The information that receivers extract from alarm calls in suricates

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Field observations and acoustic analyses have shown that suricate (*Suricata suricatta*) alarm calls vary in their acoustic structure depending on predator type. In this study, we tested whether receivers respond appropriately when hearing a call in the absence of a predator. Although the only way for suricates to escape from predators is to retreat to boltholes, responses to playbacks could be divided into distinct categories. The subjects responded differently to alarm calls given in response to aerial or terrestrial predators and to recruitment calls emitted in response to snakes and deposits on the ground. Suricates also showed rather distinct responses to low, medium and high urgency aerial calls. Differences in the responses were less obvious for different levels of urgency in the terrestrial and recruitment calls. Suricate receivers thus gain information about both the predator type and level of urgency from the acoustic structures of their calls.

Keywords: alarm calls; functionally referential; level of response urgency; receivers; suricates

1. INTRODUCTION

In order to understand the evolution of acoustic variation in animal vocalizations, it is important to consider both the contexts that elicit different calls by signallers and the information that receivers extract from these calls (Marler *et al*. 1992; Macedonia & Evans 1993). In the case of alarm calls, two different meanings that are extracted by receivers have been described. In some species, the acoustic structure of the alarm calls varies depending on predator type and this variation is sufficient to allow receivers to respond appropriately to different types of predators, even in the absence of visual cues. Such calls have been described as functionally referential. Vervet monkeys (*Cercopithecus aethiops*), for example, typically show obviously different responses to different types of alarm calls. They run into trees in the case of leopard alarm calls and to the next bush when hearing eagle alarm calls (Seyfarth *et al*. 1980). Several species of sciurids, such as some ground squirrels (Robinson 1981) and marmots (Blumstein & Armitage 1997*a*), also give more than one call type in response to different predators. However, their calls appear to be less predator specific and rather denote slow-developing 'low-risk' and fast-developing 'high-risk' situations', respectively (Robinson 1981; Sherman 1985). The only way of escape, independent of what call type is played, is to run into their burrow. The alarm calls of these species have therefore been assumed to provide listeners with information about the urgency of the situation rather than the predator type.

The selective force causing some species to evolve functionally referential alarm calls, as opposed to only response urgency alarm calls, might be the way of escape from a predator (Cheney & Seyfarth 1990; Macedonia & Evans 1993). When reviewing alarm calls in several primate and sciurid species, Macedonia & Evans (1993) concluded that the predation pressure on small-bodied

terrestrial mammals living in an open habitat might explain why vervets' and ring-tailed lemurs' (*Lemur catta*) alarm calls denote predator classes and possibly also urgency, while the alarm calls of arboreal-ruffed lemurs (*Varecia variegata*) appear to be threat and recruitment/mobbing calls (Macedonia 1990). However, this explanation does not explain why ground squirrels have evolved alarm calls that are urgency based but not functionally referential. Macedonia & Evans (1993) suggested that functionally referential-specific alarm calls are favoured by natural selection when animals confront different predator species with different hunting strategies where different modes of escape are advantageous (Marler 1967; Cheney & Seyfarth 1990; Macedonia & Evans 1993). According to this view, the degree of referential specificity of each alarm call and also the number of call types within a species' repertoire are determined by the function of the call. For example, because vervet monkeys confront a variety of different predators with different hunting strategies, they have evolved different escape strategies. Presumably as a result, the monkeys possess a number of acoustically distinct predator-specific alarm calls (Struhsaker 1967; Seyfarth *et al*. 1980). In contrast, predator type is less important for some sciurid species than the immediacy of danger, since they escape from any predator by fleeing to their burrows (Blumstein & Armitage 1997). The question arises as to whether only species with multiple ways of escape evolve functionally referential alarm calls or whether other forces can cause the evolution of highly sophisticated alarm systems.

Suricates (*Suricata suricatta*), also called meercats which are cooperatively breeding mongooses, use several structurally distinct alarm calls for warning other group members when predators are approaching. The acoustic structure of some of their alarm calls varies depending on both predator type and the level of urgency (Manser 2001). Suricates are diurnal and live in open semi-desert areas in groups of three to 33 individuals. They forage for 5–8 h d^{-1} in the open, digging for invertebrates and small vertebrates in the sand (Doolan & Macdonald 1996).

