

The foraging behaviour of honey bees (*Apis mellifera* L) and bumble bees (*Bombus* spp) on cranberry (*Vaccinium macrocarpon* Ait)

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Summary — The behaviour of honey bees and bumble bees while foraging on cultivated cranberry in southeastern Massachusetts was studied. Bumble bees were much more consistent foragers than are honey bees. Whether collecting nectar or pollen, bumble bees almost always approached a flower in a manner that pollen transfer could occur. Honey bees foraged for nectar legitimately or illegitimately by probing at the base of the flower. Although they rarely forage pollen on cranberry, a few honey bee foragers collected pollen by drumming the anthers with their forelegs. Significantly fewer honey bees foraged legitimately for nectar or collected pollen than did bumble bees. In addition, honey bees had more mixed pollen loads and were slower foragers on cranberry than were bumble bees. Thus, bumble bees appear to be better cranberry pollinators than honey bees, and methods of using bumble bees as managed pollinators of cranberry should be developed.

Apis mellifera / *Bombus* spp / cranberry / pollination / foraging

INTRODUCTION

Cranberry is an important, high value crop in the areas of North America where it can be grown successfully (McGregor, 1976; Eck, 1990). Although the plant is native to North America, cranberry growers currently depend on the rental of colonies of introduced honey bees to ensure pollination (Robinson *et al*, 1989). Cranberry is ericaceous and thus has flower morphology adapted for vibratile pol-

lination. The single pistil is surrounded by a ring of stamens each with a basal anther sac bearing a long appendage and a terminal pore. In order to collect pollen from this type of flower, a visiting pollinator grasps the flower and vibrates its wing muscles. This causes pollen movement within the anther sac and eventually the release of a stream of pollen from the pore which results in pollination (Buchmann, 1983, 1985). Although bumble bees and many other native North American bees are known to exhibit this for-

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aging behaviour, honey bees do not. While honey bees can collect pollen from cranberry by anther drumming, they do so only rarely (Cane *et al.*, 1993). Pollen foraging bees (bumble bees and a solitary anthophorid, *Habroproda laboriosa* F) are more effective pollinators of rabbiteye blueberry (*Vaccinium ashei* Reade), another ericaceous plant, than are nectar-collecting honey bees (Cane and Payne, 1988).

Differences in pollination success among bee species have been related to foraging behaviour. For example, honey bees are poor pollinators of alfalfa (Gray, 1925; McGregor, 1976) and Delicious apples (Robinson, 1979) because they forage in a manner that allows nectar collection without pollen transfer. On cranberry, some researchers have noted that honey bees also forage without touching the stigma, and thus do not pollinate the flower (Roberts and Struckmeyer, 1942; Farrar and Bain, 1946; Franklin, 1950). Bumble bees have been cited as more effective cranberry pollinators (Franklin, 1950; McGregor, 1976; Eck, 1990). However, differences in foraging behaviour between bumble bees and honey bees on cranberry have never been properly documented. This study was designed to both describe and evaluate the foraging behaviour of honey bees and bumble bees on cranberry.

MATERIALS AND METHODS

Foraging behaviour

The study was carried out on 9 commercial cranberry bogs in southeastern Massachusetts over a 3 year period (1990—1992) during mid-June to early July. Honey bees and bumble bees were observed as they foraged on cranberry flowers and their activities were noted. Differences were observed in foraging behaviour for honey bees and bumble bees and for nectar *versus* pollen collection in both groups.

Nectar foraging

In 1991, nectar-foraging by honey bees and bumble bees was rated. Ten 5-min censuses were run. The observer walked randomly throughout the bog recording all honey bees and bumble bees encountered as either foraging normally for nectar (probing with the probocis down the staminal column or at the base of the flower while contacting the stigma with the abdominal sternites) or foraging illegitimately (probing at the base and not contacting the stigma). The percentage of honey bees and bumble bees foraging legitimately was calculated and compared by paired *t*-test after an arcsine transformation (to achieve normality) (Zar, 1984).

Pollen foraging

Honey bees and bumble bees were censused in 1992 for pollen foraging. The observer walked randomly through the bog recording all bees encountered as either having or not having a pollen load. Five 2-min counts were done for each of 7 observation periods. Percentages of foragers of the 2 bee groups with pollen loads were compared by 2-way ANOVA (bee, observation period) and Tukey's multiple comparison test after square root transformation (to account for differences in variances) (Zar, 1984).

