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Alarm calls and flight behaviour in Spanish ibex (*Capra pyrenaica*)

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Key words: Antipredator behaviour. alarm calls. *Capra pyrenaica.*

RESUME

Cris d'alarme et comportement de fuite chez le bouquetin espagnol (*Capra pyrenaica*).

Certains aspects des réactions d'une population de bouquetins espagnols (*Capra pyrenaica*) vis-à-vis de prédateurs ont été étudiés de Mai 1984 à Janvier 1985 et en Septembre 1985 dans la Sierra de « Cazorla y Segura » au Sud-Est de l'Espagne. Au cours de l'étude, 102 groupes de bouquetins comportant au total 288 animaux, ont été expérimentalement alarmés par la présence d'un humain. Dans ces conditions, les animaux se regroupent et fuient ensemble. Dans la nature, les bouquetins émettent des cris d'alarme en réponse à une présence humaine. Nous suggérons que cette perturbation rassemble les individus apparentés et leur permet de fuir ensemble, conduits généralement par une femelle adulte, ou par le mâle le plus âgé s'il s'agit d'un groupe de mâles. Lorsque les humains sont proches et ont été détectés, les cris d'alarme sont émis depuis des points où les animaux sont en sécurité (par exemple, pentes rocheuses), les résultats indiquent que la fonction principale des cris d'alarme est d'alerter les autres membres du groupe. Ceci peut être considéré comme un comportement égoïste dans la mesure où les animaux sont plus vulnérables s'ils fuient seuls. De plus, comme les bouquetins émettent des cris d'alarme plus fréquemment lorsqu'ils sont dans des groupes d'animaux apparentés que lorsqu'ils sont dans des groupes d'animaux non apparentés, nous suggérons que les cris d'alarme peuvent avoir évolué en liaison avec la sélection parentale.

Mots clés: Comportement antiprédateur. cris d'alarme. *Capra pyrenaica.*

SUMMARY

Some aspects of the reactions of a population of Spanish ibex to predator (*Capra pyrenaica*) were studied from May 1984 until January 1985 and during

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September 1985, on the Sierras de Cazorla y Segura in South-eastern Spain. During the study 102 groups of ibexes with a total of 288 animals were experimentally alarmed by the presence of a human. The ibex were put into seven age and sex classes. In our results we observed that Spanish ibex bunch closely together and flee together in response to humans. Spanish ibex give alarm calls in response to human disturbance in the wild. We suggest that this human disturbance seems to bring related ibex together, and allows them to flee together, generally led by an adult female, or by the oldest male in a male group. We found ibex call from a safe vantage point (e.g. rocky slopes) when humans are close to them and are likely to have been detected. The data indicate that the primary function of the alarm call is to alert other members of the group. This may be largely selfish, because animals are more vulnerable if they flee by themselves. Furthermore since ibex call more frequently in related than in unrelated groups, we suggest that alarm calls may have evolved by kin selection.

INTRODUCTION

The Spanish ibex (*Capra pyrenaica*) is primarily a species which inhabits some of the mountain ranges of Spain. When Spanish ibex detect a potential predator they give an attention response ; an erect stance with head and ears pointing towards the predator, and one member of the group usually gives one or more alarm call before the group flees in single file, some times the group moves to avantage point on a rocky slope and stops to look back.

Spanish ibex are cryptic in colour but in response to potential predators they give an auditory signal consisting of high-pitched explosive whistle, which begin and end abruptly. They are audible to human observers up to about 200 m. away. These charcteristics give the alarm call a strong directional quality allowing the caller to be accurately and quickly located from considerable distances by predators and conspecifics. In addition, the rapid repetition of calls give recipients ample time in which to locate the caller.

The use of alarm signals in escape situations is widespread among artiodactyls (Guthrie, 1971). Several hypotheses have been developed to explain the function of signals given in dangerous situations. These hypotheses which are not mutually exclusive include : (1) The signals are altruistic and may have evolve by kin selection (Hamilton, 1964, Maynard Smith, 1965) or group selection (Wilson, 1975). (2) The signals discourage a predator from attacking (Trivers, 1971, Tilson and Norton, 1981) and serve to inform the predator that it has been detected (Bildstein, 1983, Caro, 1986). (3) Individuals obtain direct benefits from warning others of danger by creating confusion among group members and thereby diverting the predator's attention away from the caller (Charnov & Krebs, 1975, Hoogland & Sherman, 1976, Owens & Goss-Custard, 1976). (4) The alarm call may be a cohesive signal serving to keep a group together (McCullough, 1969, Kitchen, 1972).

