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NEST-DEFENSE BEHAVIOR IN THE RED-WINGED BLACKBIRD[1]

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Abstract. We examined various aspects of nest-defense behavior in marsh-nesting Red-winged Blackbirds (*Agelaius phoeniceus*) in Madison, Wisconsin. Blackbirds used seven types of calls in nest defense. The female *scream* elicited the strongest response of any call type; attracting more birds, and eliciting the highest rate of hovers. Additionally, the *scream* caused begging nestlings to stop begging and crouch low in the nest. Female blackbirds had higher call rates to predator models than did male blackbirds; however, males were the more aggressive sex in defense of the nest. Although there were no differences in call rates to different predator models, there were differences in more overt nest-defense behavior. The ability to drive off a predator best explained the variation in aggressiveness to the predator models. Male blackbirds, when faced with a choice, defended nests of primary females more aggressively than nests of secondary females; the differences were due to neither the nests' contents nor to the stage of the nests. Call rates, but not rates of dives and strikes, were correlated with successful nests. Finally, the most aggressive males had the largest harems.

Key words: Red-winged Blackbird; Agelaius phoeniceus; *nest defense; parental care; mate choice.*

INTRODUCTION

Red-winged Blackbirds (*Agelaius phoeniceus*) have been the subject of numerous field studies resulting in many aspects of their biology being known. It is surprising, therefore, that one of their conspicuous behaviors, i.e., nest defense, is not well described. Nest-defense behavior has been examined indirectly in the context of parental investment theory (D'Arms 1978, Robertson and Biermann 1979, Biermann and Robertson 1981, Weatherhead 1982), mate choice theory (Searcy 1979, Eckert and Weatherhead 1987, Yasukawa et al. 1987), and more directly as an antipredator (Picman 1983) and antinest-parasitism strategy (Folkers and Lowther 1985). Recently, blackbird nest-defense behavior was also used to critically assess results and assumptions of studies dealing with nest-defense behavior of altricial birds (Knight and Temple 1986a, 1986b). In this paper we present results of a descriptive study of Red-winged Blackbird nest-defense behavior. Specifically, our study examined the following questions: (1) What are the types and proportions of calls used in nest defense? (2) What are the responses of other blackbirds to call types used in nest defense? (3) Do blackbirds respond differently to predators that differ in the threat they pose to adult blackbirds vs. the nest contents? (4) Do male blackbirds allocate nest defense evenly among females in their harems? (5) Is nest success correlated with the intensity of nest defense? and (6) Is harem size correlated with either male nest-defense intensity or the number of call types used by males?

METHODS

Our observations of Red-winged Blackbird nest-defense behavior were made between April and July 1982 in Redwing, Class of 1912, Gardner, and Kettle marshes within the city of Madison, Wisconsin; see Bedford et al. (1975) for descriptions of these cattail (*Typha* spp.) marshes.

Frequent observations of the marshes began in April, and we mapped male blackbird territories during the first week in May. Territorial boundaries were verified the first week in June by an observer recording responses of male blackbirds to an individual walking from nest to nest. Nest locations were marked by placing numbered plastic flagging from 1 to 4 m in any direction from the nest. Nests were then monitored weekly until their fate was determined.

We measured nest-defense responses of blackbirds to taxidermic mounts of a raccoon (*Procyon lotor*) and an adult Red-tailed Hawk (*Buteo jamaicensis*), and a rubber model of an American Crow (*Corvus brachyrhynchos*). All three predators are commonly seen on our study areas dur-

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TABLE 1. Percentage of different types of calls used in nest defense by 30 pairs of Red-winged Blackbirds and proportions of individuals that gave the calls.[a]

	Calls by males		Calls by females	
Call types	Number and percentage of all calls	Proportion of birds giving call	Number and percentage of all calls	Proportion of birds giving call
Check	1,763 (59.6%)	30/30	5,106 (85.4%)	30/30
Chatter	0 (0.0%)	0/30	54 (0.9%)	15/30
Growl	83 (2.8%)	11/30	0 (0.0%)	0/30
Scream	0 (0.0%)	0/30	819 (13.7%)	8/30
Peet	35 (1.2%)	1/30	0 (0.0%)	0/30
Cheer	970 (32.8%)	29/30	0 (0.0%)	0/30
Seeet	107 (3.6%)	9/30	0 (0.0%)	0/30
Total calls given	2,958	—	5,979	—