As a second measure of pollen foraging, collections of bees foraging on cranberry, made in 1990 and 1991, were assessed for the presence of pollen loads (pollen type was not considered). Pollen loads were divided into large loads (those completely covering the corbiculae) and small loads. Small loads could accumulate by bees picking up small amounts of pollen as they nectar foraged, while the large loads would definitely be a result of pollen foraging. Honey bees and 6 species of bumble bees (*Bombus affinis* Cresson, *B. bimaculatus* Cresson, *B. impatiens* Cresson, *B. perplexus* Cresson, *B. terricola* Kirby, and *B. vagans vagans* Smith) were examined. The sites and years of collections varied depending on the species of bee in question. Percentages of bees with any pollen load and those with large loads were compared by 3-way ANOVA (year, site, species) after an arcsine transformation (to account for differences in variances) and Scheffe's multiple comparison test (used because of unequal sample sizes) (Zar, 1984).

A subsample of collected bees was examined for the proportion of *Vaccinium* pollen in the load. Twenty bees from each species (honey bees and the 6 species of bumble bees) were examined. For each specimen, a sample from the right pollen load was viewed under 150 times magnification, and 200 pollen grains were counted as either *Vaccinium* (pollen tetrads) or not *Vaccinium* (all other pollen grains). Percentages of *Vaccinium* pollen was compared by 3-way ANOVA (year, site, species) and Tukey's multiple comparison test after an arcsine transformation (to account for differences in variances) (Zar, 1984).

Foraging rates

In 1991, individual bees were timed as they foraged on at least 10 flowers, while in 1992 the number of flowers visited in 1 min by a bee was counted. Bees were categorized as honey bees, *B. impatiens*, or as another *Bombus* species. Floral handling times in terms of bloom visited per minute were calculated. Data for each year were analyzed by ANOVA and Scheffe's multiple comparison test (used because of unequal sample sizes) (Zar, 1984).

RESULTS

Foraging behaviour

Foraging bumble bees and honey bees either crawled in the vines or flew short distances between flowers. Occasionally, longer flights between sections of bog occurred. Differences in foraging behaviour between bumble bees and honey bees were marked.

Honey bees foraged in 2 basic ways for nectar. In the first instance, the bee would hang onto a flower with its legs while probing down the stigma between the stamens. The appendages of the anthers and the stigma splayed out around the bee's face. During this kind of contact it was possible for pollen to be transferred to the stigma from areas on the bee's head. In the second method, a bee would approach the flower

from the back while holding onto the petals, the pedicel, and even adjacent flowers. It would then probe at the base of the flower between the anther sacs. Sometimes the bee circled the flower probing entirely at the base. Only rarely was the stigma touched during this type of foraging, and the location of contact on the bee could be anywhere including the dorsum and the legs. It is unlikely that much, if any, direct pollen transfer occurred due to this type of foraging. Effectively, bees foraging in this manner were 'stealing' nectar. A combination of the 2 methods was also observed. A bee would first probe at the base of the bloom, perhaps sampling for nectar, then turn around on the bloom, and forage down the staminal column. Very few honey bees collected pollen while foraging on cranberry. During observations in 1991, only 2 of the 186 honey bees observed were seen pollen foraging; however, in a cage study pollen foraging was more common (MacKenzie, 1994). To collect pollen the forager held onto a flower with 1 pair of legs while hitting the stamens with its front legs and also moved about rapidly jostling the bloom.

Bumble bees approached the bloom in a stereotypic manner. They almost always held onto the petals with their legs while the body was held below the reproductive parts of the flower. The abdomen more or less curled around the staminal column, with the stigma touching the first and second sternites. This area, which carried accumulations of pollen, appears to be a 'safe spot' for pollen on bumble bees. *B. impatiens* foragers almost always probed for nectar with their probocis down the stigma between the stamens, while other species, such as *B. terricola* and *B. affinis*, tended to forage at the base of the flower. In either case, however, the forager's body was held in the described manner so that the stigma touched the pollen on the abdominal sternites. Only rarely did bumble bees probe for nectar in such a manner that the stigma was not touched (6 of the 132 bumble bees

observed in 1991). Bumble bees collected pollen by vibrating the cranberry bloom. *B. affinis* and *B. terricola* usually probed at the base of the flower while vibrating, while *B. impatiens* probed at the base while vibrating and then probed down the staminal column, presumably to more effectively collect nectar before leaving the flower.

