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An intra- and interspecific study of body size and autotomy as a defense in Orthoptera

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Abstract

Autotomy, the 'voluntary' shedding of a limb or other body part, is a highly effective escape mechanism to avoid predation or other forms of entrapment. Autotomy, however, comes with costs to locomotion, reproductive behavior, regeneration *etc*. It has been suggested that increasing body size and 'robustness' may allow for less reliance on this extreme form of predator defense, but this theory has never been tested. Here we present behavioral observations ('willingness' or time taken to lose an entrapped limb) of Orthoptera of a range of body size and mass. These data strongly suggest that body size and mass may be an important determinant of the use of autotomy as an escape mechanism within the Order, possibly due to the effects of body size upon the efficacy of autotomy, as well as other defense mechanisms. An ontogenetic study for *Gryllus bimaculatus*, however, shows no clear trend in willingness to autotomize a limb with body mass, suggesting that this defense tactic may be less affected by body size *per se*, but rather by the tactics developed by each individual species.

Key words

defense, predation, body mass, grasshopper, cricket, leg loss

Introduction

A day without food or without sex may influence fitness in the short-term, but nothing reduces fitness as totally and effectively as being killed and eaten by a predator (Lima & Dill 1989). Predation pressure therefore, is one of the most important selective forces resulting in the evolution of escape behavior, crypsis, aposematism, armor, chemical defense (Lima & Dill 1989) and possibly the most extreme defense: sacrificing a limb or other appendage to the predator (Arnold 1988). Autotomy is the self-amputation of a body part, often as a reflexive action and along a predetermined breakage plane, which has been observed in a wide variety of taxa in defense against conspecifics or nonspecifics (Arnold 1984, 1988; Fleming *et al*. 2007; Juanes & Smith 1995; Maginnis 2006). Despite the benefits of escaping through autotomy of a body part, this loss often makes the individual more vulnerable to further attacks, negatively influences locomotion, reproductive behavior, foraging ability or social status, incurs energy costs through loss of tissues or regeneration of the structure, or can significantly reduce survivorship (see Arnold 1988, Fleming *et al.* 2007 for reviews).

Theoretically, juveniles may be able to recoup the cost of loss of a leg by regenerating it in successive instars; however limb regeneration appears to be rare or incomplete in Orthoptera. First instar *Ephippiger ephippiger* (Tettigoniidae) successively regenerate autotomized front legs, but they are only a quarter of the size of normal legs and lack a working tympanum (Lakes & Mücke 1989). Hind limbs lost by *G. bimaculatus* nymphs are not regenerated (PWB pers. obs.); this suggests that loss of a leg as a nymph is a burden necessarily carried over into adulthood. Arnold (1984, 1988) suggested that tail autotomy in lizards is reduced or absent in larger, 'robust' species of lizards that are better able to fight back against a predator with claws and teeth, whilst smaller, more 'gracile' species will be selected to autotomise tails sooner. Although he proposed this idea 20 y ago, we have found very little published data addressing the hypothesis.

But how could a relationship between autotomy and body size be measured? Various authors have collected data on the incidence of autotomy amongst different size classes of invertebrate taxa under natural conditions. However, species that are not able to regenerate a lost appendage will necessarily accumulate autotomy injuries over their lifetime, and therefore the incidence of autotomy should not be interpreted as a reflection of the relative costs or benefits to that animal at its particular point in life. For example, daddy-long-legs spiders *Holocnemus pluchei* (Pholcidae) and *Pardosa milvina* (Lycosidae) wolf spiders, accumulate injuries over time (Brautigam & Persons 2003, Johnson & Jakob 1999).

Other species are able to regenerate a lost appendage, but may still accumulate injuries due to marked differences in regeneration time between juveniles and adults (discussed by Fleming *et al.* 2007). For example, mantis shrimps *Gonodactylus bredini* (Gonodactylidae) accumulate injuries as they grow (Berzins & Caldwell 1983). In a review of crab autotomy, Juanes & Smith (1995) report an accumulation of autotomies with body size in three species, but greater incidence in smaller individuals of a further three species (for two species, injury frequency was similar for large and small individuals, and for another there were greater numbers of injuries for intermediate-sized animals). By contrast with these data, in larvae of two Odonata species (*Enallagma erbium* and *Ischnura verticalis*), the frequency of caudal lamellae autotomy is significantly correlated with the number of aggressive encounters, and smaller individuals acquire more injuries than larger individuals (Baker & Dixon 1986). These conflicting data reflect how difficult it is to interpret the relationship between the incidence of missing legs and body size in species with dynamic behavior and biology as they mature.

