Abstract: Using cub growth as an index, the influence of maternal nutrition, litter size, and cub sex on maternal care in cheetahs (*Acinonyx jubatus*) were examined and cub and litter growth rates compared with those of larger felids. Seventy-nine free-living cheetah cubs in 21 litters from 15 mothers were weighed at least once between 6 and 48 days of age. Eleven litters were weighed at the begging and end of a 5-day observation of their mothers. The mean cub growth rate varied significantly between litters, due primarily to differences in maternal food intake. Growth declined sharply when maternal foods intake was less than 1.5 kg/day, but did not increase with greater levels of food intake. Lower limits of growth rates may therefore have been set by the mother's food intake, whereas upper limits may be set by the intrinsic physiological ability of cubs to grow. Although male cubs were heavier than female cubs in the same litter when first weighed, major differences in growth rate between the sexes were not apparent at this stage. Both cheetah cubs and litters grow fast relative to other large felids, and it is argued that this may be an adaptation to the high rate of cheetah juvenile mortality from predation.

Cub growth and maternal care in cheetahs

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Using cub growth as an index, I examine the influence of maternal nutrition, litter size, and cub sex on maternal care in cheetahs (*Acinonyx jubatus*) and compare cub and litter growth rates with those of other large felids. Seventy-nine free-living cheetah cubs in 21 litters from 15 mothers were weighed at least once between 6 and 48 days of age. Eleven litters were weighed at the beginning and end of a 5-day observation of their mothers. The mean cub growth rate varied significantly between litters, due primarily to differences in maternal food intake. Growth declined sharply when maternal food intake was less than 1.5 kg/day, but did not increase with greater levels of food intake. Lower limits of growth rates may therefore have been set by the mother's food intake, whereas upper limits may be set by the intrinsic physiological ability of cubs to grow. Although male cubs were heavier than female cubs in the same litter when first weighed, major differences in growth rate between the sexes were not apparent at this stage. Both cheetah cubs and litters grow fast relative to other large felids, and I argue that this may be an adaptation to the high rate of cheetah juvenile mortality from predation. *Key words: Acinonyx jubatus*, cheetah, growth, lactation, life-history traits, maternal care, Serengeti. *[Behav Ecol 6:405–409 (1995)]*

During lactation, carnivores exhibit relatively high rates of parental expenditure in comparison to other mammals, with rapid offspring growth in a short period (Oftedal, 1984). The offspring of large felids, however, grow relatively slowly during gestation and lactation (Oftedal and Gittleman, 1989), but the ultimate factors influencing juvenile growth rates of large felids and carnivores generally are not well understood. It has been proposed, however, that the ability of large, solitary felids to capture large prey may be constrained and lead to a limitation in both offspring birth weight and maternal milk-producing ability (Gittleman and Oftedal, 1987). Furthermore, the importance of age-specific mortality rates to life-history evolution has recently regained prominence with a new theoretical focus and empirical analyses (Charnov, 1991; Gittleman, 1993; Promislow and Harvey, 1990, 1991). Fast growth rates might be advantageous by reducing the period of infant vulnerability to mortality from factors independent of growth rate such as predation, accidents, bad weather, or disease.

From a more proximate perspective, variation in maternal nutrition and food availability can indirectly affect the growth rate, an index of maternal care, of individual offspring (Costa et al., 1989; Loudon et al., 1984). Factors such as litter size (König et al., 1988), sex (Lee and Moss, 1986), environmental changes (Ono et al., 1987), maternal phenotype (Clutton-Brock et al., 1981), and genotype (Jara-Almonte and White, 1972) are also known to influence the growth of individuals.

For several reasons, cheetahs provide an appropriate model for assessing some of the proximate and ultimate factors influencing early maternal care in carnivores. Wild female cheetahs markedly increase their food intake to support the energetic demands of lactation (Laurenson, in press) and are multiparous. This article examines how mother's food intake, cub sex, and litter size influence cheetah cub growth rates, and thus maternal care, during the early part of lactation. Cheetahs suffer high juvenile mortality rates compared to other large felids and carnivores (Caro, 1994; Laurenson, 1994). Only 9% of cubs born still survived at 4 months old, with predation accounting for 73.2% of deaths. In addition, solitary cheetahs are more reliant on speed to capture their prey than other large felids and thus may be particularly susceptible to constraints on hunting ability during gestation. Therefore, I compare early growth rates of cheetah cubs and litters to those of other large felids and discuss the evolution of this life history trait.

