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Lifetime reproductive success of territorial Male Yellow-Bellied Marmots

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Abstract. Number of years as a territorial resident, number of adult females in the territory, mean age of the adult females, and mean matriline size were used to evaluate the lifetime reproductive success (LRS), measured as the number of young weaned, of adult male territorial yellow-bellied marmots residing on eight habitat patches (sites). Only mean age of females differed among sites. In univariate analyses, LRS was significantly related to the number of females present and the number of years resident. In multivariate analyses only the number of females present significantly affected LRS. When LRS was measured as the number of yearlings produced, mean matriline size and number of young were significant. Inbreeding, mainly father:daughter matings, did not affect the frequency of weaning or mean litter size, but survival of young was significantly lower. LRS of adult females was significantly related to the number of years a female was resident. Mean LRS was significantly greater in males than females and variance was much greater in males. Males that lived near a site before becoming territorial were significantly more likely to reproduce in their first year of residency than males who did not live near their site of territorial residence. LRS is greater in males that settle quickly with as many females as possible for as many years as possible.

Key words: lifetime reproductive success, male yellow-bellied marmots, inbreeding, number of weaned young, number of adult females, matriline size, number of yearlings

Introduction

It is generally recognized that the reproductive success of males is limited by the number of females with whom they mate whereas reproductive success of females is limited by their physiological capacity to bear offspring. This relationship suggests that variance in reproductive success will be much greater in males than in females because each female is likely to reproduce at or near her physiological capacity whereas the number of females with whom a male may mate may vary widely because of such factors as demographic changes in the number of females and differences in the number of females in different habitats. The difference in variance between males and females is expected to be much greater in polygynous species.

Most species of ground-dwelling squirrels are polygynous (Schwagmeyer 1990), but some species of marmots are monogamous or polyandrous (Armitage 2000). Polygynous species may defend females or resources that females require (Emlen and Oring 1977). Most ground-dwelling sciurids are territorial, but male defense, male dominance, or scramble competition occur in some species (Schwagmeyer 1990). All species of marmots are territorial (Armitage 2000, Armitage and Blumstein 2002). Male yellow-bellied marmots (*Marmota flaviventris*) disperse from their natal social group as yearlings (one-year-old) (Armitage 1974), traverse the mountain slopes seeking females (Van Vuren 1990), and if successful, become resident on a habitat patch that supports one or more female social groups (Armitage 1998). Females are defended; defense occurs primarily in late spring and early summer when intruder males are more common (Salsbury and Armitage 1994a). Annual reproductive success, measured as the number of young weaned or the number of surviving yearlings, was significantly increased as the number of females in the harem increased (Armitage 1986). This increase occurred because the number of litters increased as harem size increased and not because of larger litter sizes.

However, the tenure of a male on his territory and the number of females present from year-to-year may vary considerably (Armitage 1986). Therefore, this paper explores factors that affect the lifetime reproductive success (LRS) of adult male, territorial marmots and makes some comparisons with LRS of adult female yellow-bellied marmots. LRS of males that defended isolated, widely-spaced females is not included (Salsbury and Armitage 1994b).

The analysis presented here is based on two assumptions. First, the resident male was the only male that mated with the females in his territory and second, the males had not reproduced before becoming a territorial resident and did not move to another site and reproduce after disappearance from his territory. These assumptions are supported by two sets of observations. First, analysis of variable allozyme systems supported the hypothesis that all young were fathered by the resident male (Schwartz and Armitage 1980). Second, when there was no resident adult male living in a habitat patch, there was no reproduction even when males were living at nearby sites, sometimes within 200 m of the site without a male (Armitage 2003a). Male movements apparently are restricted during the mating season because the environment typically is snow-covered and the risk of predation in a snow-covered landscape is high (Svendsen 1974).