Klump & Shalter (1984) have analysed the different functions of various alarm calls in birds and mammals, taking into account the requisite conditions and available evidence for the evolution of alarm calls through individual selection and kin selection.

In this study we have attempted to know the responses of ibexes to human disturbances in different situations taking into account the characteristics of the group and behaviour of the group members. The use of alarm calls in the Spanish ibex was also studied.

METHODS

Ibexes were observed in Sierras de Cazorla y Segura (SE of Iberian Peninsula), a mountain reserve located between latitudes 37° 45' and 38° 10' and longitudes 2° 40' and 3° 00'. The area is 66,367 ha. A dense woody vegetation forms a protective cover in the reserve. The mountains have been afforested with *Pinus nigra, P. pinaster* and *P. halepensis,* which together with *Quercus ilex* are the main tree species. The limestone slopes are very steep and rugged.

The major predator in the evolutionary history of Spanish ibex has been the wolf (*Canis lupus*) and aboriginal man. There are alson other smaller predators such as eagles or foxes, which attack only ibex kids. Today, in the ranges where we are studying the ibex population, the wolf has been exterminated althogh some feral dogs have partially filled its ecological niche. Hirth &McCullough (1977) believe that escape and alarm behaviour are conservation characteristics that have changed little over evolutionary time and, which may have been reinforced by modern human predation. If this is the case, the results could be applied to other predators in general.

Our field work was conducted from May 1984 until January 1985 and during September 1985. Observations were made with binoculars (10 × 40) at dawn and dusk. During the study 102 groups of ibex with a total of 288 animals were experimentally alarmed by the presence of a human. Individuals were assigned to sex and age-classes based on combinations of sexually dimorphic physical characteristics and age-related variations in body size, horn size and morphological configuration (Alados, 1986). The seven age and sex classes considered were: adult females (♀ ad) older than two years, yearling females (♀ J) between 1 and 2 years old, kids (J) newly born to 1 year old, old males (♂ v) older than 8 years, adult males (♂ ad) from 4 to 8 years old, subadult males (♂ sb) from 2 to 4 years old, and, finally, yearling males (♂ J) from 1 to 2 years old.

The there basic social units of Spanish ibex included in our study were: *male groups* defined as groups of males with no females, *female-kid groups,* groups with at least one adult female with juveniles, and *mixed groups* i.e. females and males of all ages.

Three kinds of distance were recorded: detection distance—when ibexes started to move away from the human disturbance either at full speed or walking slowly; and alarm call distance—the distance between the human disturbance and prey when the prey gives the first alarm call.

When we found a group of ibexes, one of us walked towards it in a straight line at a steady speed stopping as soon as an animal walked, trotted or galloped away. We then measured the flight distance with a telemeter. We also noted the size and composition of ibex groups and noted the relative position of individuals in relation to each other before and after they were alarmed, and the direction from which the human disturbance aproached (from above or below). Other data recorded comprised: the nearest neighbour distance, the first animal to detect the human disturbance, the detection distance, the number of alarm calls, the alarm call distance, and, finally, we noted the flight behaviour. Habitat characteristics were recorded, such as inclines and orientation of the slope and wind directions. Tourist pressure was also considered (high tourist pressure areas—

where vehicles are permited, low tourist pressure areas—where vehicles are forbidden).

The flight starting index was calculated by the excentricity quotient ($q = (o\text{-}e) / \sqrt{e}$), the expected value (e) being calculated by the probability that an individual in the age and sex class shown was the group leader, and the observed value (o), the frequency of flights led by it.

At the begining of our study we tested to see if tourist pressure influences the flight distance, in order to prevent any bias.