Table 1. *The number of playback experiments performed per call type (indicating what predator type and level of urgency the calls denote) in different groups.*

call type	predator type	level of urgency	n different calls per call type	n groups	n playback experiments
aerial low urgent	aerial	low	6	6	6
aerial medium urgent	aerial	medium	12	12	18
aerial high urgent	aerial	high	6	6	12
terrestrial low urgent	terrestrial	low	6	6	6
terrestrial medium urgent	terrestrial	medium	6	6	12
terrestrial high urgent	terrestrial	high	6	6	6
recruitment low	recruitment	low	6	6	12
recruitment high	recruitment	high	6	6	12
alert	aerial	low	12	12	18
moving animal	aerial/terrestrial	low	12	10	18
panic	aerial/terrestrial	high	6	6	12

They spend most of their time foraging at a distance of 20–50 m from the next bolthole or shelter and, when passing by during foraging, they often renovate these holes. Suricates emit a variety of acoustically different calls in order to alert other individuals to the approach of aerial and terrestrial predators. Alarm-like calls are also used for recruiting group members when encountering snakes or other animals caught in boltholes or for recruiting others for investigating deposits on the ground, such as urine, faecal or hair samples of foreign suricates or predators (Manser 2001). Depending on the alarm call given, suricates either stand bipedally, run to the next bolthole or move to a burrow system. When they encounter a snake, they gather together and mob the snake. When they smell a deposit they begin to emit calls and other group members join them in order to investigate it. Although suricates frequently climb up shrubs and trees to stand guard, they never climb to escape from predators.

In this study, we use playback experiments in order to investigate how suricates respond to different alarm call types that vary in their acoustic structure depending on both the level of urgency and predator type. The range of alarm call types in suricates allows us to examine whether the variation in acoustic structure with the level of urgency elicits the same range of responses as does the variation in acoustic structure with predator type. In particular, we ask whether suricates show different responses to aerial and terrestrial alarm calls and recruitment calls and whether they respond more strongly to more urgent calls within the same predator category.

2. METHODS

(a) *Study site and animals*

Recordings of alarm calls and the playback experiments were conducted at two study sites in South Africa in the southern part of the Kalahari Desert from November 1995 to December 1996 and again from January 1999 to August 1999. For the recordings of alarm calls, we followed eight groups with 70 adult individuals along the dry riverbed of the Nossob in the Kalahari Gemsbok National Park and another 10 groups with 131 adult individuals on ranchland close to Van Zyl's Rus along

the dry riverbed of the Kuruman (for a more detailed description see Clutton-Brock *et al.* (1998)). All individuals in a group could be identified and were habituated to close-range observation by humans on foot. We made tape recordings of vocalizations from as close as 0.2 m. Alarm calls were recorded using a Sony digital audio tape recorder DAT Pro II (Sony Corporation, Tokyo, Japan) and a Sennheiser directional microphone MKH 816 (Sennheiser electronic, Wedemark, Germany).

(b) *Playback experiments*

(i) *Selection of calls for playback experiments*

Acoustic analysis of the different alarm-call types conducted prior to the playback experiments showed that the acoustic structures of the calls varied substantially within a predator type, but also depending on the level of response urgency (Manser 2001). We investigated whether the receivers would recognize these different calls as being from the correct category of predator type and show the appropriate response, and also whether there was a difference in their responses depending on the level of urgency a call conveyed. We tested responses to 11 different alarm-call types that had originally been elicited by the presence of different predator types at different levels of response urgency (aerial and terrestrial calls at low, medium and high urgency levels and recruitment calls at low and high urgency levels) (table 1). We also played three other types of call that were not correlated with specific predator types, namely 'alert', 'moving animal' and 'panic' calls. The alert and moving animal calls were given in response to a variety of predators as well as non-dangerous animals, usually in what appeared to be low-risk situations. Panic calls, on the other hand, were elicited in response to the alarm calls given by birds and a few times by aerial and terrestrial predators that were very close by. These calls almost always made the suricates run to the next bolthole and go below ground, suggesting that they represented a high-risk situation. An example of a typical spectrogram and a description of the context that elicited the different call types are given in another paper on an acoustic analysis of these vocalizations (Manser 2001).