Material and Methods

This study occurred in the Upper East River Valley, Colorado, where yellow-bellied marmots live on habitat patches consisting of rocky outcrops, talus, or scattered boulders under which burrows are constructed (Svendsen 1974). These patches occur in a mosaic formed by meadow and forest vegetation; the patches occupied by marmots are associated with meadows dominated by grasses and large showy perennials (Armitage 1991). Marmots reproduce once annually shortly after emerging from hibernation in late April or early May (Inouye *et al*. 2000). All age classes typically gain mass during the summer (Salsbury and Armitage 2003) and immergence into hibernation occurs in late August and early September. Marmots living on a habitat patch are organized into female social groups ranging from one to five closely-related females, yearlings, and young. The social group is known as a matriline and from one to five matrilines may occur on a patch (Armitage 2003a). From 1962 through 2002, all marmots at eight sites were live-trapped, weighed, sexed, and provided with uniquely numbered ear tags upon first capture. Marmots were also marked with a non-toxic fur dye for visual identification. Because most young are born to a female living solitarily in a burrow, weaned young were readily assigned to a female. In those cases where two or more reproductive females lived in the same burrow system and young were intermingled upon emergence, young were divided equally among the females. Although this procedure may incorrectly assign the number of weaned offspring to a female, it does not affect the number of young produced by the resident male.

The eight sites consisted of six large sites, formerly designated colonies and ranging in size from 1.6 to 7.24 ha and two small sites of 0.15 and 0.2 ha, formerly designated satellite sites (Svendsen 1974). The number of years a male was territorial, the number of adult females (aged two years or older) resident on the territory each year, mean matriline size, mean age of the adult females, and the number of young weaned were tabulated for each male. Adult females could be resident for two or more years. Thus, the number of adult females refers to the number of female-years (a female-year is one female resident for one year) and not to the number of different individual females. For the adult females, the number of years resident and the number of young weaned were tabulated. Matriline size and age of the adult females were included because both matriline size (Armitage and Schwartz 2000) and age (reproduction of young adult females may be suppressed by older females) (Armitage 2003b) affect reproductive success of females and thus could affect reproductive success of males.

Statistical analyses included t-test, simple and multiple linear regression, ANOVA, linear model ANOVA, and analysis of covariance. All analyses were performed in Mini tab 11.1.

Results

LRS: Number of young

ANOVA was used to determine if any of the five variables differed among the eight sites. Mean female age differed significantly among the eight sites and the number of females was nearly significant (Table 1). The lack of a significant difference for mean matriline size was expected as matriline size is a function of the social behavior of females. Nearly 93% of matrilines consist of one or two females (Armitage and Schwartz 2000); the mean size of matrilines in this study varied from 1.17 to 1.94 among sites and averaged 1.6 among males. Because males generally remain in their territories once established, there was no expectation that the number of years a male was territorial would vary significantly among sites (Table 1). The mean number of young ranged widely, but did not differ significantly among sites. For all five variables, standard deviations were high and the 95% confidence limits were broad. The high level of variation probably explains why more significant differences among colonies were not found.

The number of young was regressed against each of the other variables. Regressions were significant for number of females (p = 0.0001), number of years resident (p = 0.0001), and mean matriline size (p = 0.016), but not for mean age of females (p = 0.123). Because some of the variables are likely to be correlated, analysis of

	Among Individuals		Among Sites		
	Mean	Range	Range of Means	F	p
Number of years territorial	2.39	1 - 9	1.92 - 3.0	0.68	0.686
Number of females	5.93	0 - 42	3.1 - 8.9	1.9	0.076
Number of young	12.67	0 - 81	4.0 - 19.8	1.42	0.206
Mean matriline size	1.60	0 - 5	1.17 - 1.94	1.04	0.408
Mean female age	4.05	0 - 9.5	2.60 - 4.70	3.36	0.003

Table 1. Means and ranges for the five variables used to explain lifetime reproductive success of territorial male yellow-bellied marmots.

covariance was run with site as the main effect and the other variables as covariates. For mean age of females, site differed significantly ($p = 0.005$); none of the covariates were significant (all $p > 0.437$). In the analysis for the mean number of females, all variables were significant except mean female age. Therefore, the analysis was rerun with mean female age deleted. The remaining three variables were significant (all $p < 0.001$). When analysis of covariance was run on the number of young, both site ($p = 0.001$) and number of females ($p = 0.0001$) were significant. These results indicate that patterns of correlation occur among the five variables with site also possibly affecting LRS.

Therefore, the factors affecting the number of young were subjected to a linear model ANOVA. The number of young was not significantly affected by site ($p = 0.385$), mean female age ($p = 0.497$), number of years ($p = 0.689$) or mean matriline size ($p = 0.979$). However, the number of young was significantly affected by the number of females (Fig. 1) and this relationship explained 76% of the variation in the number of young.