METHODS

Study site and general methods

The study was carried out between October 1987 and August 1990 in a 2500-km² area (34–36° E, 1°15'–3°30' S) of the central plains of the Serengeti National Park and Ngorongoro Conservation Area in Tanzania [see Sinclair (1979) and Caro and Collins (1986) for a description of the general area and study site, respectively]. In most years rainfall increases between November and May, the wet season, while it is scarce from June to October, the dry season.

Out of approximately 60 female cheetahs that use the central Serengeti plains, 20 well-habituated females were chosen for intensive study. Fourteen of these females were fully grown, had previously raised cubs to maturity, and were classified as prime adults. Six were young adults that had not raised cubs previously. Females were immobilized using 125 mg of xylazine (Rompun: Bayer) and 100 mg of ketamine (Vetalar: Parke Davis & Co.), weighed, measured, and blood sampled. A radio collar (Advanced Telemetry Systems, Minnesota) was then fitted before the effect of xylazine was reversed using RX 821002A (Reckitt & Coleman). Females were relocated monthly by aerial radio telemetry and their reproductive status assessed by observing them on the ground as soon as possible after the flight. If well-developed mammary glands and a protruding abdomen were seen when the cheetahs were walking, sitting up, or lying down, advanced pregnancy was suspected, whereas brown rings around the nipples and full mammae indicated lactation. If I suspected pregnancy, I relocated the female as soon as possible after a further week had passed. If lactation was suspected, the female's lair site was located by radiotracking from the vehicle at daybreak when mothers were almost always with their cubs (Laurenson, 1993). Data presented in this paper were collected from 11 prime adults and four young adults (Table 1).

Table 1

Summary information on the composition of the 21 litters weighed

Mother	Litter	Litter size	Sex ratio M:F	Number of weighings	Mean cub growth rate for litter (g/day)
A	1	4	1:3	1	
A	2	3	2:1	1	
B	1	2	0:2	2	32
B	2	4	3:1	2	63
C	1	4	2:2	1	
C	2	4	2:2	3	37
D		5	4:1	2	35
E		3	2:1	2	32
F		3	3:0	3	42
G		3	3:0	3	49
H		3	1:2	2	42
I		5	3:2	2	−6
J		5	4:1	3	51
K		4	1:3	1	
L	1	3	2:1	4	35
L	2	4	4:0	3	37
L	3	5	2:3	2	42
M		4	3:1	1	
N	1	5	2:3	3	45
N	2	3	1:2	3	47
P		3	2:1	2	29

The estimated growth rate is given for those litters weighed more than once.

Data collection

Lairs were entered when the mothers had left to hunt. After it was established that mothers did not abandon or kill their cubs after they were handled (Laurenson and Caro, 1994), I recorded the mass of each cub. Disturbance to cubs and lair was minimized, and gloves were usually worn to decrease the strength of the observer's odor. Cubs were picked up, wrapped in cloth, suspended from a 5-kg spring balance, and weighed to the nearest 20 g. In most cases I recorded the circumference of the thorax behind the foreleg, tail length, sex, pattern of tooth eruption, and notes on appearance and stage of development. Cub age was estimated by comparing this information to that from cubs of known age (Adamson, 1969) and by observations on the mother's behavior and reproductive condition in previous weeks. These techniques altered neither cubs' survival nor mothers' behavior (Laurenson and Caro, 1994), nor was the mean cub growth rate in the litter affected by the number of times the litter was weighed (ANOVA, $F_{2,13} = 0.84$, ns).

Cubs were first weighed when the lair site was initially located, provided cubs were at least 6 days old. Cubs were also weighed at the beginning and end of a 5-day observation period of the mothers, carried out when cubs were between 3 and 5 weeks old. Generally, cubs were not weighed after 5 weeks of age as they were relatively mobile and seemed more disturbed by handling. Summary information on the litters that were weighed is presented in Table 1.

