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Interspecific reciprocity explains mobbing behaviour of the breeding chaffinches, *Fringilla coelebs*

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When prey animals discover a predator close by, they mob it while uttering characteristic sounds that attract other prey individuals to the vicinity. Mobbing causes a predator to vacate its immediate foraging area, which gives an opportunity for prey individuals to continue their interrupted daily activity. Besides the increased benefits, mobbing behaviour also has its costs owing to injuries or death. The initiator of mobbing may be at increased risk of predation by attracting the predator's attention, especially if not joined by other neighbouring prey individuals. Communities of breeding birds have always been considered as temporal aggregations. Since an altruist could not prevent cheaters from exploiting its altruism in an anonymous community, this excluded any possibility of explaining mobbing behaviour in terms of reciprocal altruism. However, sedentary birds may have become acquainted since the previous non-breeding season. Migrant birds, forming anonymous communities at the beginning of the breeding season, may also develop closer social ties during the course of the breeding season. We tested whether a male chaffinch, a migrant bird, would initiate active harassment of a predator both at the beginning of the breeding season and a week later when it has become a member of a non-anonymous multi-species aggregation of sedentary birds. We expected that male chaffinches would be less likely to initiate a mob at the beginning of the breeding season when part of an anonymous multi-species aggregation of migratory birds. However, their mobbing activity should increase as the breeding season advances. Our results support these predictions. Cooperation among individuals belonging to different species in driving the predator away may be explained as interspecific reciprocity based on interspecific recognition and temporal stability of the breeding communities.

Keywords: interspecific reciprocity; anti-predator behaviour; mobbing; chaffinch; *Fringilla coelebs*

1. INTRODUCTION

When a prey detects a potential predator, there are different ways it can react. The most obvious is to move away from the predator. However, a predator that is not an immediate threat may elicit mobbing behaviour. Prey animals mob predators by emitting repeated, loud and easily localizable calls, and performing stereotyped movements that quickly recruit more prey individuals around a predator (Curio 1978; Dominey 1983). This well-defined behavioural pattern is considered to be an anti-predator strategy (Harvey & Greenwood 1978) that occurs in a wide diversity of vertebrate groups, especially in birds and mammals (Altmann 1956; Curio 1978; Pitcher *et al.* 1986). Mobbing is usually assumed to decrease the hunting efficiency of the predator, either through distracting it or by driving it from the vicinity (Lorenz 1931; Pettifor 1990; Flasskamp 1994).

The general function of predator mobbing is well explained (for reviews, see Curio 1978, 1988; Frankenberg 1981; and Flasskamp 1994). However, the origin and evolution of mobbing as a type of adaptive behaviour is poorly understood. The emission of mobbing signals puts the mobber in jeopardy (Hoogland & Sherman 1976; Denson 1979; Curio & Regelmann 1985) and, if it benefits others, it is, by definition, altruistic (Hamilton 1964, 1971). The current view is that reciprocal altruism cannot be invoked as a possible selective force in explaining mobbing behaviour. As Trivers (1971) has made clear, an altruistic act helping a non-relative only pays the altruist if it is directed at a particular individual that on a later occasion reciprocates. If the altruist were to help an anonymous community, as is traditionally considered to be the case with mobbing, it could not prevent cheaters (i.e. non-reciprocators) from exploiting its altruism and thus eliminating it from the population (Munn 1986). It is considered that acoustic signals, such as alarm calls or mobbing behaviour, cannot arise through reciprocal altruism among anonymous non-relatives since they are essentially undirected and can thus not be protected against cheating (Rohwer *et al.* 1976; Sherman 1977). An additional difficulty is that under natural conditions mobbing often occurs in heterospecific company. This implies the possibility of reciprocity among individuals belonging to different species. This possibility can be admitted since many animals live in multi-species groups and they may benefit from the anti-predator behaviour of other species (Slagsvold 1980; Forsman *et al.* 1998*a*,*b*). However, reciprocal altruism between heterospecific individuals, to the best of our knowledge, has not yet been documented.