An important aspect of autotomy is that this process is, to some varying extent, at the discretion of the individual, and the 'willingness' of an animal to lose an appendage (*i.e.*, time to autotomize an entrapped limb) may therefore reflect its present circumstances. For example, Bateman & Fleming (2006) showed that, while mating history had no influence on autotomy time in male *Gryllus bimaculatus*, unmated females (that need tympana on the front legs to locate calling males) are less 'willing' to shed these legs when entrapped compared with mated females. *Gryllus bimaculatus* that have lost a limb become less ready to autotomize a subsequent

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limb (Bateman & Fleming 2005), as does the crab *Hemigrapsus oregonensis* (Grapsidae) (Easton 1972). By contrast, *Asterias rubens* (Asteriidae) starfish, autotomize consecutive arms more rapidly than the first arm (Ramsay *et al*. 2001) [which may reflect the lingering action of systemic secretory products influencing the mechanical properties of mutable collagenous tissue at autotomy sites (Wilkie 2001)]. 'Willingness' (or time taken) to lose a limb may therefore be a useful measure of autotomy as a defense mechanism.

Supporting Arnold's (1984, 1988) suggestion that the usefulness of autotomy may vary with body size, larger *Asterias rubens* starfish take longer to autotomize an arm, which is correlated with increased mechanical toughness, in itself an antipredator defense (Marrs *et al*. 2000). For *Uta stansburiana* (Phrynosomatidae) lizards, larger individuals require application of greater force to induce tail autotomy (Fox *et al.* 1998). As far as we are aware, however, the theory has not been explicitly tested in any arthropod.

Here we examine the relationship between body size and willingness to autotomize a leg in Orthoptera. We carried out an ontogenetic study for *G. bimaculatus* and then examined the relationship for a wide range of Orthoptera taxa. We hypothesized that autotomy may be an important defense for smaller animals to escape a predator, because they cannot rely on armor or retaliation (kicking, biting or struggling) which are much more effective tactics for larger animals. We therefore predict a high reliance on autotomy in smaller animals, which would correspond to shorter times taken to lose a limb. Studying a single taxon ontogenetically as well as across species offers the opportunity to determine how body size influences this important survival strategy.

Methods

For the ontogenetic study, we used *G. bimaculatus* from a laboratory-bred population kept in the Department of Zoology and Entomology, University of Pretoria. Seventy-five intact nymphs, ranging in mass from 0.03 to 0.87 g (mean 0.28 ± 0.17 g), and 156 intact adults, ranging from 0.43 to 1.91 g (mean 0.95 ± 0.29 g; females: 1.09 ± 0.29 g, N=91; males: 0.76 ± 0.14 g, N=65) were selected.

As an interspecific comparison, we collected data for adults of a total of 25 other Orthoptera species (N=109 individuals in total). The gryllid *Acheta domestica* was sourced from a pet-shop supplier, whilst *Gryllodes sigillatus* nymphs were collected on the University of Pretoria campus; both species were raised to adulthood in the laboratory. Adult *Libanasidus vittatus* (Anostostomatidae) were collected from suburban gardens in Pretoria and *Acanthoplus discoidalis* (Bradypodidae) were collected from roadsides in the Northern Cape, South Africa. *Gryllotalpa africana* (Gryllotalpidae) were collected at night from lawns on the campus of the University of Pretoria. All other Orthoptera species were opportunistically collected from fields and undeveloped land in Pretoria (Tshwane Metropolitan Area) during day and night.

