen and extends it horizontally. It is possible that motionless trapped females are simply abandoned by their mates or that tandem males are unable to free them.

L. congener has been reported ovipositing in various substrates, including dry stems of the sedge *Scirpus* 5-30 cm above the water surface (Sawchyn & Gillott 1974a), dead portions of the grass *Glyceria* (Harwood 1960), and both dead and green cat-tail leaves (Walker 1953). Kennedy (1915) recorded oviposition in a willow stem, and Cannings & Stuart (1977) in the stems of *Eleocharis palustris* 2-6 cm above the water; but these authors did not specify whether the stems were dry or green. In our study, *L. congener* oviposited in the dry stems of *E. obtusa* growing on dry land 0.5-3 m from the water. When pairs occasionally used younger, greener parts of the plant, these were in the upper 65% of stems that were destined to become brown in several weeks. All plants used by *L. congener* at our study site became submerged by heavy rainfall in late fall and covered by ice and snow throughout the winter.

Sawchyn & Gillott (1974a), studying *L. congener* in Saskatchewan, Canada, suggested that the use of dead plant material for oviposition in this species evolved along with relatively little pre-diapause embryonic development in the egg and thus with no need for external moisture prior to the onset of winter. In contrast, *L. d. disjunctus* Walker, *L. dryas* Kirby, and *L. unguiculatus* oviposit only in *Scirpus* stems that are green and thus contain moisture required for more advanced stages of embryogenesis to be reached before diapause occurs (Sawchyn & Gillott 1974b).

Our data on egg dimensions, distance between incisions, and deposition within the pith of stems are similar to those of Sawchyn & Gillott (1974a). Like these authors, we observed no more than one egg per incision, as also occurs in *L. dryas* (Sawchyn & Gillott 1974b) and in *L. barbarus* and *L. virens vestalis* (Loibl 1958; Utzeri et al. 1987). However, some other lestids may deposit two or more eggs per incision, for example *L. sponsa* and *L. viridis* (Robert 1958) and *L. d. disjunctus* (Sawchyn & Gillott 1974b). It was interesting to observe that about 16% of 1,437 oviposition scars did not contain an egg. We assume that sometimes females probe stems and (for whatever reason, unclear to us) do not find certain sites satisfactory for egg deposition.

We did not see eggs within *Eleocharis* stems at densities as high as Sawchyn & Gillott (1974a) found for *Scirpus*. Like Cannings & Stuart (1977), we observed many *L. congener* pairs ovipositing in close proximity to one another, as has also been observed in many other zygopterans (Jödicke 1997: 238; Corbet 1999: 30). However, even in those situations, incision scars covered less than 1% of the surface area of a stem. Thus, there seemed to be no shortage of oviposition sites, nor did the sedges, already past the fruiting stage and soon to die back during the winter, suffer any apparent damage. Little is known, in fact, about the short-term or long-term effects on plants of endophytic oviposition by odonates (e.g., see Jödicke 1997: 236). Since these odonates have important and varied reproductive associations with plants, this subject may be worthy of further study.

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