Breeding bird assemblages in the northern temperate zone are dynamic entities. The breeding season of most passerine birds seems to be too short for them to become familiar with their neighbours. However, in many cases

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breeding birds have known each other since the previous non-breeding season because they spend the winter as members of small, coherent and often territorial flocks (Ekman 1989). Therefore, when a migratory bird joins the local community after arriving from its wintering grounds, it may have two opposing opportunities. Its first option is to join the community composed of sedentary birds. The second option is to become a member of a community composed mainly of other migratory passerines. In the first case migrants definitely enter a non-anonymous local community. In the second case the migratory birds may join a truly anonymous community, at least at the very beginning of the season.

Mobbing reactions of the chaffinch (*Fringilla coelebs*), a small migratory passerine bird, have been widely studied (Hinde 1954; Marler 1956; Korbut 1989). The aim of this experimental study was to test whether the mobbing behaviour of the chaffinch may be explained in terms of reciprocal altruism. We expected that chaffinches would not initiate the harassment of a predator at the moment of formation of communities composed of migratory passerines only. However, chaffinches were expected to initiate a mob when joining communities composed of sedentary birds. For reciprocal altruism to work, there must be some kind of social control against cheaters, individuals receiving the benefits without reciprocating. In communities where the majority of individuals are familiar, a cheater will be recognized and quickly punished (Clutton-Brock & Parker 1995). This is more probable in communities with a stable composition. Heterospecific individuals in migratory communities may also develop closer social ties during the course of the breeding season to achieve better protection of their nests. Therefore, we expected that chaffinches in migratory communities would initiate a mob more often during repeated experiments performed towards the mid-season.

2. MATERIAL AND METHODS

The study was carried out in May 1999, 2000 and 2001 near Krāslava, southeastern Latvia. More than 60% of the total area is covered by a mosaic of forests, bogs, rivers and lakes. The forests are dominated by Scots pine (*Pinus sylvestris*) and common spruce (*Picea abies*). Forest clear-cuts, pine plantations and the secondary succession of abandoned fields increase the mosaic pattern of the landscape.

The experiments were carried out at 24 separate areas. On average, the study areas were 4.5 km apart (range of 3.2–14 km). At each of the 24 areas we carried out two experimental trials, which were done at separate sites (48 sites in total). The sites at each area were separated by a distance of 0.8 km (range of 0.6–1.3 km).

At one site in each area we presented a predator to a community composed of a pair of chaffinches and some pairs of sedentary passerine birds, such as marsh tits (*Parus palustris*), willow tits (*Parus montanus*), crested tits (*Parus cristatus*), blue tits (*Parus caeruleus*), coal tits (*Parus ater*), great tits (*Parus major*), nuthatches (*Sitta europaea*), treecreepers (*Certhia familiaris*), bullfinches (*Pyrrhula pyrrhula*), greenfinches (*Carduelis chloris*), blackbirds (*Turdus merula*) and siskins (*Carduelis spinus*). At the other site within the same area we presented the same predator to a pair of chaffinches and some pairs of other migratory birds, such as tree pipits (*Anthus trivialis*), starlings (*Sturnus vulgaris*), wrens (*Troglodytes troglodytes*), dunnocks (*Prunella modularis*), icterine warblers (*Hippolais icterina*), garden warblers (*Sylvia borin*), blackcaps (*Sylvia atricapilla*), whitethroats (*Sylvia communis*), lesser whitethroats (*Sylvia curruca*), willow warblers (*Phylloscopus trochilus*), pied flycatchers (*Ficedula hypoleuca*), spotted flycatchers (*Muscicapa striata*), redstarts (*Phoenicurus phoenicurus*), robins (*Erithacus rubecula*), nightingales (*Luscinia luscinia*), redwings (*Turdus iliacus*), song thrushes (*Turdus philomelos*) and hawfinches (*Coccothraustes coccothraustes*). All the above sedentary and migratory bird species are known as mobbers (Snow & Perrins 1997). Though starlings, treecreepers and dunnocks were not as active mobbers as other birds, we observed them giving alarm calls while mobbing.