For each individual, we attempted to evoke autotomy of the right hind leg. We chose this leg, because in a field population of *G. bimaculatus*, rear legs were most commonly missing (Bateman & Fleming 2005), and autotomy time for this leg does not seem to be influenced by mating history (Bateman & Fleming 2006). Also, as the largest and most obvious legs in the majority of Orthoptera, they are the ones most likely to be grasped by a predator. Each individual was first weighed (± 0.0001 g) and then held lightly between finger and thumb and placed on a surface of rough cardboard which they could grip. The right hind leg was grasped by forceps and the insect released. Time to leg autotomy was obtained with a stopwatch. We released the insect after 60 s, if it had not autotomized the leg and recorded this as 60 seconds.

Body mass is significantly positively correlated with three other measures of body size (measured with digital calipers in mm) across these species, including body length ($r^2 = 0.34$, $t_{20}=3.19$, $p = 0.004$), pronotum length ($r^2 = 0.65$, $t_{21}=6.30$, $p<0.001$) and pronotum width ($r^2 = 0.84$, $t_{23}=10.7$, $p<0.001$). We have therefore used body mass as a measure of body size for comparison with autotomy times.

For *G. bimaculatus*, autotomy-time data were analyzed by multiple regression with sex (male *vs* female), life stage (nymph *vs* adult) and body mass as independent variables. Data were further analyzed

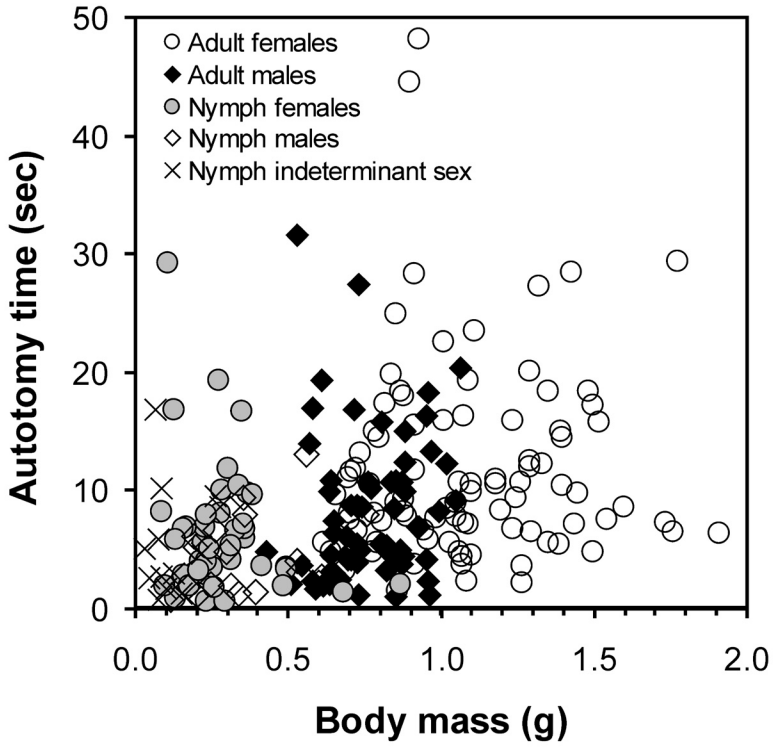


Fig. 1. Speed to autotomize their right hind limb for nymph and adult *G. bimaculatus*. Each data point represents a single individual.

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for each sex independently. For interspecific analyses, the means of autotomy time and body mass for each species were tested by regression analysis.

With phylogenetic correction, we examined the relationship between body mass and willingness to autotomize a limb. This correction was carried out using a phylogeny custom-made for the species sampled (only those that could be positively identified to genus or species), based on the Orthoptera Species File Online (Eades & Otte 2008). We used Felsenstein's (1985) independent contrasts method in the computer program PDTREE (Garland *et al.* 1992, 1993, 1999, Garland & Ives 2000). Equal branch lengths were used for all segments (*i.e.*, branch lengths were all set to one). Phylogenetically-independent contrasts (PIC) of dependent (autotomy time) and independent (body mass) variables were calculated. PIC values were standardized utilizing the branch-length transformation (Garland *et al.* 1992) and then compared by regression analysis.