Nectar foraging

Bumble bees foraged legitimately (touched stigma) $95.9 \pm 6.2\%$ of the time. This was more frequent than honey bees, who foraged legitimately $41.4 \pm 15.7\%$ of the time ($P < 0.05$, $n = 10$ pairs consisting of 103 bumble bees and 149 honey bees).

Pollen foraging

Bee type and observation period significantly affected the percentage of bees pollen foraging ($P < 0.05$, $n = 7$ observation periods

consisting of 345 honey bees and 171 bumble bees). Only $3.2 \pm 6.1\%$ of honey bee foragers collected pollen, compared with $73.7 \pm 25.6\%$ of the bumble bees.

Analyses of pollen loads in collections made from bees foraging on cranberry also showed significant differences between honey bees and bumble bees (table I). Fewer honey bees than any of the various bumble bees carried pollen loads of any size, and very few honey bees (3.5%) had large loads. While the 6 bumble bee species had similar percentages of loads of any size, there were significant differences between species in the percentage with large loads. *B. impatiens* had significantly more foragers with large loads than did *B. bimaculatus*, while the other 4 species were intermediate. No statistically significant differences in pollen loads were found between sites or years ($P < 0.05$).

Examinations of pollen loads for the presence of *Vaccinium* pollen showed significant differences between honey bees and bumble bees (table II). All 6 species of bum-

Table I. Percentages of bees with pollen loads in collections of foragers from 9 cultivated cranberry bogs in 1990 and 1991*.

Species	Sample size ^a		Mean ^b	
	n_c	n_b	All loads	Large loads
<i>A. mellifera</i>	12	442	15.9 ^{Bc}	3.5 ^C
<i>B. affinis</i>	4	26	95.8 ^A	73.7 ^{AB}
<i>B. bimaculatus</i>	9	72	73.0 ^A	53.0 ^B
<i>B. impatiens</i>	9	149	94.5 ^A	81.6 ^A
<i>B. perplexus</i>	3	16	83.3 ^A	72.2 ^{AB}
<i>B. terricola</i>	5	30	76.0 ^A	66.3 ^{AB}
<i>B. vagans vagans</i>	4	42	75.3 ^A	50.7 ^{AB}
Pooled SE			6.3	6.7

* Calculations were made separately on collections from different sites and years. ^a The number of collections used is indicated by n_c and total number of bees examined by n_b . Only those sites and years where sufficient numbers of individuals of a species ($n \geq 4$) were collected were considered in the data analysis. ^b Means were averaged across years and sites. ^c $P < 0.05$ from analysis of variance after arcsine transformation. Untransformed means are reported. No significant difference was present in year or site. For each column, different letters indicate significant differences in means by Scheffe's multiple comparison test.

ble bees had significantly purer loads (range from 88.8 to 95.5% *Vaccinium*) than did honey bees (71.6% *Vaccinium*). The percentage of *Vaccinium* pollen in loads also varied by site ($P < 0.05$).

Table II. The percentage of *Vaccinium* pollen * in loads carried by bees collected foraging on cultivated cranberry flowers in 1990 and 1991.

Species	Mean ^a
<i>A mellifera</i>	71.6 ^b
<i>B affinis</i>	93.4 ^c
<i>B bimaculatus</i>	94.7 ^c
<i>B impatiens</i>	91.4 ^c
<i>B perplexus</i>	95.5 ^c
<i>B terricola</i>	88.8 ^c
<i>B vagans vagans</i>	92.4 ^c
Pooled SE	3.6

* Determined by classifying 200 pollen grains from the right load of each bee into *Vaccinium* and non-*Vaccinium* pollen. Based on $n = 20$ per species. ^a Means were averaged across years and sites. $P < 0.05$ from ANOVA after arcsine transformation. No significant difference was seen between years, but significant differences were seen between sites. Different letters indicate significant differences in means by Tukey's multiple comparison test.