RESULTS

Spanish ibex react to human disturbance by grouping closely together from an average of 10 m (SD = 8.2) between members before

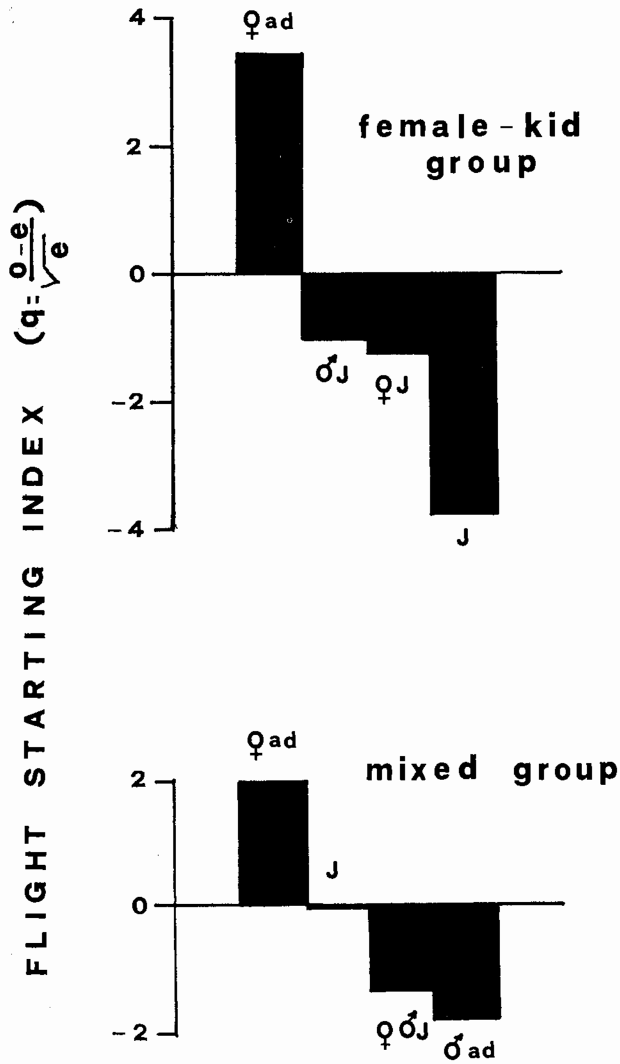

Fig. 1 : *" Flight starting index " in ordinates representing the probability that female-kid and mixed groups are led by an individual in the age and sex class shown when the animals are escaping from the human disturbance.*

Fig. 1 : *L'indice « d'initiation de la fuite » en ordonnées représente la probabilité pour des groupes de femelles-jeunes d'être entraînés à éviter l'homme par un individu d'une classe d'âge et de sexe déterminée.*

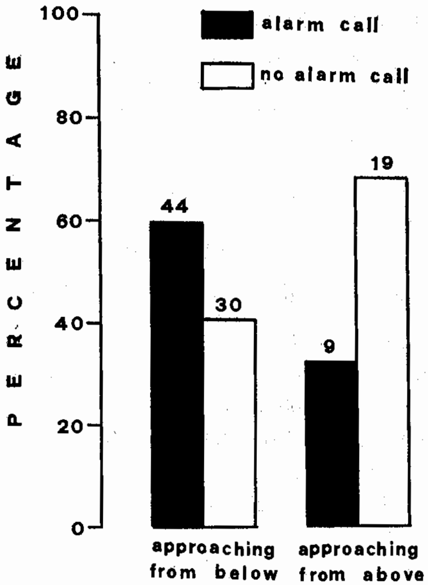

Fig. 2

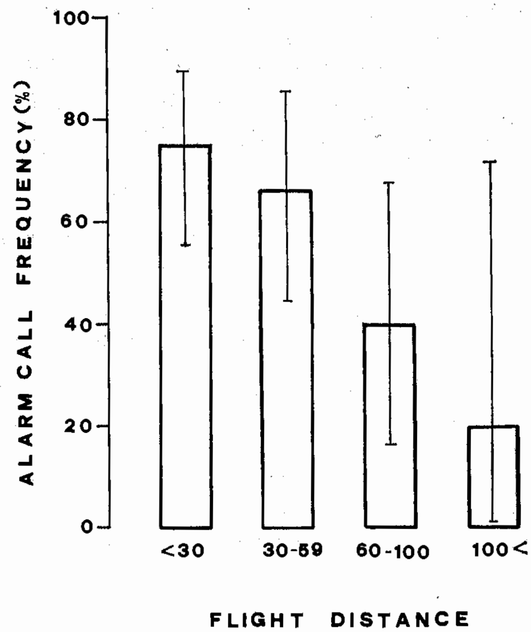

Fig. 3

Fig. 2: *Frequency of alarm calls when the human disturbance is approaching either from below (ibex at a higher level) or from above (ibex at a lower level). Number above the histogram represent the sample size.*