Results

Ontogenetic study: Gryllus bimaculatus.—All *G. bimaculatus* autotomized their entrapped limb within 60s (Fig. 1). Multiple regression analysis ($R^2 = 0.12$, $F_{3,227} = 10.29$, $p < 0.001$) revealed that there was no significant effect of body mass ($t_{227} = 0.96$, $p = 0.34$) upon time to autotomise the right hind limb, whilst life stage (nymph vs adult; $t_{227} = -1.92$, $p = 0.06$) was marginal, and sex differences were evident in these data ($t_{227} = 2.23$, $p = 0.03$; females were slower to autotomise this limb compared with males: 10.0 ± 7.8 s, N=137 compared with 7.3 ± 5.9 s, N=85; the remainder of nymphs were of indeterminate sex). The data were therefore re-analyzed for each sex independently.

For males ($R^2 = 0.09$, $F_{2,82} = 4.04$, $p = 0.02$), neither life stage ($t_{82} = 0.73$, $p = 0.465$) nor body mass ($t_{82} = 1.27$, $P = 0.21$) significantly affected autotomy time. For females ($R^2 = 0.10$, $F_{2,134} = 7.79$, $p < 0.001$), however, life stage did show a significant pattern ($t_{134} = 2.12$, $P = 0.04$), with adult females taking significantly longer to shed a leg (11.8 ± 8.2 s) compared with nymphs (6.5 ± 5.5 s); no pattern was evident for body mass and autotomy time ($t_{134} = 0.07$, $p = 0.94$).

Interspecific.—For 26 Orthoptera species (N=265 adult individuals in total, including 156 adult *G. bimaculatus*), we found a significant relationship between species' average time to autotomize the limb and average body mass, with larger species demonstrating less readiness to autotomize a limb compared with smaller species (Fig. 2; $r^2 = 0.60$, $t_{25} = 6.27$, $p < 0.001$). In fact, some of our largest species never autotomized their leg in response to this particular experimental setup (Table 1). This relationship between body mass and willingness to autotomise a limb remained significant after phylogenetic correction ($r^2 = 0.58$, $t_{24} = 5.73$, $p < 0.001$).

Discussion

There is a significant decline in readiness to autotomize a limb with increasing body size across Orthoptera species. However we found very little evidence that time to autotomize a limb was dependent upon body mass for *G. bimaculatus*. Presumably, defense mechanisms and therefore willingness to autotomize a leg, are less likely to be influenced by ontogenetic changes in body size, and more likely to be a species-specific defense characteristic.

Theoretically, juveniles may be able to recoup the cost of a lost leg by regenerating it in succeeding instars; however limb regeneration appears to be rare or incomplete in Orthoptera. First instar *Ephippiger ephippiger* (Tettigoniidae) successively regenerate autotomized front legs, but by their last ecdysis, these are only a quarter the size of normal legs and lack a working tympanum (Lakes & Mücke 1989). Hind limbs lost by *G. bimaculatus* nymphs are not regenerated (PWB pers. obs.): this suggests that loss of a leg as a nymph is a burden necessarily carried over into adulthood.

Why would body size affect time to autotomy? Firstly, as Arnold (1984, 1988) suggested, the relationship may be related to retaliatory