The mean food intake of females was estimated for each of these 5-day observation periods by following them in a vehicle and recording the age, sex, and species of each prey item and the parts of the carcass eaten (Laurenson, in press). The amount of flesh and viscera eaten was then calculated from Blumenschine and Caro (1986). I calculated the mean distance traveled each 24 h from odometer recordings, noted every 15 min during daylight hours, at twilight and at first morning sighting each day. Growth rates (g/day) over this

period were calculated for each cub, as well as the mean and total for the litter. Standard errors are provided.

Data analysis

In all cases, I tested raw data for skewness and kurtosis and compared them to a normal distribution using a Kolmogorov-Smirnov goodness-of-fit test. Parametric statistical tests were used where data met these criteria of normality. All masses were initially included in a repeated measures analysis of covariance model of the effect of age on cub mass to estimate the mean growth rate of siblings, using the GENSTAT 5 statistical package (GENSTAT Committee, 1987). I gave each separate litter ($n = 21$) an identification number so that both litter and an interaction between litter and age could be entered into the model. Only one litter from each mother ($n = 15$) was used in the final model, and so I avoided problems arising from this type of pseudoreplication. A model fitting growth rates for individual cubs rather than each litter left too few residual degrees of freedom and thus was not used. I chose not to use the mean mass of cubs on each weighing as the dependent variable because variance of cub growth within litters was small and not correlated with litter size or age. As a result I had no reason to suspect that pseudoreplication biased the estimates of growth rate. I added maternal food intake and litter size to this model to examine whether they significantly improved the model. Samples sizes were too small to test the effects of season, mother's parity, age, or size on the mean cub growth rate in the litter.

I also examined the effect of maternal food intake on cub growth rate in only the 11 litters of 3- to 5-week-old cubs whose mothers were observed between cub weighings because food intake can vary greatly on a short-term basis. The growth rates of cubs during this 5-day observation period were, however, correlated with the growth rates calculated over the longer period in the original data set ($r = .827$, $n = 11$). In this smaller data set, an asymptotic regression of mother's food intake on the mean cub growth rate in the litter, where $y = a + br^x$, did not provide a statistically better fit to the data than the logarithmic ANCOVA model ($r^2 = .664$, $F_{1,9} = 20.8$), but was chosen a priori as it was reasonable to assume that cub growth would reach an asymptote due to physiological constraints. Indeed cub growth rates reached a maximum of 46.5 g/day in the asymptotic regression, a more conservative and realistic estimate than that of 76 g/day at a maternal food intake of 10 kg/day in the logarithmic model.

RESULTS

Cub and litter growth rates

The inclusion of litter identity in a model describing cub mass with age provided a significantly better fit to the data ($F_{15,125} = 2.77$, $p < .01$) than a model without this factor. This indicated that cubs belonging to different litters grew at significantly different rates, ranging from −6.0 g/day to 63.1 g/day (Table 1). This model explained 96.4% of the variance in mass. The growth rate of the median litter (Female F, 42 ± 5 g/day) was similar to the overall estimate of growth rate (44.2 ± 1.5 g/day) calculated from all the available data by a simple regression of cub mass on cub age ($r^2 = .862$, $n = 164$, $p < .001$; Figure 1).

Mother's food intake had a significant effect on the mean cub growth rate, using an asymptotic regression, where $y = a + br^x$ (Figure 2; $r^2 = .751$, $F_{2,9} = 16.06$, $p < .003$) and parameter estimates were $a = 46.5 \pm 5.8$ g/day, $b = -108.5 \pm 35.9$ g/day, and $r = .25 \pm .15$. Maximum cub growth rate was 46.5 g/day, and there was little increase in cub growth rate above
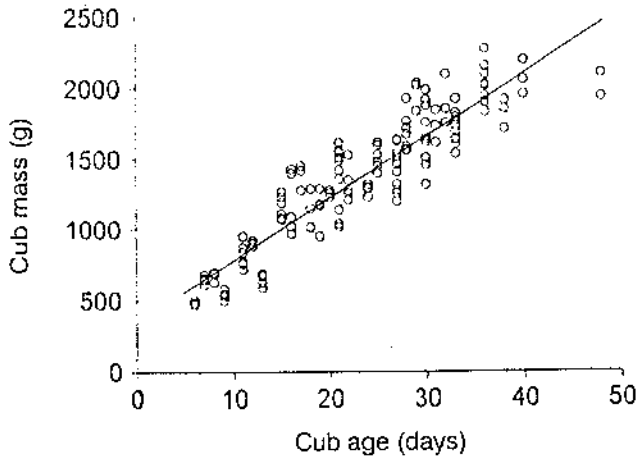
Figure 1
The relationship between the age of cheetah cubs *x* and their mass *y* (g), where $y = 0.44x + 0.32$ ($r^2 = .862$, $n = 164$), including data from all mothers and all litters. Exclusion of the two cubs weighed at 48 days of age gave a slightly higher estimate of growth rate at 45.9 g/day and explained slightly, but not significantly, less of the variation ($r^2 = .852$).