[a] Red-tailed Hawk, American Crow, and raccoon models were each presented to 10 different pairs of blackbirds when the nests contained eggs 6 to 8 days after initiation of incubation.

ing the blackbird breeding season. We also measured the response to a 14 cm × 14 cm × 25 cm cardboard box to test whether blackbird responses to our predator models differed from a neutral model. Each predator model was presented to 10 different pairs of blackbirds when their nests contained eggs 6 to 8 days after initiation of incubation. Model presentations at each nest were randomized and presented at 1-hr intervals. Presentations were made before noon, when there was no rain, and when winds were <10 km/hr. The predator models and box were placed on top of an adjustable aluminum pole within 0.5 m of the nest. Models were placed so the heads were level with and facing the nest. A cloth attached to a string covered the models and the box while the observer moved outside of the male blackbird's territory. Observations began when the cloth was removed and only after the parents had resumed "normal" behavior (i.e., had stopped responding to our presence). During a 3-min period the types of calls, the nearest distance the parents approached the potential predator, and the total number of hovers, dives, and strikes were recorded by two observers, one watching the male and the other the female. Closest distances blackbirds approached the models or the box were estimated to the nearest 0.5 m. Dives were defined as being any break in horizontal flight that was directed at the predator. Hovers were counted as separate flights from a perch over the predator then back to a perch. Call types were those we could discern and are described by Orians and Christman (1968) and D'Arms (1978).

We performed 10 replicates of a playback experiment between 24 June and 7 July at 10 different locations in Redwing Marsh. A replicate consisted of playing four 15-min tapes 20 min apart in the same location. Playback tapes consisted of 5 min of prerecorded background noise, 5 min of either pure female *check,* female *scream,* male *cheer,* or male *growl* calls, followed by 5 min of background noise. The order in which tapes were played was chosen randomly. Both the background noise and the blackbird calls were recorded in the Class of 1912 and Kettle marshes during May. Sound volume was held constant for all playback experiments and approximated that of calls heard in the marsh. Playback trials were conducted as follows: a tape recorder was placed in the marsh, away from the marsh edge and as far away from an active nest as possible, but inevitably within a male blackbird's territory. The recorder was turned on, and the observer retreated 20 to 30 m. During each 5-min segment of background noise and blackbird calls, we counted the number of Red-winged Blackbirds that flew to within 5 m of the recorder, the number of calls they gave, and the number of hovers over the recorder.

During June, nine nestlings were removed from five nests on a number of different occasions and taken indoors for a series of playback experiments. A total of 17 replicates were performed on nestlings of different ages (range 3 to 13 days old) in isolation. A replicate consisted of playing five 20-sec tapes, in random order and 30 min apart, to a nestling begging for a mealworm and noting the nestling's response while the tape was played. The tapes consisted of background noise, female *check,* female *scream,* female *chatter,* male *growl,* and male *cheer* calls. Nestlings were returned to their nests following the experiments.

TABLE 2. Responses of Red-winged Blackbirds to 10 playback experiments of *check* (female), *scream, cheer,* and *growl* calls.

Response variable	Responses ($\bar{x}$ ± SD) of blackbirds to playback of indicated call types and background noise			
	Check vs. background	*Scream* vs. background	*Cheer* vs. background	*Growl* vs. background
Blackbirds attracted	1.2 ± 1.0 vs. 1.1 ± 0.2	5.5 ± 3.9 vs. 1.4 ± 0.5*	1.7 ± 0.5 vs. 1.2 ± 0.3	1.6 ± 0.7 vs. 1.0 ± 0.0
Calls	63.2 ± 39.1 vs. 52.2 ± 41.9	194.5 ± 148.0 vs. 49.7 ± 41.1*	82.9 ± 48.9 vs. 55.4 ± 27.0	148.9 ± 73.2 vs. 53.1 ± 38.1
Hovers	0.5 ± 0.7 vs. 0.0**	7.4 ± 7.8 vs. 0.0**	0.9 ± 1.1 vs. 0.3 ± 0.6	0.3 ± 0.7 vs. 0.0**

* $P < 0.05$, ** $P < 0.001$; tests of significance (Mann-Whitney *U*-test) between responses to 5 min of the call and the average of the responses to the two 5-min presentations of background noise.