LRS: Number of yearlings

The general linear model ANOVA included all the variables used above plus the number of young. Only number of young and mean matriline size were significant. The analysis was rerun with site ($p = 0.896$), mean female age ($p = 0.596$) and number of years ($p = 0.201$) deleted. Mean matriline size ($p = 0.019$) and number of young ($p = 0.0001$) were significant and number of females nearly so ($p = 0.090$). A multiple regression of the number of yearlings as a function of number of females, number of young, and mean matriline size (MMS) revealed that number of females was not statistically significant ($p = 0.926$). Thus, the number of yearlings was best described by the following:

$$\text{No yearlings} = -0.985 + 0.475 \text{ No young} + 0.7804 \text{ MMS}.$$

The number of yearlings increased as the number of young and mean matriline size increased. Number of females was significantly related to mean matriline size (No females = 2.72 + 2.01 MMS, $p = 0.003$), but this relationship explains little of the variation between these variables (adj $R2 = 0.067$). The significant relationship of mean matriline size rather than the number of females to the number of yearlings suggests that social organization may affect the number of young surviving to become yearlings. Survivorship increases as matriline size increases (Armitage and Schwartz 2000), but how survivorship is increased is unknown.

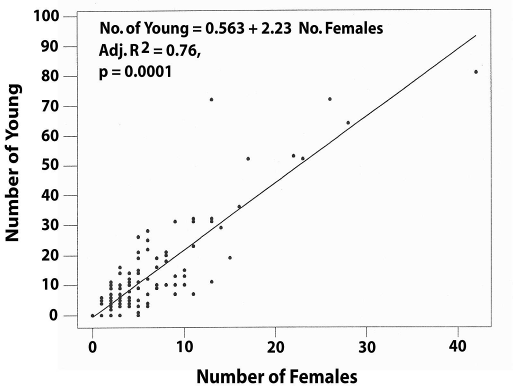

Fig. 1. The relationship between the number of young weaned by adult male yellow-bellied marmots and the number of females within the male's territory.

Effect of inbreeding

The number of females was significantly related to the number of years a male was resident (No females = 1.22 + 3.0 No. years, $p = 0.0001$). One way in which a male can increase the number of females with whom he can potentially mate is to increase the number of years that he is a territorial resident. For all males resident for more than two years, there is a possibility of inbreeding through father:daughter mating or rarely, mother:son or brother:sister. Inbreeding is generally accepted to lower reproductive success (Thornhill 1993).

First, I tested to determine if reproduction was more or less likely where inbreeding was possible. Of 780 potential matings, inbreeding was possible in 79 (10.1%). Litters were weaned in 34.1% of the probable inbreeding matings and in 48.9% of the outbreeding matings. This difference is highly significant ($G = 6.3$, $p = 0.01$); reproductive success was less likely when inbreeding was possible. However, when inbreeding occurred, there was no significant difference in litter size (means ± SE: inbreeding, 4.16 ± 0.31, N = 25; outbreeding, 4.13 ± 0.078, N = 336; $t = 0.09$, $p > 0.9$). The analysis of the likelihood of inbreeding is confounded by reproductive suppression of young adult females by older adult females (Armitage 2003a). Daughters of territorial males are most likely to be young females as a male would have to be resident for at least five years for a daughter to become an older female. Two analyses were performed. First, the frequency of reproduction of 124 2-yr-olds was determined when older females were present or absent and when father:daughter matings were possible (Table 2). When older females were present, the frequency of reproduction by father:daughter matings did not differ from that of outbreeding matings ($G = 2.0$, $p > 0.1$). When older females were absent, there was no difference in the frequency of reproduction between inbreeding and outbreeding females ($G = 0.5$, $p > 0.1$). The second analysis compared the reproductive success of potential father: daughter matings in the presence or absence of older females. Clearly,

	Older female			
	present		**absent**	
	Inbreed.	**Outbreed.**	**Inbreed.**	**Outbreed.**
Reproductive	4	15	4	31
Non-reproduc.	36	60	4	18

Table 2. Frequency of reproduction among 2-yr-old females. Inbreeding refers to father:daughter matings; outbreeding, to non-kin related matings.

the presence of older females was the major factor associated with the failure of father:daughter matings (Table 3). When older females were absent, father:daughter matings occurred 66.6% of the time, which is much higher than the 48.9% of successful outbreeding matings. I conclude that there is no evidence of inbreeding avoidance once reproductive suppression among females is taken into account.