a maternal food intake rate of 1.5 kg/day. Below this level, cub growth rates declined rapidly to an estimated loss of 62.0 ± 40.7 g/day when mothers did not eat. In comparison, cubs that did not suckle at all, in an abandoned litter, lost an average of 82 g/day over 4 days, within 95% confidence interval of the intercept of the asymptotic regression. The residuals from this regression were not significantly correlated with any other variable, although the best correlation was with litter size and was positive ($r = .344$, $n = 11$). The growth rate of the whole litter was not significantly related to maternal food intake ($r^2 = .256$). Thus I found no indication that cub growth in large litters was constrained.

I examined the effect of sex on cub mass at first weighing and growth rate only in litters that contained both male and female cubs ($n = 18$). Male cubs were significantly heavier than females in these litters when they were first weighed (paired *t* test, $t = 2.98$, df = 17, $p < .01$). The mean difference between male and female cubs of 36.1 ± 12.1 g was less than one day's growth. The mean growth rate of male cubs was 46.2 g/day and of females 41.9 g/day in litters that contained both male and female cubs ($n = 11$). This difference was not significant ($t = 1.54$, df = 10, $p < .10$, ns).

Forms of stress, other than nutritional stress, may also adversely affect cub growth rate. When a grass fire swept through an area concealing two litters 500 meters apart, one litter of four 10-day-old cubs, which could not walk, burned to death. The other litter of three 28-day-old cubs survived, although they were singed and their feet had burns on the pads. The average cub growth rate in this litter was 48.6 g/day before the incident, but cubs lost an average of 190 g over the 4-day period (not included in the overall analysis) that included the fire, despite the mother maintaining her food intake rate.

Comparative early juvenile growth rates

I compared the early juvenile growth rate of cheetahs to that of other large (>10 kg) felids by plotting data from Gittleman and Oftedal (1987, Table 1) but using the average cheetah female body mass (36 kg) and cub growth rate (44.2 g/day) from the present study. Consistent with other studies, maternal mass was scaled to the power of 0.75, as most mammalian reproductive events and energetic constituents demonstrate
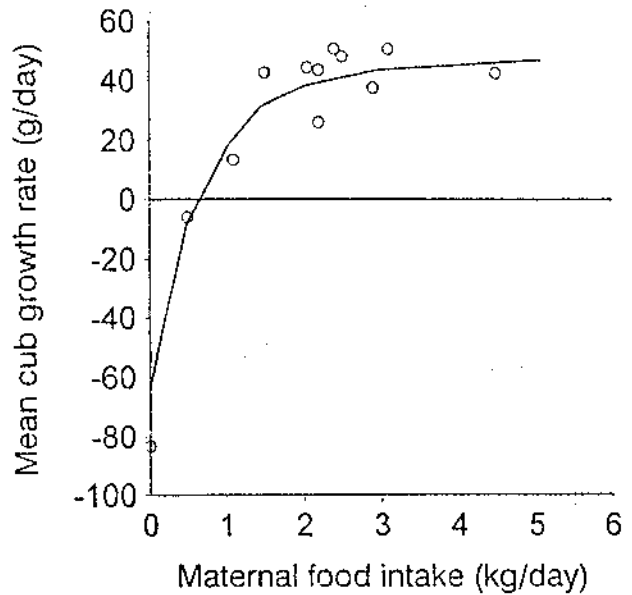

Figure 2
The relationship between cheetah mother's food intake *x* (kg/day) and offspring growth rate *y* (g/day) based on 11 litters of 3- to 5-week-old cubs. The asymptotic regression line, $y = 46.5 - 108.5 \cdot (0.25^x)$ describes the best fit to these data ($r^2 = .751$). A point (0 kg/day, -82 g/day) representing the mean mass loss in a litter of cubs that was abandoned is included but not used in the analysis.