We examined relationships between nest-defense intensity, nest success, harem size, and call-repertoire size using linear regression analyses. The number of days (beginning with the initiation of incubation) nests survived and harem size were response variables, and calls, dives, and strikes (total for both parents or just for males), and number of male call types were independent variables. This information was collected at nests of 26 primary females in three marshes 6 to 8 days after initiation of incubation. Calls, dives, and strikes of defending parents to a crow model placed at the nest were recorded during a 3-min period. A primary female is defined as the first female to begin nesting within a male's territory.

Data were analyzed with Wilcoxon's paired-sample tests, Mann-Whitney two-sample tests, contingency tables, and linear regression analysis (Ryan et al. 1976, Zar 1984). Statistical tests, where appropriate, were two-tailed. We used analysis of variance to test the null hypothesis that regression coefficients did not differ significantly ($P < 0.05$) from zero. Residuals from the regression analyses were plotted against the independent variables and the predicted y values to determine whether data transformations were necessary. The dependent and independent variables were log or square-root transformed when necessary to meet the assumption of linearity.

RESULTS

CALLS USED IN NEST DEFENSE

Red-winged Blackbirds used seven types of calls in response to the predator models placed at nests (Table 1). The *check* was the most common call, both in numbers given ($\chi^2 = 2579.1$, df = 1, $P < 0.001$) and in the proportion of individuals who gave the call; every male and female gave *checks*. The *check* call comprised a greater proportion of total calls by females than by males ($\chi^2 = 740.4$, df = 1, $P < 0.001$).

Male blackbirds used five recognizable calls. The *cheer* call was the second most common call; *seeet, growl,* and *peet* calls comprised less than 8% of total male calls, and were given by less than half of the males (Table 1). *Growls* were given only when males were diving at or striking the predator models. Females used three types of calls; the *chatter* and *scream* comprised less than 15% of total calls and were given by only half of the females.

BLACKBIRD RESPONSES TO PLAYBACKS

Of the four call-types used in playback experiments, only the female *scream* produced responses significantly different from the responses to background noise in the number of blackbirds attracted, the number of total calls given, and the number of hovers (Table 2). Additionally, the *scream* call attracted more blackbirds and elicited more hovers than any of the other call types (Mann-Whitney *U*-tests, all P values < 0.05).

In each of the playback trials of the *scream* call to nestlings, young stopped begging within 1 to 5 sec and crouched low in the nest; whereas, young neither stopped begging nor crouched low to playbacks of the other call types.

REACTIONS TO DIFFERENT PREDATOR MODELS

Total call rates of male and female blackbirds were greater to each of the three predator models than to the box (Mann-Whitney *U*-test, all P values < 0.02; Table 3). Females had higher call rates than males, to both the hawk ($P = 0.02$) and the crow ($P = 0.006$), but not to the raccoon ($P > 0.05$). There were no differences in total

TABLE 3. Rates of nest-defense behavior by male and female Red-winged Blackbirds to different predator models.

Nest-defense response variables	$\bar{x}$ ± SD of nest-defense responses of 40 pairs of male and female blackbirds to indicated predator model[a]			
	Hawk		Crow	
	Male	Female	Male	Female
Check	38.4 ± 25.6	178.4 ± 93.5	46.7 ± 24.6	176.5 ± 110.4
Chatter	0.0	3.2 ± 5.9	0.0	1.1 ± 1.3
Growl	2.7 ± 3.9	0.0	12.3 ± 20.3	0.0
Scream	0.0	1.0 ± 3.2	0.0	79.2 ± 117.1
Peet	3.6 ± 11.4	0.0	0.0	0.0
Cheer	52.2 ± 21.6	0.0	22.1 ± 17.8	0.0
Seeet	9.6 ± 12.4	0.0	0.5 ± 1.0	0.0
Total calls	106.5 ± 28.7	182.6 ± 93.3	81.6 ± 27.0	256.8 ± 131.2
Nearest distance approached (m)	0.3 ± 0.4	3.6 ± 3.2	0.0	1.2 ± 2.0
Hovers	15.5 ± 8.3	3.5 ± 4.9	27.5 ± 19.6	18.1 ± 12.1
Dives and strikes	16.5 ± 11.9	0.0	72.5 ± 56.3	10.3 ± 14.7