(ii) *Experimental procedure*

Responses to alarm calls without a predator present were investigated by playing back calls to 13 different groups (eight groups on the ranch and five groups in the park). However, not all the call types were played to all of the groups. Some call

types were tested in the same group more than once, but each time on a different subject (table 1). Only adult individuals were chosen as subjects. Because 11 call types were tested and each was tested in at least six groups, some individuals were used as subjects for more than one call type (however, the same subject was only used a maximum of three times in all of the experiments). Eighty-five subjects were tested in a total of 144 playbacks. At least six different examples of a call type were tested. High quality recordings of adult individuals in the same group were typically chosen as the playbacks were conducted. The calls were played from a Sony DAT recorder (Sony Corporation, Tokyo, Japan) connected to a Sony walkman SR A60 speaker, and responses were filmed with a Sony video high 8 camera or Panasonic digital video camera when possible (in eight out of the 144 experiments we were not able to film major parts of the response for technical reasons, and we used our notes made during the playbacks for the analysis). We adjusted the volume of the calls to the amplitude observed for calls given during naturally occurring predator encounters. All playbacks were conducted on suricates foraging at least 50 m from burrow systems and 10 m from boltholes within a range of 10–20 m of the loudspeaker. We only performed a playback if there had not been a predator encounter or group encounter during the previous 30 min. The subject was filmed for at least 30 s before the call was played and its response for a minimum of 30 s or until it relaxed. In order to minimize habituation to the playbacks, one playback experiment was typically performed per foraging session and the next was conducted 5–7 days later in the same group.

(iii) *Statistical analysis*

We analysed the response of the subject that had been filmed for each playback experiment. We then used a logistic regression model of Spss v. 10.0 in order to test the influence of predator type and the level of urgency on the frequency of specific responses. The duration of the time to relax was analysed by performing ANOVA after a logarithmic transformation of the data in order to fulfil the requirement of the data being normally distributed (Sokal & Rohlf 1995).

3. RESULTS

On the occasions when the suricates showed a response, they always did so immediately within the first few calls (2 s) of a playback. Although the only shelters for suricates are boltholes, it was possible to classify their responses within different categories. Suricates responded to the alarm calls by looking up briefly, rearing up on their hind legs to scan their surroundings, moving to a shelter and scanning the surrounding area, running back to a bolthole or burrow system without looking around or approaching the loudspeaker. Only one of these responses was possible for the analysis. The additional responses analysed, i.e. scanning the sky, gathering together, moving away together and erecting their tails and fur, did not exclude other responses. We included longer time-windows for these responses than just the first few seconds. We limited the response time for the response of scanning the sky to 20 s because they showed this behaviour either when rearing up or after they had run to a bolthole. We scored all the other non-exclusive responses if we observed them from any time when playing the call until the individual resumed foraging.

(a) *Responses to predator type-specific alarm calls*

The suricates responded in qualitatively different ways to the aerial, terrestrial and recruitment calls (tables 2 and 3). A few subjects showed no response to the aerial predator calls, but most of them either interrupted foraging and scanned the area or immediately ran to the next bolthole without first looking around. Individuals crouched down on the ground before they ran to a bolthole or resumed foraging again quite quickly in one-third of the playbacks of the high urgency aerial call. Although the subject scanned the sky within 20 s after having heard the call in only 11 out of 54 playbacks, this was still significantly more often than for any other call-type category. The time to relax after a playback was significantly shorter for aerial calls than for any other call type (ANOVA of predator type, d.f. = 1, $F = 20.49$ and $p < 0.0001$) (figure 1).

The suricates always interrupted foraging when they heard any of the terrestrial calls but, rather than running to the next bolthole, they moved in the direction of the loudspeaker, frequently scanning the area. The suricates typically gathered together 5–10 m away from the loudspeaker and often marked each other before they then either moved away together to the next bigger burrow system in 15 out of 24 experiments or resumed foraging again quite quickly. The time to relax was much longer than after an aerial call (Bonferroni *post hoc* test of terrestrial versus aerial calls, $p < 0.0001$) (figure 1).

