

Effects of dextrin and cellulose on feeding and reproduction in female brown-banded cockroaches, *Supella longipalpa*

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Abstract. Food consumption and reproduction were compared through two gonotrophic cycles in female brown-banded cockroaches, *Supella longipalpa* (F.), fed a standard rat food diet which had been serially diluted with methyl cellulose, alpha cellulose or dextrin. Females did not increase daily intake to compensate for dilution, and reproductive rate was highly dependent upon the degree of dilution of the diet. With increasing dextrin concentrations, digestibility increased, but reproductive rate, size and mass of oothecae, and efficiency of food utilization progressively decreased.

On diets containing 75% rat food and 25% methyl cellulose, females consumed minimal amounts of food and 80% of the females did not mate or produce oothecae within 30 days. On identical diets containing 25% alpha cellulose, food digestibility decreased and females ate significantly more than females fed 25% methyl cellulose, but less than females fed rat food. Many (65%) females fed 25% alpha cellulose produced oothecae which were smaller and took longer to form than in control females fed on rat food. At concentrations higher than 50% of either methyl or alpha cellulose daily intake was further reduced and females died rapidly.

Key words. Cockroach, reproduction, food dilution, cellulose, dietary compensation, nutrition.

Introduction

Many insects modulate consumption rates or alter feeding behaviour in an effort to maintain nutrient intake on low quality foods (McGinnis & Kasting, 1967; Gordon, 1968; Bignell, 1978; Simpson & Abisgold, 1985; Abisgold & Simpson, 1987; Hamilton & Schal, 1988;

Timmins *et al.*, 1988). Grasshopper nymphs (*Melanoplus sanguinipes* F.) increase feeding rates eightfold on a diet containing seven parts cellulose and one part wheat sprout meal (McGinnis & Kasting, 1967). *Locusta migratoria* nymphs compensate for a 50% dilution of dietary protein by increasing the frequency, but not the size of meals (Simpson & Abisgold, 1985). Fifth stadium tobacco hornworms (*Manduca sexta* (L.)) spend more time feeding on a high cellulose diet, increase consumption, decrease food transit time through the gut, and have slower growth rates than control caterpillars (Timmins *et al.*, 1988).

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Feeding is intimately associated with reproduction in German (*Blattella germanica* (L.)) and brown-banded (*Supella longipalpa* (F.)) cockroaches (Kunkel, 1966; Cochran, 1983; Durbin & Cochran, 1985; Hamilton & Schal, 1988; Hamilton *et al.*, 1990). Prior to production of an ootheca, females feed intensively, and use the ingested nutrients for oocyte maturation and ootheca production. However, unlike the adult female German cockroach, which alters feeding rates on high carbohydrate/low protein diets (Hamilton & Schal, 1988), brown-banded females do not increase daily feeding rates on such diets, resulting in reduced reproduction and lifetime fecundity (Hamilton *et al.*, 1990). Short-term reproductive rate is unaffected by diet composition if the nymphal diet is adequate, suggesting that adult females may mobilize nymphal reserves to supplement the adult diet (Hamilton *et al.*, 1990).

Cellulose is often treated simply as an inert, indigestible diluent of insect diets (Simpson & Abisgold, 1985; Timmins *et al.*, 1988). With cockroaches, cellulose is used as a component in artificial diets to add bulk and texture, with little regard for the chemical and physical properties or digestibility of the various types of cellulose. Preliminary evidence from our laboratory indicated that both the type and concentration of cellulose used in artificial diets might affect adult performance. We undertook the present study to determine whether female brown-banded cockroaches could alter their feeding rates to compensate for dilution of a standard commercial diet with dextrin, methyl cellulose or alpha cellulose. The information gained from these studies has important implications to routine maintenance of cockroaches, to basic studies of nutritional ecology, and to the proper formulation of toxic baits for the control of cockroaches (Schal & Hamilton, 1990).

Materials and Methods

Insects. Approximately 500 late stadium *Supella longipalpa* nymphs were maintained on Purina Rat Chow (No. 5012) and water at 27°C, 50% humidity under LD 12:12 h. Rat-food was available to the insects during the day and removed at night. Emergent adults were collected hourly during the day and held with water only

to ensure they had not fed prior to initiation of the experiment. Insects which emerged during the dark cycle (less than 24 h old and unfed) were also included in the experiments.