At all areas chaffinches started to arrive at the beginning of April, and the final bird appeared in mid-April. All of the 48 male and 28 female chaffinches were mist-netted and colour-marked at bird tables provided with sunflower seeds, song playbacks, dummies and feathers for nest building at least 10 days before the experimental trials. Other migratory birds usually arrived 3–6 days before the beginning of the first experimental trial. Robins were the only exception: they appeared at least 10 days before the experimental trials. Some blackbirds may winter in the study site, while the first migratory blackbirds appear in March or April. Therefore, we considered the blackbird as a sedentary species. Willow warblers and chiffchaffs were present at two and three sites of sedentary birds, respectively. Wrens and dunnocks were also breeding at two and three sites of sedentary birds, respectively. Robins were living at two sites, tree pipits also at two sites and blackcaps at three sites of sedentary birds, respectively. We selected the sites so that a small fraction of migratory birds (no more than one pair) was present in communities composed of sedentary birds, but sedentary birds never occurred at the sites of migratory birds. Since floaters do not sing, we were not able to detect their presence. However, we did not observe any unknown intruders appearing from the closest vegetation during the experiments. Only two male chaffinches and one pied flycatcher, all members of neighbouring communities, travelled more than 200 m to join a mobbing party.

At the study site willow tits start egg laying at the beginning of May, just when the majority of migrant birds are arriving. Male willow tits often sing in the vicinity of holes they excavate. Migratory birds often use the loud song of willow tits as a cue for a safe breeding site and join them at the places of intense singing (Mönkkönen *et al.* 1997). However, in cases of nest failure, willow tits may move away, leaving their migratory neighbours until the end of the breeding season. In nine cases willow tits moved away and entered neighbouring mixed aggregations of sedentary and migrant birds more than 150 m distant (mean and s.e. = 180 ± 9.11 m). In two cases migrant birds were left by both coal tits and willow tits, and in one case they were left by marsh tits. Thus, migrant birds were left without the company of any sedentary bird that moved owing to nest predation. In two cases willow tits abandoned their completed holes because the stumps of dead trees with the nests were destroyed by fungi and wind. These willow tits moved 160 and 210 m, respectively. In one case willow tits disappeared from their territory for unknown reasons. In two cases male willow tits often sang away from the sites where they excavated the nest holes at the beginning of the breeding season (190 and 220 m, respectively).

As soon as female willow tits started to incubate, the males tended to stay close to their nests. Thus, migratory birds were without the company of willow tits, or any other sedentary birds, until willow tits started to forage their nestlings. In six cases

migrant birds established their territories at sites where parids were absent in both winter and spring. To attract flycatchers, redstarts and starlings to aggregations of migratory birds, we placed several nest-boxes within the territories of each aggregation of migratory birds. This was done at the beginning of May to prevent attraction of the local sedentary hole-nesting birds. Finally, we did not remove any birds from either migratory or sedentary breeding communities. All of the sites of migratory birds represented patches of 25–40-year-old mixed forests 0.9–2.3 ha in size containing Scots pine, common spruce, birch (*Betula* spp.), aspen (*Populus tremula*), grey alder (*Alnus incana*) and black alder (*Alnus glutinosa*) with a rich understorey at the edges of larger 80–100-year-old coniferous forests.

The sites of sedentary birds were found in circular or peninsula-shaped habitats, 0.86–2.8 ha in size, enclosed by less productive or unsuitable habitats, such as dry pine forests, pine saplings, clear-cut areas and bogs. The habitat was mostly composed of 30–40-year-old dense stands of pine and spruce with a sparse understorey. In most cases sedentary birds either used nest-boxes or excavated the holes themselves. To prevent the attraction of migratory hole-nesters, all of the unoccupied nest-boxes were removed before the end of April.

To avoid the effect of increased dilution of risk as the arrival of migrants progressed through the spring season, we included, in the final analysis, only those communities that were not joined by any migratory individual after the first experimental trial. At both community types the number of passerine birds was similar, with between 8 and 12 individuals, including the resident chaffinches. The number of passerines at the 24 sites of sedentary birds (mean = 8.91, s.e. = 0.29) did not significantly differ from that counted at the 24 sites of migratory birds (mean = 8.83, s.e. = 0.24) (two-tailed t-test, $t = -0.22$, d.f. = 46, $p = 0.83$). So each study site was inhabited by a pair of chaffinches and some pairs of other heterospecific passerines, either migratory or sedentary. Therefore, each test, even those carried out in the same area, can be treated as an independent data point.