A different response was shown to the recruitment calls. When they heard the calls, the suricates erected their tail and often also their hair and approached the loudspeaker slowly. In two cases, when there was a bolthole between their location and the loudspeaker, they would first go down to inspect the bolthole and then walk over to the loudspeaker. The suricates began to sniff around the area after approaching the loudspeaker and often marked each other before they resumed foraging. The time to relax was substantially longer than after aerial calls, but it was approximately the same as after hearing a terrestrial call (Bonferroni *post hoc* test of recruitment versus terrestrial calls, $p = 0.37$ and Bonferroni *post hoc* test of recruitment versus aerial calls, $p = 0.0008$) (figure 1).

(b) *Influence of response urgency of the alarm calls on the response*

The acoustic variation representing the level of urgency in the alarm calls influenced the responses of the suricates to the calls in a less obvious way than did the features that changed with predator type. Nevertheless, calls of low urgency of any predator category caused the subjects just to scan the area and not to move or run for shelter (tables 2 and 3). Furthermore, the time to relax increased substantially from the low to medium and again to the high level of urgency in the case of the terrestrial and recruitment calls (ANOVA of urgency d.f. = 1, $F = 18.24$ and $p < 0.0001$) (figure 1). This was not the case for the aerial calls. This might be because the high-level urgency call elicited a rather different response from the subjects in that they crouched flat on the ground and, when they realized that nothing was happening, they resumed foraging again. On the other hand, running back to a bolthole in response to

Table 2. The number of subjects (*n*) and the percentages showing the different response categories to the playbacks of the different call types.

(The values marked by asterisks indicate the most common responses shown to the different call types. Column headings: 1, no response; 2, scanning the area; 3, crouching down; 4, scanning the sky; 5, moving to shelter and scanning area; 6, running for shelter without looking around; 7, gathering together; 8, moving away together; 9, approaching loudspeaker; 10, erecting tail; 11, erecting fur.)

call type	predator type	level of urgency	total number of playbacks	responses observed										
				1 $n(\%)$	2 $n(\%)$	3 $n(\%)$	4 $n(\%)$	5 $n(\%)$	6 $n(\%)$	7 $n(\%)$	8 $n(\%)$	9 $n(\%)$	10 $n(\%)$	11 $n(\%)$
low urgent aerial	aerial	low	6	0	3(50)*	0	1(17)	1(17)	2(33)*	0	0	0	0	0
medium urgent aerial	aerial	medium	18	0	7(39)*	1(6)	3(22)*	1(6)	9(50)*	6	6	0	0	0
high urgent aerial	aerial	high	12	0	3(25)*	4(33)*	2(17)	2(17)	3(25)*	0	0	0	0	0
low urgent terrestrial	terrestrial	medium	6	0	2(33)*	0	0	4(67)*	0	3(50)*	2(33)*	0	0	0
medium urgent terrestrial	terrestrial	medium	12	0	2(17)	1(8)	0	9(75)*	1(8)	9(75)*	7(58)*	2(17)	0	0
high urgent terrestrial	terrrestrial	high	6	0	0	0	0	5(83)*	1(17)	3(50)*	2(33)*	0	0	0
low urgent recruitment	recruitment	low	12	0	0	0	0	1(8)	0	3(25)*	0	11(92)*	11(92)*	6(50)*
high urgent recruitment	recruitment	high	12	0	0	0	0	0	0	11(92)*	0	12(100)*	12(100)*	12(100)*
alert	aerial	low	18	4(22)	11(61)*	0	4(22)*	0	3(17)	0	0	0	0	0
moving animal	aerial/ terrestrial	low	18	5(33)	7(39)*	0	2(11)	5(33)*	1(6)	1(6)	0	0	0	0
panic	aerial/ terrestrial	high	12	1(7)	2(14)	0	0	0	9(75)*	0	0	0	0	0

Table 3. Statistics for the different response categories to the playbacks of the different call types.