an exponential relationship with body size (Gittleman and Thompson, 1988). I excluded lions (*Panthera leo*) from this analysis because they may allosuckle their offspring (Packer et al., 1992) and communal care may permit higher growth rates. Individual cub growth rate for cheetahs was the second highest relative to maternal body mass among the large Felidae, slightly lower than that of the snow leopard (*P. uncia*, Figure 3). When litter growth rates, a measure of maternal
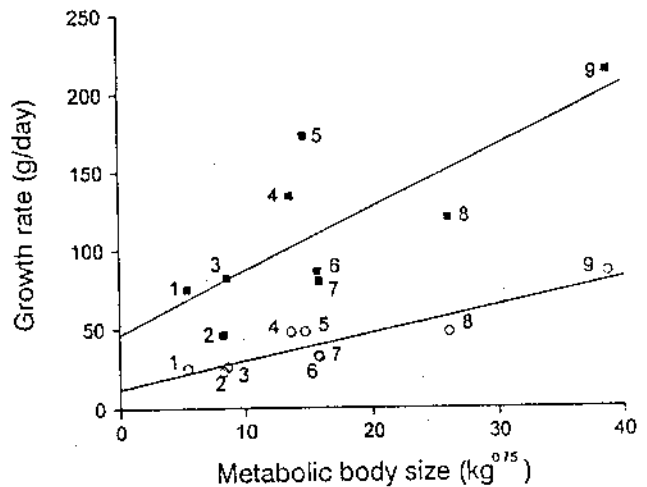

Figure 3
The relationship between female metabolic body mass [(mass)$^{0.75}$], *x*, and (a) offspring growth rate (y_1, open circles) and/or litter growth rate (y_2, closed squares) across 9 large (>10 kg) felid species, (data from Gittleman and Oftedal, 1987; this study), such that $y_1 = 12.3 + 1.76x$ ($r^2 = .84$) and $y_2 = 46.4 + 4.03x$ ($r^2 = .59$). Species: 1, *Caracal caracal*, 2, *Neofelis nebulosa*, 3, *Lynx lynx*, 4, *Panthera uncia*, 5, *Acinonyx jubatus*, 6, *P. pardus*, 7, *P. concolor*, 8, *P. onca*, 9, *P. tigris*.

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expenditure, are plotted (Figure 3), cheetahs have the highest growth rate relative to maternal metabolic body mass. Cheetahs, therefore, exhibit high offspring and litter growth rate compared to other large felids.

DISCUSSION

The mean growth rate of 44.2 g/day of cubs in free living cheetah litters between 6 and 48 days was comparable to that of similar aged cubs in captivity, where maternal nutrition is generally unlimited (40–50 g/day; Manton, 1970; Wack et al., 1991). In this study, different litters grew at significantly different rates, due primarily to differences in the level of maternal nutrition. However, the relationship between maternal food intake and mean cub growth rate was nonlinear and best described by an asymptotic regression. Cub growth rates dropped if maternal food intake was lower than 1.5 kg/day, but growth rates did not increase if the mother's food intake was greater than this. Thus, the ability of female cheetahs to meet energetic requirements for milk production appears limited if food intake drops in the short term, resulting in lower cub growth rates. Increasing food intake may be an important strategy for female cheetahs to meet the increased energetic requirements during lactation (Gittleman and Thompson, 1988); food intake approximately doubled during lactation in this study (Laurenson, in press), although mothers may also have used some metabolic stores (Laurenson, 1992).

A number of ecological and maternal factors may affect a mother's food intake, her ability to provision cubs, and ultimately her reproductive success. First, the age of the mother may be important as adolescent and young females are less successful at hunting large prey such as Thomson's gazelles (*Gazella thomsoni*) but make more hunting attempts and travel farther (Caro, 1994). Second, prey availability, which may be dependent on the season and positioning of the lair site, may be crucial in determining maternal food intake and also the energetic costs of capturing prey. The growth rate of spotted hyena cubs, for example, changed with prey abundance in their territory (Hofer and East, 1993). Last, other factors such as the height of cover may also have affected hunting success and prey capture rates (FitzGibbon, 1990). Unfortunately, sample sizes in this study were too small to test for these effects, but low prey availability around the lair and poor hunting technique may have led to prolonged low food intake and litter abandonment by a young cheetah mother (Laurenson, 1994).