Diets. All insects that emerged within a 24 h period were weighed to the nearest 0.1 mg and divided among the treatments. The treatments consisted of rat food, a dilution series with dextrin (50%, 25%, 12% or 6% rat food), two dilution series each with methyl or alpha cellulose (75%, 50% or 25% rat food), and starvation (water only). Each treatment of the dextrin dilution series contained thirty insects; the starved insects, 25% methyl cellulose treatment and alpha cellulose series each contained twenty insects, and the other methyl cellulose treatments contained ten insects.

Experimental design. Insects were housed individually in 11 × 11 × 2 cm plastic cages with experimental diet and water continuously available. Beginning 2 days after emergence, each female was confined daily with two males for 2 h in the middle of the dark period until mating was observed. Females that failed to mate by day 15 were excluded from the analysis.

Daily food consumption was monitored gravimetrically through the production of two oothecae and corrected (0.95) to estimate dry mass. Deposited oothecae were collected and individually dried to constant mass at 60°C as was each female, after the second ootheca was dropped, and her total faecal production throughout this period. Initial dry mass of individual females was estimated by multiplying initial fresh mass by a conversion factor (0.277) obtained by drying twenty newly emerged females. The dry mass was used to calculate digestive parameters which were modified from Scriber & Slansky (1981) to include reproductive output of adult females and were based on food ingested (F), faeces produced (E), biomass gained (G) and reproductive output (R). The following calculations were performed: Assimilated food (ASM) = $F - E$, Approximate Digestibility (AD) = (ASM/ F) × 100, Efficiency of Conversion of Ingested Food (ECI) = $(G + R)/F$ × 100, and Efficiency of Conversion of Digested Food (ECD) = $(G + R)/ASM$ × 100.

Data analysis. Records of daily feeding and reproductive parameters (day of mating, ootheca formation and ootheca deposition, and size and mass of oothecae) were analysed by Analysis of Variance (ANOVA) and Duncan's

new multiple range procedures on raw or ranked values where appropriate.

Results

Diets diluted with dextrin

Most females mated and produced two oothecae. However, greater dilution of rat food with dextrin progressively slowed the females' reproductive cycle compared with females fed undiluted rat food (Table 1). Females fed the 94% dextrin diet mated 2 days later and required 3 days longer to form the first ootheca

than control females. Of those females that mated and produced first oothecae ($n=24$), only 66% produced a second ootheca which was delayed by 223% compared with controls fed on rat food (Table 1). Females fed diets with intermediate levels of dextrin (75% or 88%) showed intermediate patterns of mating and oothecal production (Table 1).

Prior to mating and until production of the first ootheca, there were no significant differences in total consumption among females fed rat food or any of the dextrin-diluted diets (Table 2). Consumption between the first and second ootheca was highest in females fed the

Table 1. Time (mean days \pm SE) to reach reproductive events for female *Supella longipalpa* fed rat food diluted with dextrin or alpha cellulose.

Per cent diluent	A-M*	M-EC1	EC1-EC2	Total (A-EC2)
Rat food	7.6 \pm 0.4 ^b	4.9 \pm 0.1 ^b	8.0 \pm 0.6 ^c	20.5 \pm 0.6 ^c
Dextrin				
50	7.9 \pm 0.4 ^b	5.1 \pm 0.2 ^b	7.0 \pm 0.3 ^c	20.0 \pm 0.4 ^c
75	8.3 \pm 0.4 ^b	5.7 \pm 0.3 ^b	12.5 \pm 1.1 ^b	26.5 \pm 1.2 ^b
88	8.7 \pm 0.3 ^{ab}	6.0 \pm 0.2 ^b	11.8 \pm 1.0 ^b	26.1 \pm 1.1 ^b
94	9.5 \pm 0.4 ^a	7.9 \pm 0.8 ^a	17.8 \pm 1.9 ^a	33.2 \pm 1.8 ^a
Alpha cellulose				
25	9.5 \pm 0.4 ^a	7.8 \pm 1.0 ^a	15.8 \pm 1.1 ^a	31.8 \pm 1.7 ^a

* A=Adult emergence, M=mating, EC1=drop of first ootheca, EC2=drop of second ootheca. Means in the same column followed by the same letter are not significantly different (ANOVA, $P<0.05$; Duncan's New Multiple Range Test).