Inbreeding could result in lower survivorship of inbred offspring vs outbred offspring. Survivorship of young was significantly greater among outbred young than among inbred young (Table 4). About 10% more young survived in the outbred than in the inbred matings.

Comparison of female and male LRS

The number of young weaned varied considerably among females and was significantly related to the number of years resident (Fig. 2). If number of years resident for territorial males is treated as an independent variable, the relationship is significant (No. young = -3.58 + 6.81 No. years; adj R2 = 0.47, p 0.0001). Thus, number of years resident can be a predictor of reproductive success for both sexes, but number of years accounts for more of the variation in the number of young for females than for males.

Mean number of young and variation in the number of young was significantly greater in males than females (comparison of means, t_{309} = 3.53, $p < 0.001$). The major factor underlying this difference is that a small number of males (about 6%) were highly successful (Fig. 3). The greater number of young produced by males than by females suggests that sons might be more valuable than daughters. LRS was determined for 24 males whose mother was known and compared to the LRS of the daughters of those same mothers. The sons produced more offspring (mean ± SE = 15.1 ± 4.1) than the daughters (10.5 ± 3.3), but the difference was not statistically significant (t_{40} = 0.86, p = 0.40). This analysis assumes that all young that dispersed did not live to reproduce. This assumption is unlikely to be correct given that the 24 males were successful dispersers, but there is no way to know whether more male or female dispersers survived to reproduce. Another way to compare the success of sons and daughters is to compare the number of young per daughter with the number of young per son. The number of young per daughter decreases to 5.79 ± 1.7 and is significantly lower than the 15.1 young produced by the sons (t_{30} = 2.07, p = 0.047).

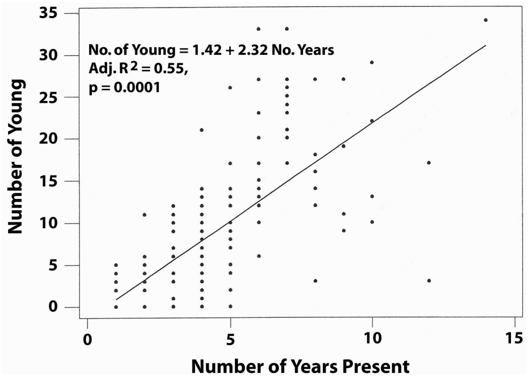

Fig. 2. The relationship between the number of young weaned and the number of years an adult female marmot was resident at a site.

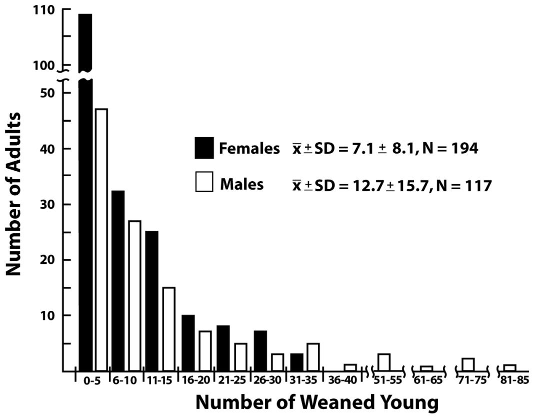

Fig. 3. The distribution of the number of young weaned in relation to the number of adult males or females producing that number of young. Young are grouped in intervals of five.

	Older Female Present	Absent
Reproductive	7	16
Non-reproductive	46	8

Table 3. Reproductive success (number of litters weaned) when a territorial male lived with close kin whose ages ranged from 2 to 4 years when older unrelated females were either present or absent. G = 21.97, p < 0.001.

	D	S
Inbreeding	65	36
Outbreeding	816	686

Table 4. Survivorship of young from inbred and outbred matings. Data were combined from all adult females (N = 351 female years). A female-year is one female in one year; all surviving females were included in subsequent years. D = disappeared and presumably dead; S = survived as determined by recapture as yearlings. G = 3.92, 0.05 > p > 0.025.