Table III. Foraging rates (number of flowers visited per min) of bees on cultivated cranberry bogs in 1991 and 1992.

Species	1991		1992	
	n	Mean	n	Mean
<i>A mellifera</i>	30	9.6 [*]	42	8.9 ^b
<i>B impatiens</i>	19	12.6 ^a	40	13.3 ^a
Other <i>Bombus</i> species	19	12.0 ^a	40	13.7 ^a
Pooled SE		0.7		0.5

* $P < 0.05$ from ANOVA. For each column, different letters indicate significant differences in means by Scheffe's multiple comparison test.

Foraging rate

Honey bees foraged significantly more slowly than did bumble bees in both years of the study (table III). Although different methods were employed, the results were fairly consistent between years.

DISCUSSION

Honey bees and bumble bees differ in their foraging behaviour on a high value, native North American berry crop, the cranberry (*V macrocarpon*). Bumble bees are very consistent foragers on cranberry. They approach the bloom so that their body curls around the reproductive parts of the flower, thus effecting pollen transfer. On the other hand, honey bees are less reliable pollinators. Most honey bees forage in a manner such that the stigma is not contacted, effectively 'stealing' nectar. Those that do forage for nectar legitimately could transfer some pollen from safe areas on the head. While few honey bees forage for cranberry pollen, the majority of bumble bee foragers do. Pollen foraging bees are more effective pollinators (MacKenzie, 1994) and deposit significantly more pollen on the stigma (Plowright, personal communication) than those that forage solely for nectar. In addition, bumble bees are faster foragers than are honey bees. Franklin (1950) also noted some of these differences between honey bees and bumble bees foraging on cranberry.

An unexpected result of this research was that a greater proportion of honey bees carried mixed pollen loads than did bumble bees. Honey bees usually have almost pure pollen loads as individuals tend to specialize on plant species during individual foraging trips (Free, 1963; Wells and Wells, 1983). On the other hand, bumble bees tend to sample as they forage and thus should carry mixed loads (Heinrich, 1976, 1979). On cranberry, however, the opposite is true.

This may be because there were few flowering weeds in the cultivated bogs and thus there were no other plants for the bumble bee foragers to sample.

Due to the great demand for nectar in the hive, many honey bees forage strictly for nectar. On cranberry, this is true as pollen foraging by honey bees is rarely seen, and varies with different years and sites (Cane *et al*, 1993; MacKenzie, 1994). Even on the same bog, there can be widespread differences in the proportion of foragers from different colonies that return with loads of cranberry pollen (Shimanuki *et al*, 1967). It appears, then, that such factors as weather, the availability of alternative pollen and nectar sources, genetics, and colony stores of pollen influence whether or not honey bees will harvest cranberry pollen. On cranberry and other ericaceous crop plants, the rabbiteye and highbush blueberries, nectar foragers are poorer pollinators than are pollen foragers (Cane and Payne, 1988, 1990; MacKenzie, 1994). In addition, honey bees are able to collect cranberry nectar without contacting the stigma. They do so by foraging at the base of the flower only. The large proportion of honey bees (almost 60%) that foraged illegitimately in this study should be of concern to commercial cranberry producers. The facts that there are few pollen collectors, that there is poor presentation of pollen while foraging, that the pollen loads are mixed, and that their behaviour varies between sites indicate that honey bees are not very well suited to cranberry pollination.

Fruit size has a direct relationship with seed number in cranberry (Roberts and Struckmeyer, 1942; Rigby and Dana, 1971; Sarracino and Vorsa, 1991). Poorer pollen deposition would result in lower fertilization rates of the ovules, and thus, ultimately, smaller berries and overall yields. Current average cranberry fruit sets of about 33% result in yields of around 370 barrels per ha (150 barrels per acre) (1 barrel equals 45.4

kg or 100 lb) (Eck, 1990). Much higher yields, sometimes nearing 740 barrels per ha, and fruit sets of about 50% have been seen in some bogs in some years (Stricker 1946; Marucci and Filmer 1964; Eck, 1990; Strick and Poole 1991). Growers would like to be able to achieve production nearer these values. Improved pollination is one way to do this. As bumble bees forage successfully for pollen and are active within the cranberry bogs of Massachusetts, they should be considered as a possible alternative managed pollinator. This is especially true now that bumble bees are being reared commercially for greenhouse pollination (van Heemert *et al*, 1990; van den Eijnde *et al*, 1991). *B. impatiens*, the species being reared and used in northeastern United States and Canada (Plowright, personal communication), was an excellent forager on cranberry. Therefore, it may be possible in the near future to rent or buy bumble bee colonies for pollination of field crops with specialized pollination syndromes such as cranberry. However, additional research on the pollination effectiveness of these bees on cranberry is needed to determine their value for increasing yield and suggested stocking rates.

