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ORIGINAL ARTICLE

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Factors affecting egg predation in Black-tailed Gulls

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Abstract In colonial seabirds, nesting density, egg-laying date and nest microhabitat affect the probability of eggs being taken by avian predators. Jungle Crows (*Corvus macrorhynchos*) are dominant predators of eggs of Black-tailed Gulls (*Larus crassirostris*). Factors affecting the probability of gulls allowing the crows to attack their nests or depredate their eggs and the probability of eggs being taken were studied by direct observation and egg census, respectively. The effect of vegetation heights, position in the colony, egg-laying date and neighbour nests on the probability of eggs being taken were examined at multiple spatial scales. Gull nests were depredated more easily by larger groups of crows. Nests in peripheral areas (< 4 m from the edge of the colony) were also depredated more easily by the crows walking on the ground. Although the nests where eggs were laid early in the season were depredated more frequently, such nests highly synchronised in egg laying within a < 2-m radius were less likely to be depredated than less-synchronised nests. The nests in tall vegetation were less likely to be depredated though those having neighbour nests in tall vegetation were not. The number of neighbour nests did not affect the probability of eggs being taken. Antipredation effects of nesting microhabitats vary with spatial scales at which the crows search and attack the nests of gulls.

Keywords Predation · Nest · Habitat selection · Spatial scale · Gull

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Introduction

As in bird species egg predation strongly limits breeding success, predation could affect various breeding properties of birds (Lack 1954; Ricklefs 1969; Wittenberger and Hunt 1985). Parents birds directly defend their nests or eggs against predators and select nesting habitats that decrease the probability of eggs being taken (Shedd 1982; Shealer and Burger 1992; Krebs and Davies 1997; Caro 2005). Seabirds decrease predation risk by nesting on cliff ledges or in places with high vegetation coverage (Montevecchi 1978; Buckley and Buckley 1980; Parrish 1995; Massaro et al. 2001) and by breeding colonially and synchronously (Wittenberger and Hunt 1985; Ims 1990; Murphy and Schauer 1996).

Predators sometimes search for prey according to characteristics of the microhabitat in some large spatial scale and decide to attack in a smaller spatial scale (Tinbergen et al. 1967; Tarvin and Smith 1995; Tarvin and Garvin 2002). Therefore, antipredation effects of breeding properties, such as nesting habitats and breeding synchronisation, may change with spatial scales. In seabirds that breed in colonies, synchronisation of egg laying at a small spatial scale is a key for avoidance of predation risk but that at a large spatial scale is not (Siegel-Causey and Hunt 1981; Murphy and Schauer 1996). There are few studies examining the effects of both the timing of egg laying and nesting habitat on the probability of eggs being taken at different spatial scales.

Eggs of ground-nesting and colonial Laridae species are highly vulnerable to avian predators. They sometimes nest in heterogeneous habitats (Buckley and Buckley 1980; Schreiber and Burger 2002). Their colony often are subdivided into small groups according to their habitats in various spatial scales (Burger and Gochfeld 1981; Bosch and Sol 1998). Therefore, they are suitable for studying the effects of spatial scales on predator–prey interactions.

Black-tailed Gulls (*Larus crassirostris*) nest on slopes with medium vegetation cover or rocks in coastal islands and lay 2–3 eggs (Watanuki 1983). The Jungle Crow (*Corvus macrorhynchos*) and Slaty-backed Gull (*L. schistisagus*) are known as effective avian egg predators of Black-tailed Gulls (Watanuki 1983). How the gulls' nesting density and nest-site characteristics affect egg predation is unknown. To find the key factor in deciding the probability of gulls allowing crows to attack their nests and depredate their eggs, egg predation behaviour by crows and the defence behaviour of gulls was directly observed. Subsequently, to detect the effect of nest-site characteristics and characteristics of neighbour nests within <1- and <2-m radii on the probability of eggs being taken at the nest sites, an egg census was taken to examined following hypotheses. First, the probability of eggs being taken from nests in the central areas of the colony is different from the edge areas. Second, that the probability of nest sites varies with vegetation height or that of neighbour nests. Third, that the probability of nest sites varies with egg-laying date or that of neighbour nests. Fourth, that the probability of nest sites varies with the number of neighbour nests.

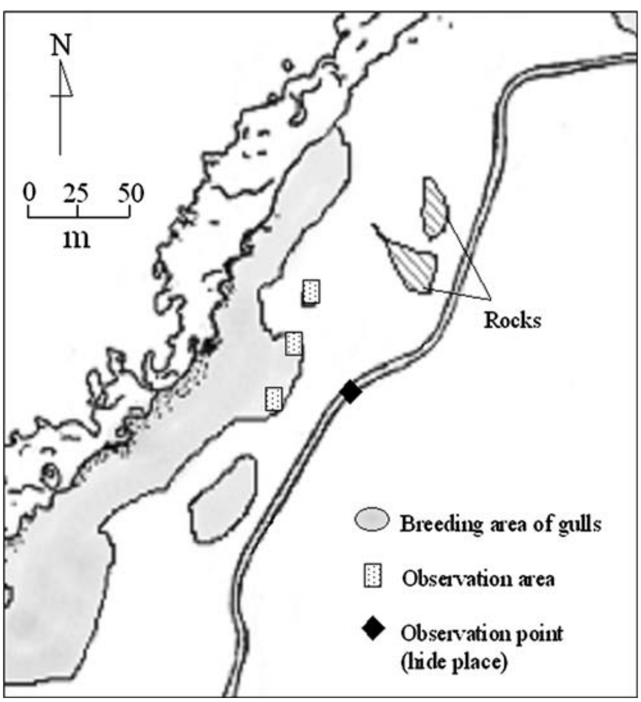

Fig. 1 Location of breeding area of Black-tailed Gull, three observation areas, observation point (hiding place) and rocks where Jungle Crow often landed (see text) at Oiso, Rishiri Island, in 2003