Table 2. Consumption (mean mg \pm SE) between reproductive events by female *Supella longipalpa* fed diets diluted with dextrin or alpha cellulose.

Per cent diluent	A-M	M-EC1	EC1-EC2	Total
Rat food	43.3 \pm 1.6 ^{ab}	13.9 \pm 1.0 ^b	32.6 \pm 1.6 ^b	89.8 \pm 1.9 ^{bc}
Dextrin				
50	46.6 \pm 1.8 ^a	16.7 \pm 1.4 ^b	23.6 \pm 1.5 ^c	87.0 \pm 2.3 ^c
75	48.1 \pm 1.9 ^a	16.8 \pm 1.7 ^b	34.9 \pm 2.7 ^{bc}	99.0 \pm 3.7 ^b
88	46.1 \pm 2.1 ^a	18.1 \pm 1.2 ^b	28.8 \pm 2.9 ^{bc}	91.2 \pm 3.5 ^{bc}
94	48.5 \pm 1.4 ^a	17.6 \pm 2.5 ^b	38.6 \pm 4.0 ^b	95.7 \pm 4.1 ^{bc}
Alpha cellulose				
25	39.2 \pm 2.3 ^b	25.8 \pm 2.4 ^a	50.4 \pm 3.2 ^a	111.5 \pm 4.8 ^a

Abbreviations and statistical treatments as in Table 1.

most diluted diet, but this group of females took the longest to produce the second ootheca. Consumption was lowest in females fed 50% dextrin and they produced second oothecae faster than other females. Females on the highly diluted diet had smaller daily food intake prior to production of both first and second oothecae than either controls fed on rat food or females fed less diluted diets (Table 3). The effect of dextrin dilution on daily consumption became especially apparent prior to production of the second ootheca: as dextrin content of the diet increased, the average daily intake progressively decreased (Table 3), resulting in a longer preovipositional interval. Interestingly, this decrease was significant between the first and second ootheca for all females fed dextrin-diluted diets, but not for females fed on rat food.

There were no differences between females fed 100% rat food and 50% rat food in either number of eggs per ootheca or dry mass of first and second oothecae. However, the number of eggs and dry mass of the first and second oothecae were progressively reduced as the level of dextrin in the diet increased (Table 4). The second ootheca was, on average, significantly smaller and lighter than the first ootheca for females fed on diets containing at least 75% dextrin (Table 4).

As the dextrin content of the diet increased, ASM and AD increased significantly, while ECI and ECD decreased steadily. Faecal production

was inversely related to dextrin content of the diet: as dextrin was doubled, faecal production was halved (Table 5).

Diets diluted with cellulose

Adult performance was drastically reduced by the addition of cellulose to the diet. Both daily and total food intake decreased as dietary cellulose levels were increased (Table 6). Of twenty females fed 25% methyl cellulose and

Table 3. Average daily consumption (mean mg \pm SE) prior to production of the first and second ootheca in *Supella longipalpa* fed diets diluted with dextrin or alpha cellulose.

Per cent diluent	First ootheca	Second ootheca
Rat food	4.6 \pm 0.1 ^{ab}	5.1 \pm 0.3 ^a
Dextrin		
50	4.9 \pm 0.2 ^a	* 4.0 \pm 0.2 ^b
75	4.6 \pm 0.1 ^{ab}	* 3.3 \pm 0.2 ^{bc}
88	4.4 \pm 0.1 ^b	* 2.7 \pm 0.2 ^{cd}
94	3.9 \pm 0.1 ^c	* 2.5 \pm 0.2 ^d
Alpha cellulose		
25	3.9 \pm 0.1 ^c	3.9 \pm 0.2 ^b

Statistical treatments as in Table 1. An asterisk between means indicates a significant difference between values for first and second ootheca (Students' paired *t*-test, *P*<0.05).

Table 4. Size (mean number of eggs \pm SE) and mass (mean mg \pm SE) of oothecae from female *Supella longipalpa* fed diets diluted with dextrin or alpha cellulose.

