Interaction between phenology and density effects on mortality from natural enemies

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Summary

1. The gypsy moth is one of many early spring-feeding Lepidoptera that have outbreaks. Previous work has revealed that mortality from natural enemies varied between egg hatch dates separated by only a few weeks. However, this phenology effect was confounded with density differences caused by differential dispersal and early larval survival of the releases.

2. Five different densities of larvae were released at two different times in early spring, and monitored for the causes and amount of mortality in the field. We thus sought to separate the effects of timing and density on mortality.

3. Mortality in the larval stages due to parasitoids, disease and physiological causes was density-dependent for both release date treatments, but the slope of the mortality vs. density line was much steeper for the early release. Total mortality over the entire generation, which included additionally mortality from predation, was density-dependent for the early release but not for the late release.

4. The timing of egg hatch thus affects fecundity, mortality from natural enemies and the form of the relationship between density and mortality. These compounding effects may help explain why spring-feeding insects are liable to have outbreaks.

Key-words: density dependence, parasitoids, population dynamics.

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Introduction

Debates about the relative importance of different factors in determining animal and plant population dynamics are typically framed as dichotomies, for example in terms of density dependence vs. density independence (Dennis & Taper 1994; Turchin 1995) or in terms of bottom-up vs. top-down (Hunter & Price 1992). Most populations in nature, however, are likely to be influenced by both density-dependent and density-independent factors (Turchin 1995), and both bottom-up and top-down factors. An additional possibility is that different factors may interact so that, for example, density-independent factors may strongly influence density-dependent factors.

This study examines the interaction between density-dependent effects of natural enemies and the density-independent effect of weather-driven events for a forest insect. Outbreaking forest insects are much studied because of the impact of their defolia-

tion on forestry and recreation, but there is little consensus on the causes of their population fluctuations (Price 1987; Harrison & Cappuccino 1995). The study also considers how timing of hatch affects the relative importance of a bottom-up influence, host plant quality, and a top-down influence, natural enemies.

Spring-feeding forest insects are especially liable to have outbreaks, compared to summer-feeding species (Hunter 1991, 1995; Haack & Mattson 1993; Larsson, Bjorkman & Kidd 1993). Many authors have hypothesized that variable synchrony with host budburst is the cause of this association (Embree 1965; Varley & Gradwell 1968; Holliday 1977; Witter & Waisanen 1978; Nothnagle & Schultz 1987; Hunter M 1990; Hunter A 1991; 1993), Watt & McFarlane 1991). Insects that emerge from winter dormancy too early starve, and those that emerge too late must feed on low-quality food. Fluctuations in abundance could thus be driven by the effects of timing on survival, growth and fecundity. Since insects that do not synchronize with leaf emergence do not experience these effects on population growth parameters, their populations should not be so variable, i.e. they are less likely to have outbreaks.

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Traditionally, this hypothesis only involves food availability and quality, and not natural enemies. However, if feeding on older foliage extends larval development and increases the exposure of vulnerable stages to natural enemies, higher mortality from natural enemies would also be expected (Moran & Hamilton 1980; Schultz 1983; Benrey & Denno 1997). On the other hand, disruptions in synchrony between predators and prey could reduce enemy mortality. Here, the impact of the timing of gypsy moth (*Lymantria dispar* L., Lymantriidae) egg hatch relative to budburst on mortality from natural enemies is examined.

In previous work manipulating the phenology of gypsy moth egg hatch, we found different amounts and sources of mortality from natural enemies at release dates differing by only a few weeks (Hunter & Elkinton 2000). However, these differences were confounded by differences in density. That is, releases just before or at the time of budburst had higher mortality rates in the late instars, but also higher densities, than releases after budburst. Thus, the differences in mortality rate could be due not to the phenology treatment but to density-dependent responses of natural enemies. Of course, both phenology and density could be important if the effect of density depends upon the timing.

To separate the effects of density and phenology, a range of densities were released at two times in spring. Changes in mortality rates with density at the two release times were measured. If mortality rates change in the same way with density for both times, then the density difference alone would explain the lower mortality rate of the late release. Alternatively, there may be different effects of density at the two release times, in which case both phenology and density could contribute to the mortality rate differences.