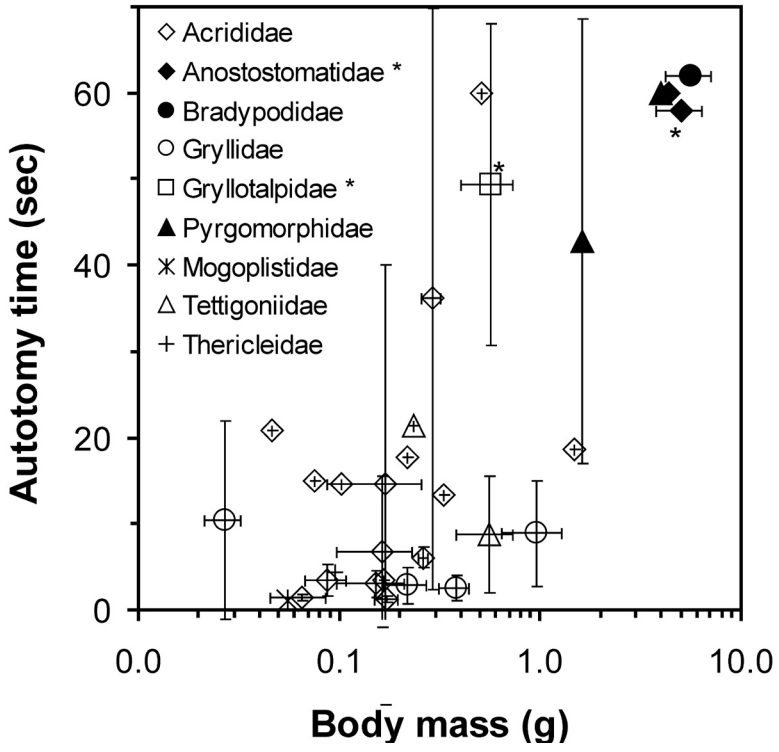


Fig. 2. Within Orthoptera there are significant differences between species in 'willingness' to autotomize limbs. This graph summarizes mean (± 1s) time to autotomize a hind limb for 26 adult Orthoptera species (N=265 individuals in total). Families that exhibit known chemical defense are shown with filled symbols; fossorial groups are indicated with an asterisk. Those that did not autotomize the entrapped limb are recorded with an autotomy time of 60 s. Note log scale for *y*-axis.

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Table 1. Species used for this study.

Suborder Family Subfamily	Species	N	Body mass (g)	Mean autotomy time (s)	
Ensifera					
Tettigoniidae	*Ruspolia* sp.	4	0.56±0.18	8.72±6.75	
	Conocephalus sp.	1	0.23	21.45	
Bradypodidae	*Acanthoplus discoidalis*	4	5.64±1.47	60	Did not autotomise, kicked vigorously, turned to bite the restraining forceps; chemical defense
Anostostomatidae	*Libanasidus vittatus*	3	5.08±1.32	60	Did not autotomise, kicked vigorously, turned to bite the restraining forceps; chemical defense
Gryllidae	*Acheta domestica*	30	0.38±0.07	2.53±1.45	
	Gryllodes sigillatus	14	0.22±0.05	2.84±2.08	
	Gryllus bimaculatus	156	0.95±0.29	10.27±7.66	
Oecanthinae	*Oecanthus* sp.	3	0.03±0.01	10.42±11.58	
Gryllotalpidae	*Gryllotalpa africana*	10	0.57±0.17	49.32±18.63	Only two autotomized; fossorial
Mogoplistidae	Unidentified sp.	1	0.06	1.01	
Caelifera					
Pyrgomorphidae	*Dictyophora spumans*	1	4.12	60	Did not autotomize; chemical defense
	Zonocerus elegans	7	1.6±0.61	42.78±25.7	Only three autotomized; exuded an acrid-smelling yellow liquid when restrained
Acrididae	*Acrida acuminata*	1	1.49	18.6	
	Acrida sp.	2	0.26±0.01	6.08±1.2	
	Acrotylus sp.	7	0.16±0.07	6.77±8.76	
	Anacridium moestum	1	0.17	3.47	
	Catantops humeralis	1	0.22	17.71	
	Locustana pardalina	1	0.51	60	Did not autotomise, kicked vigorously with spiked back legs
	Oedalus sp.	3	0.17±0.02	1.31±0.38	
	Orthoctha dasycnemis	3	0.15±0.06	3.04±1.54	
	Paracinema sp.	5	0.17±0.08	14.56±25.46	
	Sphingonotus scabriculus	1	0.33	13.4	
	Truxalis sp.	2	0.30±0.03	36.14±33.75	
Gomphocerinae	Unidentified sp.	2	0.07±0.02	1.5±0.32	
Lentulidae	Unidentified sp.	1	0.16	3.96	
Thericleidae	*Pseudothericles* sp.	1	0.09	4.45	

defense. Smaller animals may not rely on other defense mechanisms such as armor or retaliation (kicking, biting or struggling) to escape a predator, mechanisms that are more effective for larger species. In *G. bimaculatus*, adults and larger nymphs turned to bite the restraining forceps or occasionally kicked with the unrestrained hind leg (hind limbs of *G. bimaculatus* are armed with spines); such behavior was not evident for smaller animals. Furthermore, though we could not induce hind-leg autotomy (trials terminated after 60 s, by which time a predator might have succeeded in trapping the animal) in most individuals of the largest orthopterans included in our study (Anostostomatidae, Pyrgomorphidae, Bradypodidae and Acrididae), most individuals we tested kicked vigorously with their spined back legs and turned to bite the restraining forceps (Table 1). Similar behavior has been recorded in the large (approx. 6 cm in length) weta *Hemideina crassidens* (Anostostomatidae), which kick vigorously with spiny back legs and bite when seized by geckos, resulting in escape without resort to autotomy (Field & Glasgow 2001).