Fig. 2: *Frequence des signaux sonores d'alarme à l'approche de l'homme, soit par le haut (les bouquetins sont au-dessous). Le chiffre au-dessus des histogrammes indique la taille de l'échantillon.*

Fig. 3: *Relationship between the frequency of alarm calls and the flight distance, when the human disturbance approaches from below in areas with high touristic pressure.*

Fig. 3: *Relation entre la fréquence des appels sonores d'alarme et la distance de fuite, lorsque le perturbateur approche d'en bas dans les zones où la pression touristique est forte.*

the disturbance, to an average of 3 m (SD = 3.5) afterwards (when the members have grouped together before fleeing), as measured from 33 observations in each case ($t = 4.51$, $P < 0.001$, two tailed t test). The flight is coordinated and usually occurs in single file. The flight of male groups is led by one of the oldest males in the group (81.8 %) with the last animal being one of the youngest males (72,7 %). An adult female usually leads the flight in female kid groups (*fig. 1*) ($G = 22.34$, $df = 3$, $P < 0.001$), and in mixed groups, although this tendency is not significant ($G = 6.68$, $df = 3$, N.S.).

However we observed that giving an alarm call does not lead to an increased probability of bunching ($\chi^2 = 1.81$, $df = 1$, N.S.) for $N = 27$.

We observed that the flight distance of individuals in areas of high

Table I: *Comparison of the values of the various distance types (flight distance, detection distance) for the different types of groups in usually and unusually disturbed areas and according to the approaching direction (above or below).*

Tableau I: *Comparaison des valeurs de plusieurs types de distances (distance de fuite, distance de détection) pour les différents types de groupes dans des aires habituellement et inhabituellement agitées et d'accord à la direction d'approximation (d'en haut ou d'en bas).*

Detection Distance in areas of High Tourist Pressure

	From Below			From Above		
	Mean	Number	Variance	Mean	Number	Variance
Female-kid group	72.97	20	2812.70	54.46	12	1080.34
Male group	59.00	4	310.67	73.67	3	785.33
Mixed group	100.10	8	5251.09	48.00	3	772.00
	F (2,29) = 0.93, P = 0.40, N.S.			F (2,15) = 0.57, P = 0.57, N.S.		

Flight Distance in areas of High Tourist Pressure

	From Below			From Above		
	Mean	Number	Variance	Mean	Number	Variance
Female-kid group	36.15	23	340.30	44.09	11	570.09
Male group	36.50	6	393.10	64.33	3	703.33
Mixed group	55.03	7	1329.61	36.33	3	186.33
	F (2,33) = 1.89, P = 0.17, N.S.			F (2,14) = 1.24, P = 0.32, N.S.		

Detection Distance in areas of Low Tourist Pressure

	From Below			From Above		
	Mean	Number	Variance	Mean	Number	Variance
Female-kid group	150.56	8	10267.53	—	—	—
Male group	34.0	1	0	34.	1	0
Mixed group	—	—	—	—	—	—
	F (1,7) = 1.18, P = 0.31, N.S.					

Flight Distance in areas of Low Tourist Pressure

	From Below			From Above		
	Mean	Number	Variance	Mean	Number	Variance
Female-kid group	78.81	8	1685.42	—	—	—
Male group	67.0	3	823.0	34	1	0
Mixed group	52	1	0	—	—	—
	F (1,9) = 0.20, P = 0.7, N.S.					

tourist pressure is not as far as in areas of low tourist pressure (Mann-Whitney U test, $z = 2.24$, $n_1 = 12$, $n_2 = 21$, $P < 0.02$, two tailed test), in subsequent tests these bias were taken into account, because separate studies were carried out in areas of high and low tourist pressure respectively.