Methods

STUDY SITE

Field studies were conducted on Otis Air National Guard Base, Cape Cod MA in 1997. Although densities of gypsy moth egg masses were very low (at less than five egg masses per hectare), this site is highly suitable for the gypsy moth. Outbreaks have occurred on Cape Cod in the past more frequently than anywhere else in Massachusetts (Liebhold & Elkinton 1989). Forests in this area are dominated by black oak (*Quercus velutina* Lam.) (70% of stems greater than 2·45 cm d.b.h.), white oak (*Quercus alba* L.) (12% of stems), pitch pine (*Pinus rigida* Mill.) (9% of stems) and red maple (*Acer rubrum* L.) (6% of stems). Blueberry (*Vaccinium* sp.) dominates the understorey. Trees in these stands are relatively short, about 6–8 m high, so the canopy can be readily sampled with pole pruners. The Air National Guard collects weather data at Otis Air Base.

GYPSY MOTH EGGS AND RELEASE PLOTS

Gypsy moth eggs were collected from outbreak populations in Michigan in mid-winter in 1997. Eggs were placed in hardware-cloth packets, each packet holding 5·3 g of eggs, and stored at 4–76 °C until needed. These packets allow larvae to emerge while retaining eggs. Upon removal from cold storage, egg packets were sterilized in 10% formaldehyde for 1 h, then rinsed for 1 h under running water. This treatment kills virus on egg surfaces (virus commonly occurs in high density populations). The fungus *Entomophaga maimaiga* Humber does not appear to be transported on egg masses (Yerger & Rossiter 1996).

Egg packets were divided into groups of five, placed in paper lunch bags and warmed at room temperature until they began to hatch. Ten subsamples of 100 eggs each were held at the same temperature as the packets. The subsamples of eggs were used to monitor the timing of emergence as well as the percentage hatching. When at least 30% of eggs had hatched in the subsamples, larvae were released into the field. The emerging larvae were gently brushed from the packets and onto the paper bags, then the bags were stapled to the trees. The packets were placed in fresh bags and returned to the lab to continue warming, until over 80% of eggs had hatched. Then the packets were stapled to the trees so the remaining larvae could emerge. Releases were begun on 30 April ('Early') and 30 May ('Late') (Fig. 1).

Five plots were set up at each release date. Plots were separated by at least 300 m so that dispersal of ballooning gypsy moth larvae between plots was negligible. We aimed to release 1×10^6, 5×10^5, 2.5×10^5, 1.25×10^5 and 6.25×10^4 larvae in the plots to create a range of densities.

Natural densities of gypsy moth were extremely low and it was not possible to find egg masses, but several laboratory colony egg masses were placed in the outdoor insectary in February, and we monitored the timing of their hatch. Tree phenology was gauged by visual estimates of the proportion of leaves emerging from the buds on 15 trees of each species. Budbreak is markedly synchronous at this site, perhaps because the topography is flat and temperatures are strongly influenced by coastal air masses.

DIRECT FOLIAGE AGE EFFECTS ON SURVIVAL AND GROWTH

To measure the direct effects of foliage age on survival and growth, newly hatched larvae were placed in
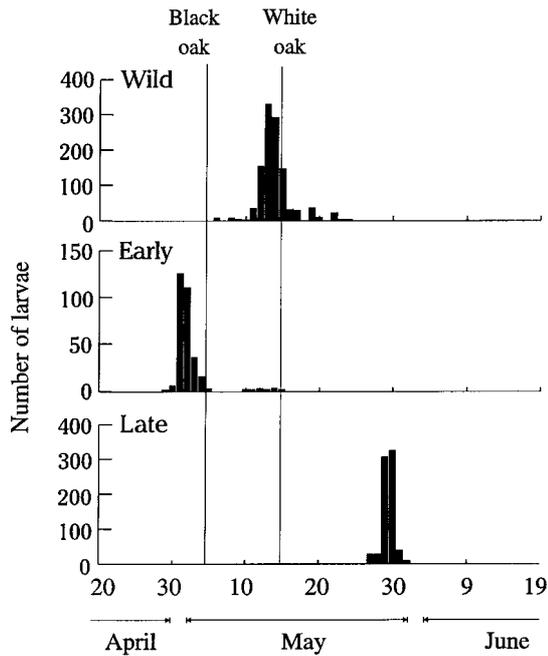
Fig. 1. Egg hatch dates of (a) laboratory colony eggs placed in an outdoor insectary in February, (b) the early release and (c) the late release. Vertical lines denote timing of black oak and white oak budburst.