To avoid influence by birds from other aggregations, we selected study sites that were as isolated as possible. The minimum distance to any nearest neighbouring bird aggregations (distance between territories of outer community members) was not less than 150 m (range of 150–310 m), separated by less suitable areas, such as dry pine forests, bogs and fields. Thus, the study sites were rather isolated and bird distribution was clumped owing to habitat constraints. Although some meadow birds, such as skylarks (*Alauda arvensis*), yellow wagtails (*Motacilla flava*), whinchats (*Saxicola rubetra*) and meadow pipits (*Anthus pratensis*), were present in the open habitats, they did not enter the forest and did not participate in mobbing predators. The average territory occupied by communities of sedentary birds was 1.38 ± 0.08 ha (range of 0.86–2.21 ha), and they did not vary much in size (one-way ANOVA, $F_{23} = 0.44$, $p = 0.85$). Similarly, the average size of areas occupied by communities of migratory birds was 1.51 ± 0.07 ha (range of 0.91–2.32 ha), and we found relatively little variation in size (one-way ANOVA, $F_{23} = 5.95$, $p = 0.31$). We also found no significant difference between the sizes of the territories of the two community types (two-tailed t-test, $t = 1.20$, d.f. = 46, $p = 0.23$). All of the spatial data were collected by GPS (Global Positioning Systems, Trimble Scoutmaster). Though habitats of sedentary birds and migratory birds differed, other features of the aggregations were similar.

A life-like stuffed tawny owl (*Strix aluco*) served as the predator stimulus in all 48 trials. This is a common predator of birds in Northern Europe (Mikkola 1983), whose presence strongly affects the behaviour of passerine birds (Bautista & Lane 2000). The owl was mounted on a small platform 1.5 m above the ground at the top of a pole. The predator was positioned *ca.* 10 m from the chaffinch nest, but was not visible from the nest. The owl was looking towards the nest. The predator was kept under cover. It was uncovered and presented so that a male chaffinch was the first individual to find it. At the time of the experimental trials female chaffinches were either laying eggs or had just completed their clutches. The response of each chaffinch was observed and evaluated for 5 min after the predator was detected. We also investigated whether the mobbing calls of chaffinches could lure other neighbouring passerine birds. The experimental trials were carried out on the same day at each area, and all the experimental work over all areas took 4–5 days for each type of experiment. The trials were carried out during the first half of the day (06.00–12.00) in calm, warm and dry weather. The weather conditions were similar during the three field seasons. Previously unfamiliar non-breeding parids often need at least several days, or weeks, to form a group with a stable composition and dominance hierarchy (Smith 1991). Supposedly, previously unfamiliar migratory birds can also form closer social bonds during the course of the breeding season. In order to test the ability of birds to cooperate in mobbing, we repeated the experimental trials a week later at each site. The experimental work took no more than 15 days each spring.

We divided the mobbing response of male chaffinches, according to their displays and voice, into four categories: (i) no response (0 points); (ii) weak response (1 point); (iii) average response (2 points); and (iv) strong response (3 points). Our categorization follows Korbut (1989), who divided the behaviour of a mobbing chaffinch into four easily distinguished categories reflecting the intensity of alarm. The first category of mobbing is no response to a predator: the chaffinch leaves the dangerous place without any alarm calls, and investigates the predator from a distance, while continuing its usual activities, such as foraging or singing. The second type of response is a weak response: frequent approaching and retreating from the predator and inspecting it. The third type is an average response: it is a real alarm when the birds tend to be close to the predator, they move restlessly around the object of alarm by bowing, pivoting and tail-flicking. Chaffinches often raise their crest and their neck is usually somewhat extended. The fourth type is a strong response: chaotic movements and intense display, perhaps including dive attacks on the predator. While mobbing predators, chaffinches use 'chink' and 'rain' calls (Hinde 1954; Marler 1956; Korbut 1989). During the second type of alarm chaffinches use mainly 'rain' calls and only some 'chink' calls. During the third type of alarm both call types are used in approximately equal proportions. During the fourth type of alarm almost all calls given by chaffinches are 'chink' calls.

To determine whether the presence of a predator affected the behaviour of chaffinches showing 'no response', we estimated their singing rate. To obtain this measure, we recorded the number of songs given by an individual during the 5 min before the experimental trial and during the presentation of the predator. In total, we obtained singing rates of 19 male chaffinches with 'no response' to the owl. None of the chaffinches included in the analysis suffered from nest predation between the experimental trials.