[a] Red-tailed Hawk, American Crow, raccoon models, and the box were each presented to 10 different pairs of blackbirds when the nests contained eggs 6 to 8 days after initiation of incubation.

call rates to the different predator models, either for males (all P values > 0.05) or females (all P values >0.16). There were differences, however, among the proportions of the various call types to the different predator models (Table 3). For example, males gave more *cheer* calls to the hawk than to either the crow ($P = 0.007$) or the raccoon ($P = 0.01$). Females gave more *screams* to the hawk and raccoon than to the crow (both P values = 0.04).

As with calls, blackbirds showed differences in the more overt forms of nest defense to the predator models than to the box (Table 3). Whereas female blackbirds had higher call rates than males, males were more aggressive in nest defense. Males approached closer to the predator models than did females; the differences were significant for both the hawk (Mann-Whitney U-test, $P = 0.0003$) and the crow ($P = 0.02$), but not for the raccoon ($P = 0.15$). Males hovered more than females over both the hawk and crow models, though the differences were significant only for the hawk ($P = 0.001$); there were no intersexual differences in hover rates to the raccoon ($P = 0.91$). Finally, males dove and struck the predator models more often than did females (all P values < 0.002).

Blackbirds were most aggressive to the crow, intermediate in aggressiveness to the hawk, and least aggressive to the raccoon. Males approached the hawk and crow equally close ($P = 0.19$) but this was much closer than to the raccoon (both P values < 0.0002). Likewise, males hovered over the crow and hawk equally ($P = 0.19$) but far more than over the raccoon (both P values < 0.001). Males dove at and struck the crow more than the hawk ($P = 0.02$), and the hawk more than the raccoon ($P = 0.0002$). These differences were dramatic; 725 dives and strikes against the crow, 165 dives and strikes against the hawk, and two dives (no strikes) against the raccoon. Females showed a similar pattern. They approached the crow closer than the hawk ($P = 0.01$), and the hawk closer than the raccoon ($P = 0.05$). Females only dove at and struck the crow.

We examined whether individual blackbirds were consistent in their nest-defense intensity (i.e., call rates, closest distance approached, dives, and strikes), regardless of predator type, by use of Kendall's coefficient of concordance (Zar 1984). That is, was an individual that was aggressive (or timid) to one predator type equally aggressive (or timid) to the other predator models? Individual male and female blackbirds were consistent in nest-defense intensity across predator types (all P values < 0.05).

MALE ALLOCATION OF NEST DEFENSE AMONG HAREM FEMALES

Others have suggested that male nest defense is a form of parental care that is shareable among females in a male's harem (Patterson 1979, Orians 1980, Patterson et al. 1980a). We examined an aspect of this generalization by presenting two crow models simultaneously at nests of primary and secondary females and counting the number of dives and strikes directed at each crow by the male during a 3-min period. This experiment

TABLE 3. Extended.

$\bar{x}$ ± SD of nest-defense responses of 40 pairs of male and female blackbirds to indicated predator model[a]			
Raccoon		Box	
Male	Female	Male	Female
91.1 ± 35.8	161.5 ± 180.0	43.1 ± 28.7	19.5 ± 30.0
0.0	1.3 ± 1.9	0.0	0.8 ± 1.0
0.0	0.0	0.0	0.0
0.0	1.7 ± 5.4	0.0	0.0
0.0	0.0	0.0	0.0
23.4 ± 25.7	0.0	2.3 ± 3.7	0.0
0.6 ± 1.9	0.0	0.0	0.0
115.1 ± 47.6	164.3 ± 106.1	45.4 ± 30.4	10.3 ± 10.1
4.6 ± 5.1	5.8 ± 3.6	6.7 ± 4.2	2.0 ± 3.1
3.8 ± 4.0	3.8 ± 4.6	0.6 ± 0.7	0.0
0.2 ± 0.6	0.0	0.0	0.0

was conducted at 20 male territories in four marshes between 6 and 9 June.