When food is unlimited, cub growth and thus also the amount of care mothers can give may eventually be constrained by physiological limits on the rate that cubs can grow. However, the rate that mothers can produce milk may be limited, leading to a predicted inverse relationship between litter size and growth rate. Consistent with this, many studies in other species have found that maternal care did not increase in proportion to litter size, leading to lower offspring birth mass and slower growth and physical development (e.g., *Mus musculus* König et al., 1988; *Sigmodon hispidus* Mattingley and McClure, 1982; *Felis catus* Braagstad and Heggelund, 1984; Deag et al., 1987). In other studies, however, maternal care does increase in proportion to litter size (*Felis catus* Hall and Pierce, 1934; Loveridge, 1987; *Peromyscus maniculatus* Millar, 1977; *Peromyscus leucopsus* Fleming and Rauscher, 1978; see Mendl, 1988, for a review). Mendl (1988) suggested that unlimited maternal nutrition in laboratory studies could account for these contradictory results. This may not be a general explanation as free-living cheetah cubs in larger litters grew at a similar rate to those in smaller litters in this study. Similarly, in a small sample (n = 21) of zoo cheetah cubs, litter size had no effect on mass (Wack et al., 1991).

Male cheetah cubs may require slightly greater amounts of maternal care than female cubs during the early part of lactation because male cubs in mixed sex litters were heavier than female cubs. Sex differences in growth rates were not, however, significant until cubs ate solid food (Caro, 1990). Similarly, sex differences in offspring mass occurred after lactation ceased in both domestic cats (Latimer and Ibsen, 1932; Loveridge, 1987) and lions (Smuts et al., 1980). Sexual dimorphism in felids may, therefore, result primarily from differences in growth rate, or duration of growth period, after weaning rather than during lactation.

Cheetahs have a relatively low litter birth mass amongst carnivores despite large litter size (Oftedal and Gittleman, 1989), which can be explained in one or both of two ways. First, low litter birth mass might be advantageous when juvenile mortality is high and mothers are unable to mitigate its effects. Cheetahs suffer high offspring mortality rates compared to other large felids both before and after emergence from the lair (Laurenson, 1994; Caro, 1994). At birth, cheetah cubs had only a 26.6% chance of emergence at 8 weeks of age, and an 8.8% and a 4.8% chance of reaching 4 months of age and independence, respectively (Laurenson, 1994). In these circumstances cheetah mothers that put little effort into each reproductive iteration might be at an advantage. Second, cheetahs rely on short, fast sprints to catch their prey, and it is possible that the mass of cubs near term might slow females and impair hunting success. Thus, there may be constraints on the ability of female cheetahs to invest in their young during gestation. If, however, cubs are protected in a lair, there is no theoretical disadvantage to an altricial state at birth and a slow rate of growth.

In practice, however, cheetah cubs and litters grow fast compared to other large felids, and cub mortality is high both before and after emergence from the lair. Predators accounted for 73.2% of cheetah cub deaths in this study, and the ability of cubs to run away from predators is probably responsible for a decline in mortality rates after 4 months of age (Laurenson, 1994). Thus, cubs that grew fast and reduced the period of juvenile vulnerability to predators would be more likely to survive.

In addition, costs and constraints are associated with denning, which might limit the period cubs could be concealed in a lair and lead to the evolution of fast growth rates. Lactating cheetahs with cubs in a lair were on the move for a longer time each day, traveled farther, had restricted ranging patterns, and made more kills in the heat of the day than when accompanied by their cubs (Laurenson, in press). Thus, cubs that grew fast to become mobile at an earlier age would again be at a selective advantage. This may be particularly true where prey are migratory and availability varies seasonally, as in the Serengeti ecosystem. Scant data are available from large felids for comparison, although the extreme seasonality of the snow leopard's environment might have led to the relatively fast cub growth rates observed in this species (Figure 3). Nevertheless, I propose that the high individual and litter growth rates in cheetah cubs evolved primarily to reduce the period of extreme juvenile vulnerability.

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