(The statistics were performed with the original frequency data and show the results of the logistic regressions testing for differences in the responses for predator type and level of urgency. There were no data available for the no response category for any of the three variables. A dash indicates a *p*-value of < 0.0001. The values marked by asterisks indicate significant results. Column headings: 1, scanning the area; 2, crouching down; 3, scanning the sky; 4, moving to shelter and scanning area; 5, running for shelter without looking around; 6, gathering together; 7, moving away together; 8, approaching loudspeaker; 9, erecting tail; 10, erecting fur.)

variable	responses observed									
	1	2	3	4	5	6	7	8	9	10
predator type (d.f. = 2)										
χ^2-value	26.53	5.73	10.56	34.85	16.36	42.83	23.37	79.66	73.65	50.74
p-value	—*	0.057	0.005*	—*	—*	—*	—*	—*	—*	—*
urgency (d.f. = 2)										
χ^2-value	4.88	4.80	1.91	0.75	1.84	9.69	2.36	4.59	0.0	10.36
p-value	0.09	0.09	0.39	0.69	0.4	0.008*	0.31	0.10	1.0	0.006*
intercept (d.f. = 4)										
χ^2-value	18.25	10.71	14.63	35.38	22.13	45.69	29.01	92.00	100.51	70.65
p-value	—	0.03	0.006	—	—	—	—	—	—	—

low and medium urgency aerial calls required much more time.

The playback experiments of the three alarm-call types that were not elicited by specific predator types supported the pattern of responses seen in the predator-specific calls changing from the low to high level of urgency. The moving animal and alert calls, both of which are call types representing a low urgency situation, elicited the least strong responses in that the suricates more often either did not show any response at all or only scanned the area (tables 2 and 3). On the other hand, the panic call, which represents a high urgency situation,

evoked a very strong response. Only one subject did not interrupt its current occupation at all. Two subjects out of 12 only looked up briefly and then continued foraging, while nine out of 12 immediately ran to the next bolthole.

4. DISCUSSION

The suricates responded to the alarm-call playbacks with adaptive escape strategies that depended on two sorts of acoustic variation in call structure. Calls that were given in response to aerial predators, terrestrial predators, snakes and deposits evoked qualitatively different responses. Furthermore, within each of these call categories, calls that had been recorded in situations of high, medium and low urgency evoked the strongest, intermediate and the weakest responses, respectively.

These results indicate that call recipients are able to extract specific information about predator type and also the level of urgency from the acoustic structures of alarm calls in the absence of stimuli. Together with the high production specificity of aerial and terrestrial calls in response to different predator types, this suggests that suricates have evolved functionally referential alarm calls, as described for vervet monkeys (Seyfarth *et al*. 1980) and ring-tailed lemurs (Macedonia 1990). In addition, suricate alarm calls also vary depending on the level of response urgency, and receivers are able to extract that information and show adaptive responses within this dimension as well. However, the differences in the responses between low urgency and high urgency calls were less obvious than between the different predator types.

Although the receivers in this study showed a high perception specificity to the recruitment calls, it is not clear whether this call type is functionally referential or the expression of the affective state of a caller in order to manipulate other group members. Recruitment calls are not predator type specific as is the case with aerial or terrestrial calls (Manser 2001). Although they are mainly emitted in response to snakes and deposits, other animals such as suricates and terrestrial predators caught in boltholes elicit the same calls. Recruitment calls may denote the context of more or less stationary animals or deposits on the ground or in boltholes. It may be that it is not the predator type, but how a predator approaches or is encountered that elicits different call types (Evans 1997). However, the response of other group members to these calls for approaching the caller also supports the management hypothesis (Owings & Morton 1998). These calls may express the affective state of the caller who wants the group to gather together. More detailed observations and experiments need to be performed in order to draw conclusions on whether recruitment calls are the expression of the affective state of the caller or whether they denote a specific behaviour of an approaching animal.

A similar question arose in the analysis of the moving animal call. This call is given in response to different predator types and also non-dangerous animals, but only when they are moving (Manser 2001). The question that arose was whether the call was a higher urgency version of the alert call and the expression of the affective state of the caller or whether it was functionally referential and denoted a specific behaviour of the approaching animal. The responses to the playbacks of moving animal calls
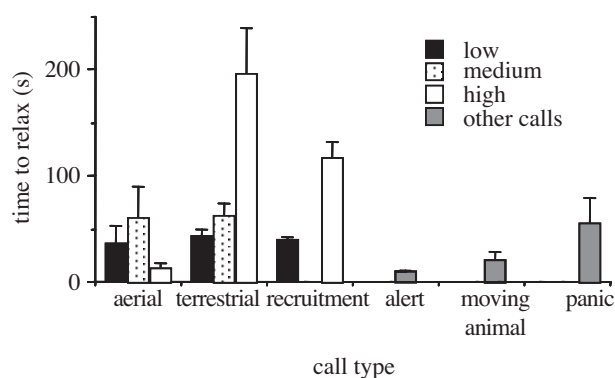

Figure 1. The time to relax (s) (mean ± s.e.) after the playbacks of the different call types.

and alert calls were not obviously different, indicating a low perception specificity. Therefore, according to our analysis, this call type cannot be considered as functionally referential. The experiments suggest that the moving animal call is the expression of the affective state of the caller.