spun polyester bags (100 × 50 cm) at each release date. The bags protect larvae from predators and parasitoids. Bags were doubled and sewn shut at one end, and closed at the other end with electric-cable ties. On each release date, 40 larvae were placed in each of 20 bags: 10 on white oaks and 10 on black oaks. Larvae were carefully transferred from the sterile plastic containers into which they had been counted onto the foliage and the inner surface of the bag, with sterile fine paintbrushes. At the first check, in the third instar, surviving larvae were split into smaller groups, and after that bags were moved among trees as necessary to provide sufficient foliage to prevent defoliation. Each bag was on a different tree, and trees were not re-used. Pupae were weighed, then held in the insectary until adults emerged. Males and females were mated and the eggs laid by females were counted.

SOURCES OF MORTALITY: PATHOGENS AND PARASITOIDS

To measure the contributions of pathogens and parasitoids to mortality, larvae were collected from each plot at weekly intervals after the releases. Larvae were placed directly into plastic cups containing wheat germ-based diet. We always moved from the lowest density plots to the higher densities when making collections, to try to minimize the spread of disease. The larval instar was scored, and

larvae were held for 1 week in an outdoor insectary. Larvae that died in this week were held for at least 2 days to allow for emergence of parasitoids, then autopsied under a light microscope at 400× to check for pathogens. First instar larvae suffer little mortality, so more (100 per replicate) were collected. In the later instars, 50 larvae were collected from each release plot each week. Larval mortality was expressed as marginal rates (Elkinton *et al.* 1992) and converted to *k*-values.

The most common parasitoids in this area are the specialist braconid wasp *Cotesia melanoscela* (Ratzeburg) and the generalist tachinid fly *Compsilura concinnata* (Meigen). The fungus *Entomophaga maimaiga* and a nuclear polyhedrosis virus (NPV) are common pathogens of gypsy moth but no virus was detected in the samples. The surface sterilization of eggs prevented the transfer of NPV from the high density source populations. Many early instar larvae died at the time of moulting from one instar to the next, but showed no pathogens when examined under the microscope. This was classified as 'moulting stress.'

MORTALITY IN THE FIELD: BURLAP COUNTS AND PREDATION

From the late fourth instar on, gypsy moth larvae seek daytime resting locations under bark flaps or in the litter, where they are concealed from some predators. This behaviour can be used to produce a relative estimate of density. Larvae will use burlap skirts as daytime hiding places and pupation sites and can easily be counted. Burlap skirts were provided on the boles of trees at 5-m intervals to a maximum of 40 m along transects in the main compass directions in the release plots (65 trees per plot). The number of larvae and pupae under or near the burlaps was counted three times for each release, at weekly intervals. Individuals were also counted later in the season, first when all larvae had pupated and later when adults had emerged. Females are flightless and do not walk far, so egg masses are typically found close to the pupation site.

k-values for total mortality in the field were calculated. These can be compared to the *k*-values from the weekly collections for the same period. The collections reveal mortality from pathogens and parasitoids and unknown causes, while the burlap *k*-values encompass mortality from these sources, plus predation.

POPULATION GROWTH RATE ESTIMATES

To integrate the opposing effects of host plant quality and mortality from natural enemies, the population growth rates were calculated, based on the survival and fecundity. Survival to adulthood was

Table 1. Proportion of larvae surviving to pupation in protective bags, on two host species, when released at different times in spring. *t*-test performed on arcsin–square-root transformed data

	Mean survival (proportion)	SD	*t*-test
Black oaks			
Early release	0·27	0·185	$t_{18} = 0·31$
Late release	0·32	0·213	$P = 0·76$
White oaks			
Early release	0·12	0·116	$t_{18} = 1·56$
Late release	0·22	0·184	$P = 0·14$

estimated from the burlap band counts. No adults or egg masses were found on trees that did not have burlap bands. The fecundity estimates from the two oak species were combined by assuming that at the early release, 80% fed on black oak and 20% on white oak, while at the late release 70% of larvae fed on black oak and 30% on white oak. This approximates the availability of these species and changes in the proportion of larvae using them at the two dates (A.F. Hunter & J.S. Elkinton, unpublished). A 1 : 1 sex ratio is assumed.