Males were significantly more aggressive in defense of nests of primary females ($\bar{x}$ ± SD: 36.8 ± 22.6 dives and strikes) than of secondary females (11.2 ± 10.6) (Wilcoxon's paired-sample test, $P < 0.001$). This difference was not due to the nest contents (in 14 of 20 cases nests of primary females had fewer eggs or young than nests of secondary females [Sign test, $P = 0.012$]) nor was the difference due to the time interval between the primary and secondary females' nests. The difference in the number of dives and strikes between the primary and secondary nests was independent of the time interval (as measured from the initiation of incubation) separating the nests (range 1–22 days) ($Y = 3.08 + 0.16X$, $t = 0.10$, df = 19, $P > 0.50$).

NEST SUCCESS, HAREM SIZE AND NEST-DEFENSE INTENSITY

Total calls given by both parents was a significant explanatory variable for nest survival ($Y = 2.45 + 0.112X$, $t = 1.80$, df = 24, $P < 0.05$); however, total dives and strikes by parents was not ($Y = 3.08 - 0.00876X$, $t = -1.60$, df = 24, $P > 0.05$).

The number of male dives and strikes to the crow model was a significant explanatory variable for harem size ($Y = 1.99 + 0.0143X$, $t = 4.19$, df = 24, one-tailed test, $P < 0.0005$). Male calls, however, showed a significant negative relationship with harem size ($Y = 2.23 - 0.0705X$, $t = -2.91$, df = 24, one-tailed test, $P < 0.005$). Dives and strikes, and calls by males were negatively correlated ($r = -0.423$, $P < 0.05$). Number of male call types used in nest defense was not a significant explanatory variable for harem size ($Y = 3.23 - 0.134X$, $t = 1.55$, df = 24, one-tailed test, $P < 0.10$).

DISCUSSION

Orians and Christman (1968:68–69) demonstrated that polygamous species of birds have a greater number of vocalizations and displays than do monogamous species. They also showed that males in strongly polygamous species have more call notes than females, while in monogamous species there are little or no intersexual differences in the number of call types. Our observations extend these generalizations to calls used in nest defense. We documented seven recognizable call types in blackbird nest defense, while monogamous species use no more than two (e.g., Greig-Smith 1980, Patterson et al. 1980b, East 1981, Buitron 1983, Knight and Temple 1986c). Likewise, male blackbirds used more call types (five) than females (three) while defending the nest while males and females of monogamous species use an equivalent number of call types (previously cited studies).

Our results are consistent with recent findings of Beletsky et al. (1986) in that call types appear to be largely interchangeable, most being used regularly in all situations of disturbance ranging from mild (the box) to severe (the raccoon). Our results also corroborate earlier observations suggesting the female *scream* call has tremendous drawing power for other blackbirds (Orians and Christman 1968:41, Knight et al. 1985). Additionally, we showed that the *scream* caused nestlings to crouch low in the nest and stop begging, thereby decreasing their visual and audible conspicuousness. Greig-Smith (1980) and Knight and Temple (1986c) found that the Stonechat (*Saxicola torquata*) and American Goldfinch (*Carduelis tristis*), respectively, have calls which serve similar functions.

Female blackbirds had higher call rates while males showed the most aggressive nest-defense behavior. Calls are neither particularly costly energetically nor risky, whereas, dives and strikes are both expensive and risky (Andersson et al. 1980, Greig-Smith 1980, Shields 1984, Curio and Regelmann 1985; but see Knight and Temple 1986b:324). Female blackbirds on our study areas receive little male assistance during the breeding season (Nero 1956; Snelling 1968, unpubl. data). In species where the sexes share the duties more equitably, there is little intersexual difference in nest-defense behavior (e.g., Greig-Smith 1980, Buitron 1983, Knight and Temple 1986c; but see discussion in Regelmann and Curio 1986). Interestingly, male call rates were negatively correlated with dives and strikes ($r = -0.49$, $n = 27$, $P < 0.01$) while female call rates were positively correlated with dives and strikes ($r = 0.41$, $n = 27$, $P < 0.05$). This suggests a trade-off in effort by individuals. For example, males that have high rates of dives and strikes are not able to maintain high call rates. Females, on the other hand, are far less aggressive than males (fewer dives and strikes) so can maintain moderate levels of dives and strikes with moderate levels of calls. Alternatively, the functions of male and female calls could differ resulting in different mixtures of calls and overt nest-defense behavior (Beletsky et al. 1986).