Table 1. Mobbing responses to a life-like tawny owl by male chaffinches (number of individuals) in communities composed of sedentary and migratory birds during experimental trials at the beginning of the breeding season and during repeated trials two weeks later.

	first trials		repeated trials	
type of response	sedentary communities	migratory communities	sedentary communities	migratory communities
no response	0	17	0	0
weak response	3	7	1	3
average response	18	0	20	19
strong response	3	0	3	2

3. RESULTS

In the company of sedentary birds, chaffinches were usually scored as showing an 'average response' to the tawny owl (table 1). The chaffinches showed either no response or a weak response when surrounded only by migratory passerines (table 1). We observed strong responses in three cases in sedentary communities and there were no 'no response' trials. There was a significant difference in the intensity of alarm between the two types of communities (two-tailed Mann–Whitney *U*-test, $z = -6.04$, $n_1 = 24$, $n_2 = 24$, $p < 0.0001$).

In sedentary bird communities all the alarms were attended by other community members. The heterospecifics usually appeared within the first 2 min of the alarm. More than half of the local passerines joined the mobbing chaffinches (mean = 6.16, s.e. = 0.18). When chaffinches ($n = 7$) mobbed the owl in the company of migratory birds, we also observed more than half of the local heterospecific individuals near the owl (mean = 6.0, s.e. = 0.53). The numbers of neighbouring birds that joined in mobbing in the sedentary communities and in seven migratory communities did not differ significantly (two-tailed *t*-test, $t = 0.37$, d.f. = 29, $p = 0.71$).

The male chaffinches with 'no response' to the owl were, however, affected by the owl's presence. Their singing rate significantly decreased from 8.05 songs min^{-1} (s.e. = 0.25) to 2.35 songs min^{-1} (s.e. = 0.34) (two-tailed paired *t*-test, $t = 14.12$, d.f. = 18, $p < 0.001$).

A week later the mobbing intensity of chaffinches at sites of sedentary birds showed no increase by comparison with the behaviour they showed at the beginning of the breeding season (two-tailed Wilcoxon matched-pairs signed-ranks test, $T = 13.5$, $n = 24$, $p = 0.53$). Chaffinches in communities of migratory birds significantly increased the intensity of alarm (two-tailed Wilcoxon matched-pairs signed-ranks test, $T = 0$, $n = 24$, $p < 0.0001$). When they were scored at the beginning of the breeding season they were scored mostly as 'no response'; during the later trials the intensity of their alarm was mainly scored as 'average response' (table 1). The intensity of alarm did not differ between the two types of communities (two-tailed Mann–Whitney *U*-test, $z = -0.97$, $n_1 = 24$, $n_2 = 24$, $p = 0.33$).

At both types of experimental sites more than half of the neighbouring passerines arrived to mob the owl during the experiments, and the community types did not differ in the number of attending heterospecifics (sedentary communities: mean = 6.25, s.e. = 0.23; migratory communities: mean = 6.21, s.e. = 0.20; two-tailed *t*-test, $t = 1.38$, d.f. = 46, $p = 0.89$).

4. DISCUSSION

Animals must continually decide between various alternative behaviours in order to maximize their fitness. The severity of a decision depends on how much it affects the animal's fitness. During the breeding season it would be enough for a male chaffinch to warn its mate about a predator simply by giving some short-range alarm calls. It is important to keep the mate alive until the end of the breeding season since it would be difficult to remate in time to fulfil successful breeding. Therefore, warning its mate increases the caller's inclusive fitness. However, the observed males did not always behave in this way: they have a choice either to initiate a mob or to keep silent.

Harassment entails a real risk to the prey animal involved owing to its proximity to the predator (Hoogland & Sherman 1976; Denson 1979; Curio & Regelmann 1985, 1986). Conspicuous long-distance calling can attract other predators (Krams 2001*a*,*b*) and is, therefore, costly in terms of predation. The risk decreases with increasing group size owing to the effect of dilution (Hamilton 1971). Thus, the responses of neighbouring birds have a major influence on the survival prospects of the initiator. Taking a higher risk would make sense only if the benefit was to increase accordingly. If no neighbours join the first individual to mob, there is no dilution effect and the lone harasser takes a deadly risk (Curio & Regelmann 1986). Therefore, the initiator has to be confident about the response of its closest neighbours before the harassment. It seems that when surrounded by sedentary heterospecifics chaffinches were quite confident about their prospects of receiving external help. Indeed, in all of the observed cases the initiator chaffinches attracted the majority of their sedentary neighbours.