A comparison of the mean detection distance of all of the groups (female-kid, male and mixed groups) showed there is no significant difference in the detection distance of ibexes which live in areas of high tourist pressure and those which live in areas of low tourist pressure. The direction from which the human disturbance approached was irrelevant (*table I*). Similar results were found when we compared the mean flight distance of different groups in areas with high and low toutist pressure and when the human disturbance approached from different directions.

Figure 2 shows that Spanish ibex are more likely to give alarm calles if they are on a higher level than the human disturbance than when they are on a lower level ($G = 6.16$, $df = 1$, $P < 0.02$ two tailed test).

We analysed the relationships between flight distance and the giving of alarm calls. *Figure 3* shows that the shorter the flight distance the higher the probability that a warning has been given ($G = 8.95$, $df = 3$, $P < 0.05$ two tailed test). Also, when the predator is close, the ibex tend to give alarm calls more frequently. The average alarm call distance for 27 groups of ibexes were 38 m ($SD = 19.29$).

In order to control the effect of an intervening variable, we analysed the relationship between group size and flight distance, and we observed that it is not significant ($r_{xy} = 0.14$, $df = 32$, N.S.) in female groups in areas of high tourist pressure.

Spanish ibex tend to give alarm calls more frequently when they are in groups than when they are on their own (*fig. 4*). There is a significant difference in the frequency of alarm calls given by animals on their own compared with groups of 2 or more animals ($G = 5.72$, $df = 1$, $P < 0.02$, two tailed test). When we compared the frequency of alarm calls given by different age and sex classes, we observed more alarm calls being given by females ($\chi^2 = 15.21$, $df = 3$, $P < 0.001$). Futhermore, *figure 5* shows that groups of females with kids give more alarm calls than groups without kids ($G = 7.37$, $df = 2$, $P < 0.05$, two tailed test).

DISCUSSION

Spanish ibex usually respond to human disturbance, and presumably to that of other predators, by giving alarm calls, which appear to be used in critical situations when the predator is close by. Similar behaviour has also been observed in klipspringers (*Oreotragus oreotragus*) by Tilson & Norton (1981).

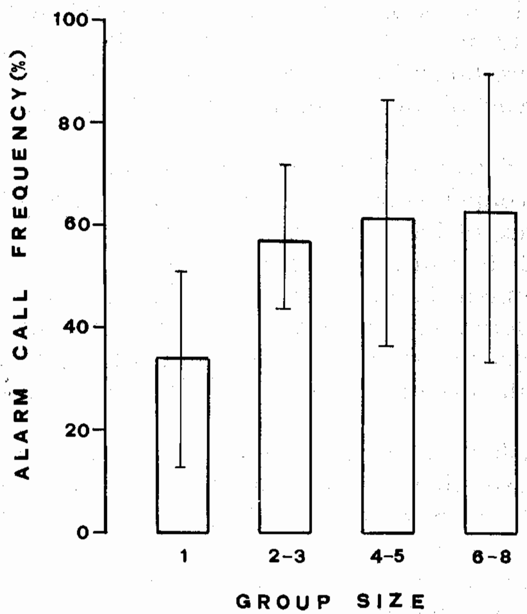

Fig. 4

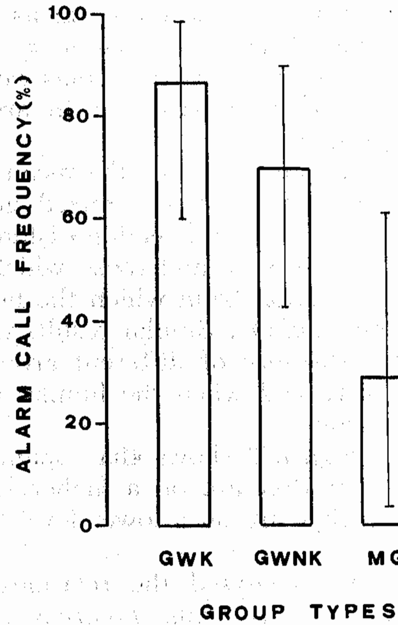

Fig. 5

Fig. 4 : *Relationship between group size and the frequency of alarm calls, when the human disturbance approaches from below in areas with high tourist pressure.*

Fig. 4 : *Relation entre la taille du groupe et la fréquence des appels sonores d'alarme, lorsque le perturbateur approche d'en dessous dans des zones où la pression touristique est forte.*