Per cent diluent	No. of eggs		Dry mass	
	Ootheca 1	Ootheca 2	Ootheca 1	Ootheca 2
Rat food	16.3 \pm 0.3 ^a	16.6 \pm 0.3 ^a	7.9 \pm 0.2 ^{ab}	8.1 \pm 0.2 ^a
Dextrin				
50	16.6 \pm 0.3 ^a	16.3 \pm 0.3 ^a	8.3 \pm 0.2 ^a	8.4 \pm 0.1 ^a
75	15.6 \pm 0.7 ^{ab}	* 13.3 \pm 0.7 ^b	7.6 \pm 0.3 ^{bc}	* 6.5 \pm 0.4 ^b
88	15.9 \pm 0.3 ^{ab}	* 13.7 \pm 0.3 ^b	7.8 \pm 0.2 ^{abc}	* 6.4 \pm 0.3 ^b
94	14.7 \pm 0.5 ^b	* 11.6 \pm 0.5 ^c	6.9 \pm 0.2 ^c	* 5.1 \pm 0.4 ^c
Alpha cellulose				
25	12.8 \pm 0.5 ^c	12.0 \pm 0.4 ^c	5.8 \pm 0.3 ^d	5.4 \pm 0.2 ^c

Statistical treatments as in Tables 1 and 3.

Table 5. Digestive parameters of female *Supella longipalpa* fed diluted diets.

Per cent diluent	ASM* (mg)	AD (%)	ECI (%)	ECD (%)	Faeces (mg)	Female mass	
						Initial (mg)	Final (mg)
Rat food	64.2 ^c	70.5 ^c	24.7 ^a	35.3 ^a	27.2 ^c	15.9 ^{ab}	22.5 ^{ab}
Dextrin							
50	73.4 ^b	84.2 ^d	24.4 ^a	29.1 ^b	13.7 ^c	15.4 ^b	19.7 ^c
75	91.6 ^a	92.6 ^c	22.7 ^{ab}	24.6 ^c	7.4 ^{fs}	15.9 ^{ab}	24.1 ^a
88	86.2 ^a	94.4 ^b	23.6 ^{ab}	25.1 ^c	5.1 ^{fbh}	15.9 ^{ab}	23.0 ^{ab}
94	94.8 ^a	96.5 ^a	22.0 ^b	22.8 ^c	3.4 ^{sh}	15.9 ^{ab}	24.9 ^a
Cellulose							
25 methyl	54.4 ^d	61.0 ^f	—	—	36.2 ^b	16.0 ^{ab}	21.0 ^c
25 alpha	53.5 ^d	46.6 ^{gh}	14.5 ^c	30.2 ^b	58.2 ^a	15.7 ^{ab}	21.2 ^{bc}
50 methyl	15.6 ^e	45.7 ^h	—	—	18.5 ^d	15.6 ^{ab}	13.2 ^{def}
50 alpha	11.4 ^{ef}	30.8 ⁱ	—	—	26.4 ^c	15.9 ^{ab}	15.0 ^d
75 methyl	5.0 ^f	52.5 ^e	—	—	4.5 ^{sh}	14.9 ^b	12.5 ^{def}
75 alpha	3.1 ^f	27.8 ⁱ	—	—	9.1 ^f	17.0 ^a	14.2 ^{de}

* See Materials and Methods for abbreviations. Means in the same column followed by the same letter are not significantly different (ANOVA, $P < 0.05$; Duncan's New Multiple Range Test; for AD, ECI and ECD the test was conducted on ranked values).

Table 6. Longevity (mean days \pm SE) and diet consumption (mean mg \pm SE) up to day 30 of female *Supella longipalpa* fed rat food diluted with cellulose.

Cellulose concentration	Longevity	Food consumed	
		Daily	Total
25% methyl	>30	2.3 \pm 0.1 ^b	73.0 \pm 2.6 ^p
25% alpha	>30	3.7 \pm 0.2 ^a	105.3 \pm 4.7 ^a
50% methyl	18.5 \pm 0.9 ^a	1.9 \pm 0.1 ^c	34.1 \pm 2.2 ^c
50% alpha	18.4 \pm 0.9 ^a	2.0 \pm 0.1 ^{bc}	38.1 \pm 3.7 ^c
75% methyl	7.9 \pm 0.9 ^c	1.1 \pm 0.1 ^d	9.5 \pm 0.9 ^c
75% alpha	10.4 \pm 0.6 ^b	1.1 \pm 0.1 ^d	11.0 \pm 1.6 ^c
Starved	11.4 \pm 0.7 ^b	—	—

Statistical treatments as in Table 1.