Mobbing is usually assumed to decrease the hunting efficiency of the predator, either through distracting it or by driving it away from the vicinity (Lorenz 1931; Hoogland & Sherman 1976; Bildstein 1982; Buitron 1983; Pettifor 1990; Flasskamp 1994; Zuberbühler *et al.* 1999). Mobbing behaviour is defined as the joint assault on a predator too formidable to be handled by a single individual (Wilson 1975). The origin and success of the mobbing assembly are thus critically dependent on the number of attendants and social context. Chaffinches breeding in

communities composed of heterospecific migratory individuals behaved in two distinct ways during successive experimental trials. At the beginning of the breeding season most male chaffinches gave no alarm calls at all. Although during spring migration many birds sing at their stop-over sites, only a few of them remain in these areas as residents. Therefore, the initiator individual should assess whether it can involve its neighbours in a mobbing party. Non-residents may not benefit from costly mobbing activities. This could explain why resident chaffinches did not rely on their migrant neighbours during the first experimental trials. Presumably they considered their neighbouring heterospecifics as birds of passage. Passerine birds can discriminate between conspecific and heterospecific individuals (e.g. Marler 1957; Sorjonen 1986; Hurd 1996). We suggest that a week later chaffinches had developed the ability to recognize their heterospecific neighbours individually. This assumption is supported by the result that chaffinches initiated harassment of the owl during all of the repeated experimental trials. Korbut (1989) has shown that any substantial increase in the mobbing activity usually takes more than a week. Therefore, it is doubtful that the difference in the bird activity between the two trials can be explained by other factors, such as mating status, reproductive value of a mobber, prospects of another breeding episode the same season, etc.

In many biological situations the future is more or less uncertain, so that future gains may be worth less than current ones. However, in this study all community members had a certain minimum probability of meeting again. Under such conditions it is beneficial to follow a strategy called tit-for-tat, which leads to mutual cooperation (Axelrod & Hamilton 1981). This requires that the cost of initiating a mob is 'paid back' by other community members at a later event (Alatalo & Helle 1990). We judge that individuals in all of the sedentary bird communities cooperated as soon as they established their territories. Individuals in communities composed of previously unfamiliar migratory birds adopted this behaviour during the course of the breeding season. This suggests that the intensity of defensive behaviour is influenced by the cooperative ability of the members of the local community. Cooperating individuals have a greater opportunity to drive the predator from the neighbourhood than those that are not cooperating. Cooperation should be of particular value for species with a high rate of nest predation, such as the chaffinch (Hanski & Laurila 1993). This suggests that inciting or joining in mobbing should increase personal fitness in the communities composed of individuals that cooperate (Greig-Smith 1980). Under such conditions mobbing behaviour can be explained in terms of reciprocal altruism. Moreover, flocking with heterospecifics may be profitable in the breeding season because there is no risk of being cuckolded while driving the predator away.

Single- and mixed-species flocks are a common phenomenon throughout the world. In tropical areas in particular, flocks can be very tight and can exist year round (Greig-Smith 1978; Munn & Terborgh 1979). In temperate and boreal areas flocking has usually been observed outside the breeding season (Ekman 1989). However, recent studies have revealed that mixed-species foraging flocks also exist during the breeding season (Mönkkönen *et al.* 1996). Our results indicate that birds in such associations can engage in mutual cooperation. This may also mean that in temperate regions many birds are members of non-anonymous social groups year round except during the season of migration and when forming new groups. In a non-anonymous community, any altruistic act that helps a non-relative can, thus, be directed at particular individuals. If this is correct, reciprocal altruism can be used to explain the evolution of alarm calls in general and mobbing calls in particular. Our results, thus, suggest a link between the benefits of gregariousness and the clumped distribution of forest passerines during the breeding season (Mönkkönen *et al.* 1996, 1997; Forsman *et al.* 1998*a*,*b*).

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