Timing of residency

When compiling the data on reproductive success, I noted that reproduction frequently did not occur in the first year of a male's residency. Therefore, I determined the likelihood that males produced offspring in their first year as a territorial resident. Males were more likely to reproduce than not (Chi-square: 10.6, $p < 0.005$). Many of the males lived in a nearby habitat patch or peripherally to their site of territorial residency in the previous year. I tested whether a male was more likely to reproduce if he lived at or near his site of residency. If not present the year previous to becoming territorial; males were equally likely to not reproduce or to reproduce. But if males were present the previous year, they were five times more likely to reproduce than not (Table 5). Thus, previous presence provided a significant advantage for reproducing in a male's first year as a resident territorial.

	Present	Not Present
Reproduced	41	27
Non-reproduction	8	27

Table 5. The number of males reproducing in the first year of residency in relation to their presence one or more years before becoming territorial. G = 13.6, p < 0.001.

Discussion

This analysis examined the relationship between five variables (number of years resident, number of females present, mean age of females, mean matriline size, and number of young) and lifetime reproductive success (LRS) of adult, territorial male marmots. Only mean age of females differed significantly among colonies, but this variable was not significantly related to LRS. In linear regressions, number of years resident, number of females, and mean matriline size (adj R2 = 0.041) were significantly related to the number of young. But when co-variation was accounted for, only the number of females was significant. A male could be associated with many females for one or two years or with a few females for several years; in each case the critical factor is the number of females not the number of years. However, if the only data available were the number of years a male was a territorial resident, a reasonable estimate of his LRS could be made (see Fig. 4). This estimate is possible because the number of females is significantly related to the number of years (No. females = -1.22 + 3.0 No. years; p = 0.0001, adj R2 = 0.60).

The production of yearlings is an important indicator of reproductive success because yearlings have a much greater probability of reaching reproductive age than young (Schwartz *et al.* 1998). A male's success in producing yearlings was significantly affected by the number of young he fathered. However, the number of yearlings was also affected by MMS. This result indicates that male LRS is affected by the social organization of adult females. Male LRS could be greater if the number of females is concentrated in larger matrilines (2 or 3) rather than dispersed in small matrilines (e.g. 1).

A polygynous mating system is one in which the variance in the LRS of males is greater than that of females (Trivers 1972). The greater variance in LRS of male than of female yellow-bellied marmots verifies that yellow-bellied marmots are polygynous. A similar difference in the variance of LRS occurs in black-tailed prairie dogs, *Cynonys ludovicianus* (Hooglund 1995, p. 272).

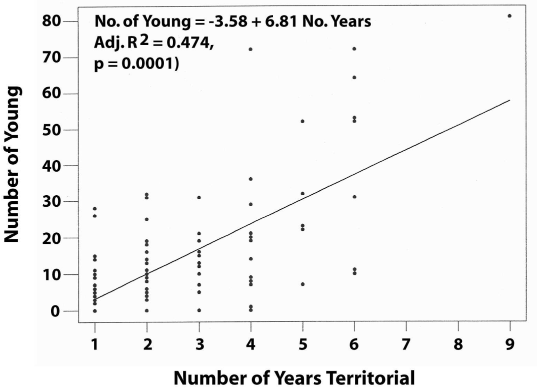

Fig. 4. The relationship between the number of young weaned and the number of years an adult male was a territorial resident.

About 24% of the variation in the number of weaned young is unexplained by the number of females. Some of that variation probably results from the failure of many males to reproduce in their first year of residency regardless of the number of females present. In addition, the number of young weaned is reduced in large matrilines when young females are present with older females (Armitage 2003b, Armitage and Schwartz 2000). Also, competition between matrilines within a male's territory may reduce the number of litters weaned (Armitage 1986, 2003b). Thus, some of the variation in male LRS results from the reproductive strategies of females.

Because the number of females in the male's territory is the single most important factor determining LRS, males should attempt to defend as many females as possible. Some large sites may have two or three male territories; when one or two males die, the surviving male may extend his territory to encompass the entire site (Armitage 1974). In some instances, all the males on a site disappear over winter and may be replaced in the spring by a new male who occupies the entire area previously divided into two or more territories. This behavior on major sites indicates that males do attempt to include as many females in their territories as possible. However, the size of male territories is not related to the number of females defended, but to the dispersion of females (Salsbury and Armitage 1994b). Some males defend isolated, widely-spaced females and have large home ranges that include these females whereas clumped females are readily defended within small home ranges (territories). In all cases, the size of the male territory is consistent with the interpretation that males include as many females as possible within their territories.