Results

MORTALITY AND FECUNDITY IN PROTECTIVE BAGS

Survival rates to pupation of insects in protective bags were about 30% on black oak and 16% on white oak (Table 1). There were no differences in survival rate to pupation between the early and late releases on either host species.

The fecundity differed between release dates and host species (Table 2, Fig. 2). For both host species, females produced on average 100 fewer eggs at the late release compared to the early release, and females reared on white oak produced 180 more eggs than those on black oak (Fig. 2).

**Table 2.** Analysis of variance comparing fecundity of gypsy moth reared on two host species from two release dates

	Degrees of freedom	*F*	*P*
Release date	1	20·9	< 0·001
Host species	1	64·2	< 0·001
Release * host	1	0·003	0·956
Error	146		
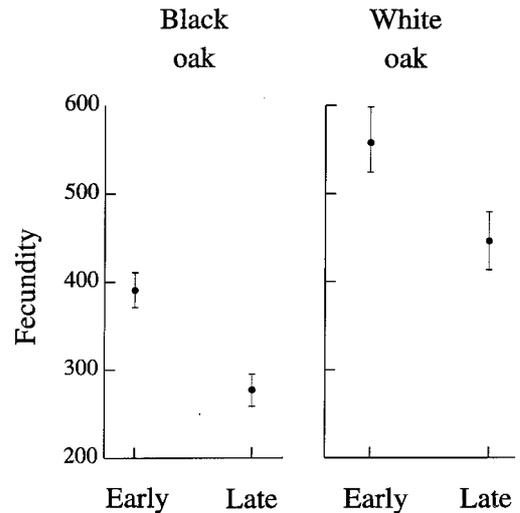
Fig. 2. Fecundity (mean $\pm$ SEM) of moths reared from two release dates on black oak and white oak hosts.

MORTALITY IN COLLECTIONS

Analysis of the mortality from collections was complicated by the fact that we could not find enough larvae to collect from the two lowest-density late releases in the last 4 weeks of collections. Gypsy moth densities decline dramatically from week to week, and with the low initial density and large spatial spread of the late releases, densities were so low that we could not find sufficient numbers of larvae in a reasonable amount of time. It was possible to count them under burlaps, however. Collections were not made from burlapped trees in any of the plots.

For the collections, mortality rates depend on both the density at release and the timing of release (Fig. 3). There is a significant interaction between
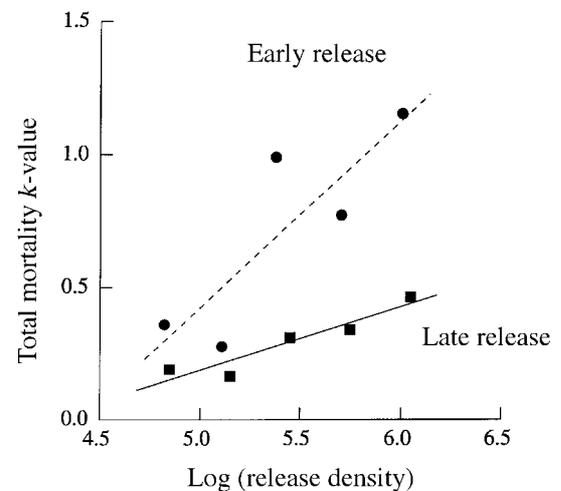
Fig. 3. Mortality in collections: total mortality vs. density at release. Mortality rate is expressed as a *k*-value, based on the marginal rate of mortality. Collections extend from the second instar to the sixth instar, at weekly intervals.

release date and density ($F_{1,7} = 15\cdot4$, $P = 0\cdot006$), indicating that the slopes of the lines in Fig. 3 differ. Mortality rates from parasitoids and disease are much higher in the high-density plots, and in the earlier release. The differences are largely due to the parasitoid *Compsilura concinnata* and the fungus *Entomophaga maimaiga* (Fig. 4). Mortality from the parasitoid *Cotesia melanoscela* is higher at the later release and in the intermediate density of that release.