We measured blackbird responses to predator models that differed in: (1) their threat to adult blackbirds, (2) their threat to the nest's contents, and (3) the ability of blackbirds to drive them off. The results enable us to examine explanations for differing levels of aggressiveness towards different predators (Kruuk 1964, Patterson et al. 1980b). The first two factors listed above relate to the parents' motivation for nest defense, whereas, the third deals with the ability of the parents to effect a change in the predator's behavior (i.e., to drive the predator away). Call rates did not differ for the three predator models; there were differences, however, in more overt behavior such as dives and strikes. Blackbirds were most aggressive to the crow, least aggressive to the raccoon, and intermediate in aggressiveness to the hawk. Because hawks are a threat to adults (Orians and Kuhlman 1956, unpubl. data) and crows are of almost no threat, we can discount the "threat to adult blackbirds" explanation for the differences in aggressiveness. Because the hawk is of no threat to a nest with eggs but crows and raccoons are, there is little support for the "threat to the nest's contents" explanation. Birds are more effective in driving off birds than mammals (Kruuk 1964, Horn 1968, Roell and Bossema 1982, Buitron 1983, Knight et al. 1985); this agrees with our findings and supports the "ability of blackbirds to drive them off" explanation. Our data does not allow us to separate among the two underlying motivations for nest-defense aggressiveness: concern for nest, and safety of adult and mate. In another study we have shown that when the threat of a predator to an adult's safety is minimized the adults defend a nest much more aggressively (Knight et al. 1987).

When presented with a choice between defending nests of primary and secondary females, males chose to defend the primary female's nest. There are at least four potential explanations for our findings: (1) primary nests may have larger clutches, (2) males may have invested more parental care in primary nests, (3) primary nests may have a greater chance of success due to a seasonal increase in nesting failure, and (4) primary females may have genetically superior offspring. We observed that neither the difference in number of offspring nor the time difference between nests of primary and secondary females explained differences in male nest defense, thereby discounting the first two explanations. We do not have the data necessary to separate the importance of the final two factors; however, Patterson (1979) observed that male Red-winged Blackbirds continued to invest in renesting attempts of the primary female rather than the initial nesting attempt of secondary females. This suggests that the male is influenced by traits of the female per se.

We found that call rate was positively correlated with nest success. Based on our correlations between rates of calling, and dives and strikes, our evidence suggests that blackbirds which successfully avoided nest predation were males who had high call rates and females with both high rates of calling, and dives and strikes. Because most nest predation in our marshes was by raccoons and minks (*Mustela vison*), our findings agree with the generalization that mammalian predators are difficult to repel with overt aggression but that high call rates may be effective in distracting or confusing them (Kruuk 1964, Horn 1968, Greig-Smith 1980, Röell and Bossema 1982, Buitron 1983, Knight and Temple 1983c). Neither Searcy (1979) nor Yasukawa et al. (1987) have found positive correlations between blackbird nest-defense intensity and nest success (but see Biermann and Robertson 1983). Neither of these studies included responses of both parents nor did either separate call rates and rates of dives and strikes in their analyses.

We found that male harem size was positively correlated with intensity of male nest defense (i.e., dives and strikes) and number of call types used (statistically nonsignificant). Likewise, Yasukawa et al. (1987) found that harem size in marsh-nesting blackbirds was correlated with nest-defense intensity, but no correlation existed for blackbirds nesting in fields. Nest-defense aggressiveness increases with age and experience (Pugesek 1983; Smith et al. 1984; Knight and Temple 1986a, 1986b) suggesting that the aggressive males in our study were older individuals. Both Picman (1980) and Yasukawa (1981) found that older males had larger harems.

An inconsistency in our findings is that nest survival did not correlate positively with dives and strikes but did with call rate. In contrast, harem size varied in the opposite manner; overtly aggressive males had larger harems. This suggests that females are not using estimates of defensive behavior (at least dives and strikes) in choosing males or territories. If it is not advantageous for females to choose males with high aggressiveness towards predators, then it would seem that the correlation between aggressiveness and harem size is an indirect consequence of some other effect or correlate of aggressiveness (e.g., age).

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