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Résumé — Comportement de butinage des abeilles domestiques (*Apis mellifera* L) et des bourdons (*Bombus* sp) sur can-

neberges (*Vaccinium macrocarpon* Ait).

Le comportement de butinage des abeilles domestiques et des bourdons a été étudié sur des cultures de canneberges dans le sud-est du Massachusetts. Les bourdons abordent les fleurs de telle façon qu'il peut y avoir transfert de pollen : ils s'agrippent aux pétales avec leurs pattes tandis que leurs corps est maintenu en-dessous des parties reproductrices de la fleur. Ils puisent le nectar en bas de la colonne staminale ou à la base de la fleur et font vibrer la fleur pour récolter le pollen. Les abeilles domestiques butinent le nectar soit par la voie normale en puisant celui-ci à la base de la colonne staminale, soit par la voie détournée à la base de la fleur sans toucher le stigmate. Bien qu'elles soient rarement butineuses de pollen sur les canneberges, les abeilles domestiques peuvent le récolter en tambourinant sur les anthères avec leurs pattes antérieures. En 1991 on a dénombré les abeilles et les bourdons qui butinaient soient de façon normale, soit de façon détournée. Pour chacune des 10 séries, l'observateur parcourait au hasard la tourbière durant 5 min et notait l'activité de toutes les abeilles rencontrées. Un nombre significativement plus grand de bourdons que d'abeilles domestiques butinaient de façon normale (95,9 + 6,2% contre 41,4 + 15,7% respectivement, test-*t* par paires, $P < 0,05$). En 1992 on a noté, pour toutes les abeilles domestiques et les bourdons rencontrés au cours d'une période d'observation, la présence ou non de pelotes de pollen. Cinq comptages de 2 min ont été faits pour chacune des 7 périodes d'observation. Le type d'insecte et la période d'observation étaient tous deux statistiquement différents (test F ANOVA, $P < 0,05$). Seuls 3,2 + 6,1% des butineuses d'abeilles domestiques ont récolté du pollen, contre 73,7 + 25,6% des bourdons. Lors d'une seconde mesure de la récolte de pollen, on a noté la taille des pelotes (petite ou grosse). Les différences étaient significatives pour l'espèce d'abeilles considérée, mais pas pour l'année

ni pour le lieu (test F ANOVA, $P < 0,05$). Moins d'abeilles domestiques que de bourdons portaient des pelotes de pollen toutes tailles confondues et elles étaient très peu nombreuses à porter de grosses pelotes (tableau I). Les 6 espèces de bourdons différaient significativement par le pourcentage de grosses pelotes (tableau I). Le pourcentage de pollen de *Vaccinium* dans les pelotes a été examiné chez 20 individus de chaque espèce étudiée. Le comptage a porté sur 200 grains de pollen de la pelote droite. Les 6 espèces de bourdons avaient des pelotes de pollen significativement plus pures que les abeilles domestiques (tableau II). Le pourcentage de pollen de *Vaccinium* a aussi varié en fonction du lieu (test F ANOVA, $P < 0,05$). Les taux de butinage (nombre de fleurs butinées par min) ont été mesurés en 1991 et 1992. Les abeilles domestiques butinaient significativement plus lentement que les bourdons (tableau III, test F ANOVA, $P < 0,05$). Les bourdons sont donc mieux adaptés que les abeilles domestiques à butiner sur les canneberges et sont probablement de meilleurs pollinisateurs. Des méthodes de gestion des colonies de bourdons pour polliniser la canneberge devraient être mises au point.