MORTALITY UNDER BURLAPS

Disappearance rates from under burlap also increased with density in the early release, but not in the late release (Fig. 5; $F_{1,7} = 13\cdot5$, $P = 0\cdot008$ for the interaction between density and release date). Note that the data here cover the period from the neonate to the adult stage, a greater period than the collection data (second instar to sixth instar), and encompass predator mortality as well as disease, parasitism and physiological causes.

POPULATION GROWTH RATES

Although the early release insects had higher fecundity on both host species than the late release insects, this was not enough to make up for the much lower survival of the early release (Table 3). All populations are shrinking, that is the expected number of eggs next year is much lower than the amount of larvae released this year. No pupae or adults were found in the lowest density early release plot, and very few were found in the other densities.

Discussion

There is a strong interaction between the density-independent factor, the timing of release, and the density-dependent mortality rates from natural enemies. While mortality rates of larvae from parasitoids, disease and physiological causes were density-dependent at both release dates, the slope was much steeper for the early release. Total mortality, from egg to adult and including predation, was density-dependent for the early release but not for the late release. It is difficult to imagine two more disparate
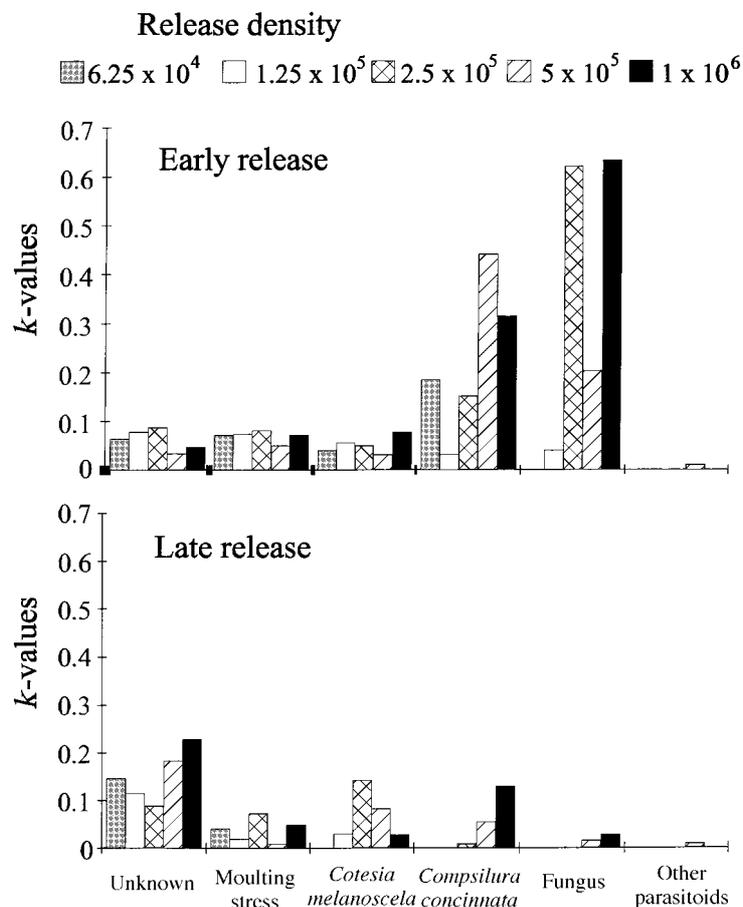
Fig. 4. Mortality (k-values) in collections: mortality sources for each release and density.
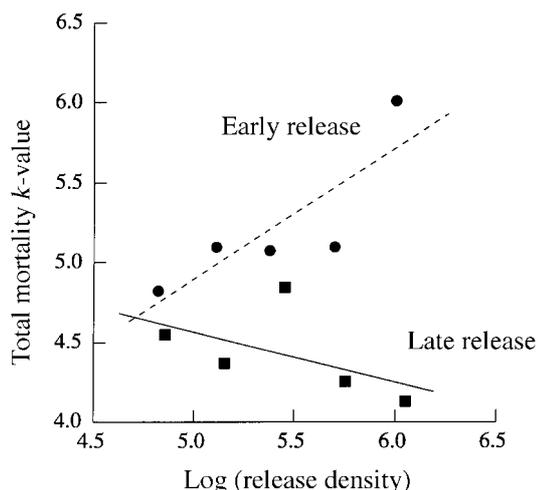
Fig. 5. Mortality (*k*-values) in the field: disappearance from newly hatched larvae to adult stage vs. release density.

pictures of the same system, yet these releases are only 4 weeks apart.