Male territorial defense is costly. Energy expenditure of males was best explained by a defensibility index that was based on the dispersion and number of females defended; expenditure increased as number and dispersion of females increased (Salsbury and Armitage 1995). Males spend more time active above ground than all other age-sex groups (Armitage *et al*. 1996), have a survivorship curve significantly lower than that of females (Schwartz *et al.* 1998), have higher metabolic rates than females, and have reproductive energetic costs greater than those of adult females (Armitage 2004). Although reproductive females have elevated energy expenditures during lactation, this expenditure lasts for only about 30 days whereas males under social conflict defending their territories may have high-energy expenditures for about 60 days (Armitage 2004). The higher mortality of males than of females at all ages ≥ 1 year is related to dispersal. Dispersers have higher mortality than philopatrics (Van Vuren and Armitage 1994); because all males disperse and about half the females do so, males suffer higher mortality. Additionally, males move through the environments seeking females and during these movements are susceptible to predation (Van Vuren 1990).

Inbreeding did not affect the likelihood that mating would occur or litter size. However, survival of young from inbreeding was significantly less than that from outbreeding. This difference raises the question of why inbreeding is not avoided. To answer this question we must consider the alternative costs of not reproducing. Marmots are annual breeders (Armitage 1981, 1998, 1999, 2000). Because an adult female on average is resident for 3.7 years, she loses about 27% of her reproductive opportunities if she fails to mate for any reason. Because the average female produces 7.15 young in her lifetime, failure to breed reduces her LRS by 1.93 young. Likewise, a male is resident on average for 2.4 years; he would lose about 42% of his reproductive opportunities by failing to mate. However, other non-kin females may be present in the matriline, which would reduce the cost of not mating for males to about 10%. Because the average male produces 12.7 young, failure to reproduce reduces his LRS by 1.27 young. This analysis indicates that the average female would have a greater reproductive loss than the average male. Another way to calculate the loss in LRS is to examine what happens if one litter is not produced. Failure to reproduce results for each sex an average loss of 4.1 young (mean litter size, Schwartz *et al*. 1998). On average, 1.86 young of each litter would not survive their first year (Schwartz *et al*. 1998). Thus, failure to breed produces a net loss of 2.14 young. The additional loss from inbreeding represents about 0.4 young. Thus, inbreeding gains an average 1.7 young over not breeding. I conclude that inbreeding is a better reproductive strategy than not breeding as gains in young exceed the losses.

The higher LRS of males (average of 12.7 young) than of females (average 7.1 young) suggests that sons are more valuable than daughters. A successful son would produce 1.79 more grandoffspring than a successful daughter. Theory suggests that females should bias the sex-ratio of their offspring toward the sex that would have the greatest effect on their own fitness (Clutton-Brock and Iason 1986). Because yellow-bellied marmot males produce more offspring than females, sex-ratio should be biased toward males. However, population sex-ratio is 1:1 in yellow-bellied marmots (Schwartz *et al*. 1998). Survivorship of males and females may affect sex allocation. The average age of first reproduction of females is 3.02 years (Schwartz *et al*. 1998). I determined the age of first reproduction for a sample of 24 known-aged males, the mean was 3.2 ± 0.98SD years. In effect, both males and females have a mean age of first reproduction of three years. By age three years, adult females out number adult males by 2.16 times. This number is similar to the 1.79 times more young produced by males than females. In brief, a female must produce two sons for each daughter to have the same probability that each sex will reproduce. But it takes two surviving daughters to produce the same number of offspring as a surviving son. Thus, it can be expected that two sons will have the same reproductive success as two daughters. In other words, sons and daughters contribute equally to a female's fitness and population sex ratios are stable at 1:1.

To summarize, adult male marmots can maximize lifetime reproductive success by establishing a territory with as many adult females as possible as early as possible and defending the females from male intruders as long as possible. The key determinant of male LRS is the number of females with whom he mates during his lifetime.

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