Individuals that have other defenses against a predator may be less likely to autotomize a limb than those lacking such defenses. For example, in *Petrolisthes* spp. (Porcellanidae), porcelain crabs, increased body size is associated with less reliance on cheliped autotomy as an escape mechanism, and greater reliance on struggling and pinching the predator with the chelipeds (Wasson & Lyon 2005). Also hermit crabs such as *Pagurus bernhardus* (Paguridae) do not autotomize their hind limbs, these being protected within the shell, but do autotomize exposed anterior legs (Needham 1953).

Secondly, larger animals may require greater force to shear a limb, and therefore may have slower autotomy response compared with smaller individuals. Speedy loss of the appendage may be a key requirement for successful escape through autotomy. Certainly for *A. rubens* starfish, longer times for arm autotomy are correlated with increased mechanical toughness (Marrs *et al.* 2000) and possibly the same may be true for tail autotomy in *Uta stansburiana* lizards (Fox *et al.* 1998).

Burnside & Robinson (1995) examined the breaking-joint diameter of Odonata larvae caudal lamellae as an index of the amount of cuticle holding each lamella. For four species of damselfly larvae, the size of the breaking joint increases not in proportion to body mass, but in proportion to the size of the lamellae themselves (Burnside & Robinson 1995). Similarly, Wasson & Lyon (2005) found that although female porcelain crabs are more likely to autotomize a cheliped, compared with males, this gender difference disappears when claw size is taken into account, because females have smaller

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chelipeds compared to males.

Although these studies all suggest a direct relationship between appendage size and the force required to autotomise that body part, we have little data to support a mechanical explanation for time to autotomy in *G. bimaculatus*. We found no difference in times to autotomy of nymphal *vs* adult males (range 0.12 to 1.06 g in body mass), and for females only slight differences in autotomy times between the life stages, but no significant effect of body mass (range 0.08 to 1.91 g in body mass).

Thirdly, body size influences predator tactics and therefore the efficacy of autotomy as an escape mechanism. The spider *Gladicosa pulchra* (Lycosidae) can survive predation attempts by scorpions, due to leg autotomy when grasped by the leg; however the tendency for scorpions to use their sting increases with size of the spiders, and larger spiders have more attacks directed at their abdomen and cephalothorax compared to their legs (Klawinski & Formanowicz 1994). Larger spiders therefore have reduced opportunity to use leg autotomy to escape (Klawinski & Formanowicz 1994).

Body size therefore influences predator tactics (as well as the efficacy of alternative defenses) and therefore, the usefulness of autotomy. Larger species may consequently experience less advantage through autotomy, and other tactics may become more valuable: for example armor (Irish 1992); retaliation (*e.g.*, *Hemideina crassidens* Anostostomatidae, Field & Glasgow 2001) or chemical defenses such as poisons sequestered from plants (Seibt *et al.* 2000), vile-smelling feces (Bateman & Toms 1998, Monteith & Field 2001, Wolf *et al.* 2006), reflex bleeding (Glenn 1991, Grzeschik 1969, Seibt *et al.* 2000), or regurgitation of crop contents (Lymbery & Bailey 1980, Sword 2001).

Finally, larger animals may have additional costs associated with loss of an appendage. Due to greater body mass, individuals may have additional costs of locomotion associated with adjustment of load carrying after leg loss. The link between autotomy and increased cost of locomotion has only been investigated for *G. bimaculatus* (Fleming & Bateman 2007), but was not tested for individuals differing in body size. If different sized species have different life spans, such costs may also be carried for longer. Selective forces for autotomy are therefore driven by a very wide range of factors. For many species, the costs incurred are such that other defense mechanisms, especially those that work in conjunction with increased body size — thereby reducing the need for autotomy — become worthy investments.

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