75% rat food, only four mated and produced an ootheca (12.5 \pm 2.6 eggs; 5 \pm 1.2 mg), and two of these produced a second ootheca (nine eggs; 3.7 mg). In contrast, 3 times as many (65%) of the females fed 25% alpha cellulose mated and produced two oothecae, although their reproductive cycles were slower and they produced

lighter oothecae containing fewer eggs than either control females or females fed up to 88% dextrin (Tables 3 and 4). Daily consumption was significantly less in females fed a 25% alpha cellulose diet than in those fed on rat food (Table 2), but they consumed significantly more during their longer reproductive intervals (Table 1).

Females fed on diets containing 50% rat food and 50% methyl or alpha cellulose died within 20 days (Table 6), without mating or producing any oothecae. Further increases in cellulose concentration caused females to lose mass and die significantly sooner than starved females (Table 6).

Addition of either alpha or methyl cellulose to the diet decreased the amount of food assimilated and its digestibility (Table 5). However, the Approximate Digestibility of diets containing methyl cellulose was greater than that of diets containing the same level of alpha cellulose (Table 5).

Discussion

Our results confirm the observation that female

Supella longipalpa fail to increase feeding rates to compensate for high carbohydrate/low protein diets (Hamilton *et al.*, 1990). Higher carbohydrate content of the diet actually depresses daily food intake (Table 3). When either alpha or methyl cellulose are added to the diet, feeding rates also decrease. This is surprising because many insects, including cockroaches, increase feeding rates on cellulose-diluted diets (Bignell, 1978; Peterson *et al.*, 1988; Timmins *et al.*, 1988). Male German cockroaches raise intake and maintain nearly normal levels of sucrose intake when their sucrose diet is diluted to 75% cellulose (Gordon, 1968). American cockroaches (*Periplaneta americana* (L.)) consume greater volumes of food when dietary cellulose replaces dextrin in the diet (Bignell, 1978). However, American cockroaches can digest cellulose (Bignell, 1977; Wharton & Wharton, 1965) which may partly explain their tolerance of very high cellulose levels. The brown-banded cockroach, on the other hand, has a very limited ability to digest cellulose (Wharton & Wharton, 1965) and even on a diet containing 25% cellulose, feeding rates in female brown-banded cockroaches are reduced compared with those of females fed either rat food or diets diluted with dextrin (Tables 3 and 6). As the dietary cellulose increases above 25%, feeding rates decline even further, and females die rapidly.

Because reproductive success is dependent upon feeding in the brown-banded and other oviparous cockroaches (Bell, 1969; Cochran, 1983; Hamilton & Schal, 1988; Hamilton *et al.*, 1990; Rollo & Gunderman, 1984), a reduction in food intake has negative effects upon reproductive performance. As the carbohydrate content of the diet increases, feeding rates are depressed (Table 3), and oothecae become smaller and lighter than in females fed on rat food. This is in contrast to females of the German cockroach which increase feeding rates and produce oothecae of normal size when fed on 5% protein diets during the first gonotrophic cycle (Hamilton & Schal, 1988). A comparative study of dietary dilution with the German cockroach would be useful to elucidate their different response to food quality.

Control females and females fed a 50% dextrin-diluted diet produced similar sized first and second oothecae, while in females fed diets containing at least 75% dextrin the second ootheca was smaller than the first. Since total

food intake did not decrease between the two oothecae, this may indicate that nymphal reserves are used to supplement the first gonotrophic cycle. Hamilton *et al.* (1990) showed that nymphal diet significantly affected adult reproduction when the adults fed on a low protein diet. Adult females fed rat food diluted with 25% alpha cellulose did not appear to benefit from nymphal reserves as indicated by the significantly smaller first ootheca than in any other group of females, and the lack of a reduction of either size or weight of the second ootheca. This might suggest that reserves are selectively mobilized under specific conditions such as a high carbohydrate diet lacking sufficient protein. In support of this hypothesis, adult female American cockroaches fed only sucrose can reproduce (Rollo, 1984), and they mobilize stored urates for oothecal production when switched to a low-protein diet (Mullins & Cochran, 1975).