The different patterns for the two releases largely result from the fact that the two most important mortality agents in this year, the fungus *Entomophaga maimaiga* and the tachinid *Compsilura concinnata* caused little mortality at the late release compared to the early release. This temporal pattern for *E. maimaiga* has been consistent in the 3 years we have made releases at different times at this site, and it has always been the largest source of mortality at the early releases. Thus, our previous results in 1996 showing that early releases had higher mortality rates but also higher densities, would probably also be a combination of both phenology and density effects.

Patterns for the parasitoids varied substantially among years. In 1995 and 1996 *C. concinnata* was not an important contributor to total mortality, although it was in 1997. Also, in 1995 the total mortality was high at the late release because of high *C. melanoscela* mortality. Mortality rates in 1997 overall were much lower than for any of the releases at a

Table 3. Expected number of eggs produced by adults of each release and density. See text for details of calculation

Release size (larvae)	Early release		Late release
6.25×10^4	0		356
1.25×10^5	221		1068
2.5×10^5	441		712
5×10^5	882		5518
1×10^6	221		14 952

comparable density (5×10^5) in previous years. Thus, there is considerable variation from year-to-year in the amount and sources of mortality. Similarly, Auerbach (1991) found considerable inter-annual variation in the causes and amount of mortality of a leaf-mining insect.

Parry, Spence & Volney (1998) also found an interaction between phenology and natural enemy mortality in spring-feeding forest tent caterpillars (*Malacosoma disstria* Hubner). First instar larvae from earlier releases developed more rapidly, and suffered less predation, than larvae from later releases. It was unclear in this study whether development rate or timing *per se* were the most important factors. This is because several of the releases occurred before the most important predator was active, and these releases also had high development rates. In other studies, development rate has a significant impact (Raupp & Denno 1984; Loader & Damman 1991; Benrey & Denno 1997), although the development rate differences were not due to host phenology.

The timing of egg hatch thus affects the fecundity, survival in the presence of natural enemies and the form of the relationship between density and mortality rate. However, in apparent contradiction to expectations there was a cost to hatching at the natural time for gypsy moth. Although fecundity was higher in the early release, in this and all years of our study (Hunter & Elkinton, in review), the fecundity was not high enough to counteract the lower survival rate of the early releases. Why do gypsy moth larvae hatch early, risking starvation if they emerge too long before budburst? (this is the same question Feeny 1970 asked about winter moth). For gypsy moth, we offer two possible explanations:

1. *E. maimaiga* epizootics, which imposed higher mortality on the early releases in all years, are a relatively new phenomenon in gypsy moth dynamics in this region. It has only been detected in populations since 1989, despite intensive sampling and the easy detection of the conspicuous resting spores of late-instar fungus-killed individuals. Gypsy moth may not have had time to adjust its phenology to this new factor. *E. maimaiga* thrives on the cool and wet conditions that prevail in early spring on Cape Cod (Hajek, Carruthers & Soper 1990; Weseloh & Andreadis 1992).

2. Natural enemy mortality varies unpredictably from year to year (Hunter & Elkinton, in press), but there was a consistent decline in fecundity with leaf age, as is found in many other studies of foliage age effects in folivorous insects. The abundance and impact of natural enemies could depend on many other factors, such as alternate hosts or prey, higher trophic levels or weather. Although they have a large impact on gypsy moth success, their variability

would not lead to consistent selection for a late hatch phenology. The consistent effect of leaf age on fecundity could drive gypsy moth to early hatch.

There is not enough information on gypsy moth mortality from natural enemies at different times, nor the availability of genetic variation in gypsy moth phenology for selection to act upon, to assess the relative merits of these hypotheses.

Density dependence is rarely detected in observational data of predator and prey insects (Stiling 1988). While the length of the time series (Hassell, Latto & May 1989), the type of test used (Holyoak 1993) and the existence of time lags can affect the potential detection of density dependence, the perturbing effect of density-independent factors may also be important.

Acknowledgements

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