(a) *The evolution of referential and response urgency alarm calls*

The reason why a species evolves functionally referential rather than only response urgency alarm calls has been explained by the different escape strategies that are needed (Macedonia & Evans 1993). While vervet monkeys respond by running up a tree in the case of the leopard call or running to the nearest bush when hearing an eagle alarm call (Seyfarth *et al*. 1980), the only way of escape in sciurid species is to run to a burrow. Suricates are in a similar situation to sciurids because their only escape from predators is retreating into a bolthole. However, they have evolved several different graded responses to intruders within this way of escape. On hearing an aerial alarm call they run to the nearest bolthole, since there is not much time to respond and the danger is usually only of short duration, whereas on hearing a terrestrial alarm call they gather together at the same safe place with the rest of the group in order possibly to leave the area together, since jackals in particular will watch a group for a long time (sometimes for longer than an hour) (M. B. Manser, personal observation). Similar subtle differences in ways of escape have been described in Belding's ground squirrels (*Spermophillus beldingi*), which run to the next burrow in the case of an aerial alarm and to burrow systems with more than one entrance in response to a terrestrial alarm (Sherman 1985). In addition, as described for Belding's ground squirrels, suricates not only emit calls in response to potential predators, but also to non-dangerous birds or herbivores approaching the group. The question therefore arises as to why suricates have evolved highly predator type-specific alarm calls, but Belding's ground squirrels have not.

Suricates are small terrestrial carnivores that dig for food in the sand. They travel from one sleeping burrow to the next and forage as a cohesive group up to several hundreds of metres away from larger burrow systems. However, they do maintain boltholes, which they

regularly dig out whenever they pass by. Unlike sciurids, suricates use a much larger territory and, if they encounter a terrestrial predator in part of the area, they often sneak away to another part several hundreds of metres away (M. B. Manser, unpublished data). By moving away from a stationary predator, either terrestrial or a perched raptor, they can resume their foraging in another area earlier than if they simply barked at the predator (Manser 1998) and waited for it to leave. However, this escape strategy requires coordination of their movements because, for each individual, losing the group could have severe consequences. Single individuals and small groups suffer a much higher predation rate than larger groups (Clutton-Brock *et al*. 1999). This might explain why, in the case of a terrestrial call, members first gather together, mark each other and then finally move to the next bigger burrow system together.

The advantage of emitting calls that are not only in response to potential predators but to any approaching non-dangerous animal becomes obvious when we consider the habitat that suricates occupy and their diet. They live in open semi-desert areas and dig for mobile prey, such as scorpions, small reptiles and insect larvae in the sand (Doolan & MacDonald 1996). Therefore, when they search for food they have their head on the ground or in digging holes and cannot see very far around them. By individuals emitting calls with specific information about predator type, the risk level of the animal and the level of urgency, they are able to adjust their responses. If suricates had to run for shelter each time an animal approached their foraging efficiency would drop substantially. The mobile prey that a suricate had just pursued would most probably have moved away by the time it returned to the spot after an alarm call. Therefore, in contrast to sciurids, suricates inhabiting large home ranges and digging for moving prey live under pressure to coordinate their movements and their vigilance behaviour in order to increase their foraging efficiency (Manser 1999).

The pressure for maintaining group cohesion and co-ordinating their vigilance behaviour might explain why suricates have evolved functionally referential alarm calls that also convey information about the level of urgency of the situation. The fitness benefit for suricates of using different escape strategies, although they are much more subtle than in vervet monkeys, may have been enough to evolve different call types with specific information. Subtle differences in their responses to different predator types may not be as important for some sciurid species, as the pressure to coordinate their group movements as a cohesive unit is not as high. Therefore, the evolution of functionally referential alarm calls in a species may not only depend on the presence of predators with different hunting strategies, but also on the social complexity under which the species is living (Blumstein & Armitage 1997*b*).

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