The observation that daily food intake drops significantly with time and with increasing dietary dextrin content, but not in control females fed on rat food or in females fed on diets containing 25% alpha cellulose diets, awaits a physiological explanation. In blowflies, there is no evidence to suggest 'counting calories' or feeding to optimize caloric intake (Gelperin, 1971; Simpson & Bernays, 1983). In both blowflies and locusts, feeding rates are generally presumed to depend upon feedback from stretch receptors in the crop, abdominal wall or alimentary canal and osmotic pressure of the haemolymph (Bernays & Chapman, 1974; Barton Browne, 1975; Dethier, 1976; Gelperin, 1971; Bernays & Simpson, 1982; Simpson, 1983; Simpson & Bernays, 1983). Regulation of feeding has not been well studied in cockroaches, but as in locusts and blowflies, the rate of crop emptying is thought to depend on feedback from stretch receptors and on the texture of the food (Engelmann, 1968). Haemolymph osmolality and amino acid concentrations are important regulators of feeding rates in locusts fed on diets of various carbohydrate content (Abisgold & Simpson, 1987), but it is currently unclear if these factors have any role in regulating cockroach feeding.

The digestive parameters calculated in this study are often used to study food utilization during growth in immature insects (Waldbauer, 1968; Scriber & Slansky, 1981). We modified

them to include not only biomass change in adults (which is minimal), but also reproductive output which is the major 'growth' in adult females. Addition of dextrin to rat food increases the amount of food assimilated (ASM) by increasing digestibility (AD), but it decreases the utilization efficiency of digested food (ECI and ECD) (Table 5). This is expected since high levels of dextrin, which is readily digested and assimilated, increase the need to catabolize the excess dextrin and reduce the availability of other nutrients which are needed for oocyte maturation and ootheca production. In contrast, adding 25% alpha cellulose to the diet decreases both digestibility and the conversion of food to body mass and oothecae. In tobacco hornworm caterpillars, dietary cellulose decreases food digestibility and transit time in the gut, and at high levels, reduces the efficiency of conversion of ingested food (Timmins *et al.*, 1988).

The differential response of females to the two types of cellulose is surprising. When dissected on day 30, non-reproducing females fed on 25% methyl cellulose had small basal oocytes with evidence of oosorption. In contrast, females fed on 25% alpha cellulose had well developed oocytes and produced oothecae. Differences in the digestibility of the two types of cellulose are insufficient to explain the differential performance of female brown-banded cockroaches since diets containing methyl cellulose are more digestible than those containing alpha cellulose. It is doubtful that methyl cellulose has a direct toxic effect because females which ate the greatest total amount of methyl cellulose (25% cellulose and 75% rat food) lived the longest. Rather, increasing levels of cellulose depressed consumption, and females which died within 11 days ate the least amount of total cellulose. The observation that females fed 50% or more cellulose die sooner than starved females suggests that the added cost of handling and digesting cellulose may have contributed to the mortality and poor performance of females. It is generally recognized that diets high in fibre are associated with faecal energy loss, especially in the form of protein and fat (Kritchevsky, 1988). In humans, dietary fibre has been suggested to reduce food digestibility and increase excretion of dietary nitrogen (Kelsay *et al.*, 1981). Also, soluble fibres (e.g. methyl cellulose) tend to exert hypolipidaemic

effects, including reduced absorption of fat-soluble vitamins, whereas insoluble fibres (e.g. alpha cellulose) do not, and hydrophilic fibres can swell and cause bolus obstruction in humans (see Kritchevsky, 1988) and possibly in insects. However, the effects of cellulose on protein, lipid and carbohydrate digestion, assimilation and excretion are incompletely understood in both humans (Kritchevsky, 1988) and insects.

Acknowledgments

We thank T. Casey, G. Collier, R. Cooper and D. Sutherland for comments on the manuscript. Supported in part by grants to C.S. from U.S. Public Health Service (NIH Grant HD-21891) and USDA-CSRS (Grant 88-341-3-370) and by a New Jersey Pest Control Association scholarship to R.L.H. New Jersey Agricultural Experiment Station Publication No. D-08170-20-89, supported by State funds and by the U.S. Hatch Act.

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