Fig. 5 : *Frequency of alarm calls in different group classes when the human disturbance approaches from below, in areas of high touristic pressure. The ibex were in groups of 2-6 individual. In all cases, the flight distance was between 30 and 100 m. (GWK = groups with kids, GWNK = groups with no kids, MG = males groups).*

Fig. 5 : *Fréquence des appels sonores d'alarme dans les différentes classes de groupes lorsque le perturbateur approche d'en bas, dans les zones où la pression touristique est forte. Les bouquetins sont en groupes de 2 à 6 individus. Dans tous les cas, la distance de fuite est entre 30 et 100 m. (GWK : groupes comprenant des jeunes, GWNK : groupes sans jeunes, MG : groupes de mâles).*

MacArthur *et al.* (1982) observed that mountain sheep have a higher cardiac response when the human approach is from over a ridge, rather than directly from the road. And, that when sheep were feeding on slopes with inclines 10-34°, the heart rate was significantly lower than when the same animals were feeding on open meadows (inclines 0-6°). In agreement with behavioural studies of mountain sheep, our data also imply greater security when the animals are on a higher level than the human disturbance.

The ibexes were more likely to give alarm calls when they were at save vantage points. Similar behaviour has been observed in *Odocoileus virginianus* (Bildstein, 1983) or *Gazella thomsoni* (Caro, 1986).

Since ibexes give warning only when the human disturbance is close to them and most probably has already been detected by them, and only when they are at vantage points (e.g. up rocky slopes), we suggest that the Spanish ibex give a relatively cost free call, and that ibexes give alarm calls only when the human disturbance has approached within a certain distance and their cryptic behaviour has failed.

The ibex alarm calls can have the effect of attracting the attention of others in the group, which then escape in an orderly and highly coordinated fashion, being generally led by an adult female in female-kid groups. The advantage in being led by an experienced individual can be particularly important to mountain species because the rugged terrain may only permit a successful flight in one or two directions.

The fact that we did not observe differences in the tendency of bunching together wether an alarm call was given or not may sometimes be due to the visual contact between the group members permiting them to bunch together without the necessity of giving alarm calls.

The negative correlation found between group size and time dedicated to vigilance per individual in Spanish ibex (Alados, 1985a) may be the reason that the Spanish ibex does not detect the predator any earlier in big groups than in small ones and why the flight distance was not affected by the group size.

The Spanish ibex is a highly gregarious species, living in herds of females with kids or in all-male groups. This segregation of the sexes is only broken during the rut, when they form mixed groups of both sexes and of all ages. During the birth season, yearlings are expelled from the female groups at the time of the new births. The first to separate from the female groups are the males, which finally join the adult male groups. However the yearling females return to their mothers after the birth season. If the mother has lost the neonate, both male and female yearlings return to her (Alados, 1985b).

Since the frequency of alarm calls is higher in related (female-kid groups) than in unrelated groups, we suggest that alarm calls have evolved by kin selection to alert relatives of danger (Hamilton, 1964, Maynard Smith, 1965). Similar observations have been made about the squirrel *Spermophilus californicus* by Leger & Owings, 1978, and in *S. tridecemlineatus* by Schwagmeyer, 1980, where the maternal breeding state influences the readiness to call in the presence of a predator. Moreover in social species such as ibexes, the young may thus learn from their parents how to recognize predators (see also Curio *et al.*, 1978). Recently the benefits conferred on alarm callers have come to be increasingly understood in terms of kin selection (Sherman, 1977, 1985, Holmes & Sherman, 1983, Klump & Shalter, 1984).

Some author support the hypothesis that alarm calls discourage a predator from returning to an area in the future by reducing its overall hunting success (Trivers, 1971, Tilson & Norton, 1981). Moreover, Morse (1973), MacDonald & Henderson (1977), Leger *et al.* (1980) and Tilson & Norton (1981), point out that raptors do not attack after their presence has been detected.

Since ibexes in response to danger bunch together allowing an orderly and highly coordinated escape, we conclude that the primary function of the alarm call is to alert other members of the group. This may have a selfish function, because of course animals are more vulnerable if they flee by themselves. Moreover Spanish ibex alarm calls may have evolved through kin selection since ibexes call more frequently in related than in unrelated groups.

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