Apis mellifera* / *Bombus* spp / pollinisation / butinage / *Vaccinium macrocarpon

Zusammenfassung — Das Sammelverhalten von Honigbienen (*Apis mellifera*) und Hummeln (*Bombus* sp) auf Blüten der Preiselbeere (*Vaccinium macrocarpon* Ait). Das Verhalten von Honigbienen und Hummeln auf Preiselbeerkulturen wurde im Südosten von Massachusetts untersucht. Hummeln nähern sich den Blüten fast immer so, daß es zur Bestäubung kommt (legitimer Besuch): Sie halten sich mit den Beinen an den Blütenblättern fest, wobei sich der Körper unterhalb der Fortpflanzungsorgane der Blüte befindet. Sie suchen entlang des Griffels hinunter oder am Blütenboden nach

Nektar oder sie schütteln die Blüte, um Pollen zu sammeln. Honigbienen sammeln 'legitim' nach Nektar, indem sie am Griffel entlang suchen, oder 'illegitim', indem sie am Grunde suchen und sich dabei an der Rückseite der Blüte festhalten. Obwohl sie an Preiselbeeren nur selten Pollen sammeln, sind Honigbienen dennoch dazu imstande, indem sie mit ihren Vorderbeinen auf die Staubbeutel klopfen. Im Jahre 1991 wurden Honigbienen und Hummeln gezählt, ob sie legitim oder illegitim sammelten. Bei jeder seiner zehn Touren ging der Beobachter 5 min lang ohne Plan durch die Kultur, wobei er die Aktivitäten aller angetroffenen Bienen notierte. Signifikant mehr Hummeln als Honigbienen sammelten legitim ($95,9 \pm 6,2\%$ gegenüber $41,4 \pm 15,7\%$; gepaarter *t*-Test, $P < 0,05$). Im Jahre 1992 wurde das Sammeln von Pollen beurteilt. Alle während einer Beobachtungsperiode angetroffenen Honigbienen oder Hummeln wurden entweder als 'Pollenträger' oder 'ohne Pollen' eingestuft. Für jede der sieben Beobachtungsperioden wurden fünf Zählungen von je 2 min Dauer durchgeführt. Sowohl Art der Bienen wie Beobachtungsperiode waren verschieden (ANOVA F-Test, $P < 0,05$). Nur $3,2 \pm 6,1\%$ der Honigbienen sammelten Pollen, gegenüber $73,7 \pm 25,6\%$ der Hummeln. Als ein zweites Maß für die Pollensammeltätigkeit von Bienen an Preiselbeeren wurden sie danach unterteilt, ob sie überhaupt Pollen trugen oder ob sie große Ladungen hatten. Der Unterschied zwischen den Bienenarten war signifikant, während dies bei Jahr und Sammelort nicht der Fall war (ANOVA F-Test, $P < 0,05$). Weniger Honigbienen trugen Pollenladungen irgendeiner Art als die sechs untersuchten Hummelarten und nur wenige Honigbienen hatten große Ladungen (Tabelle I). Die sechs Hummelarten waren untereinander im Prozentsatz großer Ladungen sehr verschieden (Tabelle I). Von jeder Art wurden die Pollenladungen von 20 Bienen auf den Anteil von *Vaccinium*-Pollen untersucht. Von jedem Tier wurden vom

rechten Pollenhöschen 200 Körner als '*Vaccinium*' oder als '*Nicht-Vaccinium*' klassifiziert. Alle sechs Hummelarten hatten signifikant reinere Pollenladungen als die Honigbienen (Tabelle II). Der Anteil des '*Vaccinium*'-Pollens schwankte je nach der Sammelstelle (ANOVA F-Test, $P < 0,05$). Die Sammelgeschwindigkeit, ausgedrückt in Blüten per Minute, wurden sowohl 1991 wie 1992 gemessen. Honigbienen sammelten in beiden Jahren signifikant langsamer als Hummeln (Tabelle III, ANOVA F-Test, $P < 0,05$). Hummeln sind also an die Sammeltätigkeit bei Preiselbeeren besser angepaßt und wahrscheinlich sind sie auch bessere Bestäuber als Honigbienen. Es sollten Methoden zum Einsatz gezüchteter Hummelvölker in der Bestäubung von Preiselbeeren entwickelt werden.

***Apis mellifera* / *Bombus* sp / Bestäubung von Preiselbeeren / Sammelverhalten**

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