Study area and methods

Observation of predatory behaviour of crows and defence behaviour of gulls

The study was conducted at Rishiri Island (45° 12′N, 141° 10′E) located 40 km from the southwestern shore of Wakkanai, Hokkaido, Japan, from late April to late July 2003. The island supported $>20{,}000$ breeding pairs of Black-tailed Gulls in 2003 (Kosugi et al. 2005). Three 10×10-m observation areas containing 75, 55 and 64 nests, respectively, were established in the edge areas of the main colony at Oiso, the gentle northwestern slope of the island. All observation areas were established along the edge of the colony at intervals of approximately 20 m (Fig. 1). Gulls nested in almost flat area covered with short (<50 cm) vegetation of Sasa bamboo (*Sasa kurilensis*) and Japanese butterbur (*Petasites japonicus*). All nests in the observation areas were marked with numbered stakes and mapped when eggs were laid.

Observation of antipredator behaviour of gulls and predatory behaviour of crows was done at three observation areas simultaneously from 3 May to 12 June. The observations were made from the hiding placed 40 m from the observation areas (Fig. 1). Observation was done for 8 h in the morning (0300–1100) or afternoon (1100–1900) and almost evenly across the stages of egg laying and incubation. To check the effect of gulls' breeding stage, an observation period was divided into three stages: Early, from 3 May when observation began to 13 May when the accumulatednumber of eggs laid reached 50% of all eggs; Middle, from 14 to 23 May when the accumulated number of eggs laid reached 80% of all eggs; and Late, from 24 May to 12 June when observation ended. Total observation times were 208 h (88 h in Early, 64 h in Middle, and 56 h in Late).

Attack attempts by crows were defined as the occasion when a crow swooped down on the observation areas, tried to intrude into observation areas from the air (attack from the air) or ground (attack from the ground) or approached <10 m from the observation areas, and when a Black-tailed Gull within the area responded to a crow. Two attack attempts at the nest where the parent bird was absent during disturbance by a Peregrine Falcon (*Falco peregrinus*) were observed. These two attempts were excluded from the analyses. Gulls allowing crows to attack their nests was defined as the occasion when one or more crows landed on the observation area from the air or approached from the ground and walked inside the area. Gulls allowing crows to depredate their eggs was defined as the occasion when a crow flew away with one or more eggs in its billfrom a nest within the observation area or broke and ate one or more eggs in the observation area. When an attack attempt was observed, the number of crows attacking—that is, the number of crows participating in the attack attempt, and the number of gulls defending—that is, the number of gulls flying towards or chasing the attacking crows, were recorded. The number of crows landing on the rock where many crows clustered in the colony (Fig. 1) was recorded at 20 min intervals in the observations and the maximum number in those observations were employed in the analysis as an index to the number of crows visiting the colony during the observations.

Egg census and factors affecting probability of eggs being taken

Nest contents were checked before and after the observations. Thus, eggs depredated by the crows were distinguished from those that had disappeared. All eggs were marked with black ink. Egg-laying date was classified in three stages according to the three observation periods—Early, Middle and Late. Vegetation height of 95 nest sites in the observation areas (27, 36 and 32 nests, respectively) were recorded at the end of breeding season (from 2 to 8 July) to minimise disturbance. To examine the growing patterns of vegetation, vegetation height was measured at random points near the observation areas after the observations. Sasa bamboo (mean 11.8 cm at the beginning of the study, $n = 6$) and the other grasses (mean 25.6 cm at the beginning of the study, $n = 7$) grew at 3 cm and 12 cm, respectively, during the observation period, and neither grew quickly afterwards. Therefore, the height measured at the end of breeding season could be suitable for the index of those of nest sites throughout the study period. Mean vegetation height at nest sites was 14.6 cm (range 0–45, $n = 95$). Vegetation of 0–19 cm that did not conceal gulls incubating were classified as short vegetation while that of ≥20 cm was classified as tall. Nests within ≤ 4 m of the edge of breeding areas were classified as peripheral nests and the others as central nests for the sake of convenience.

Statistical analysis

All data except for egg-laying date are shown as mean ± SD, n = sample size in parentheses in the text. Egg-laying date is shown as the mean elapsed date from 3 May ± SD, n = sample size in parentheses.

Variations in the maximum number of crows visiting the colony, number of attack attempts per observation and number of crows attacking per attempt among gull breeding stages (Early, Middle, Late) were analysed by the Kruskal–Wallis H test. To detect which stages were significantly different from others, pairwise multiple-comparisons tests were employed on certain transformed data sets. To asses the effects of attack tactics (from the air or the ground) and the time of day (morning or afternoon) on the number of crows attacking and interaction of those factors, the number of crows attacking between the two groups was compared using the two-way analysis of variance (ANOVA), in which attack tactics and time of the day were the factors.

To examine the effects of factors selected from all factors (number of crows attacking, attack tactics and time of day) to eliminate their correlations on the probability of gulls allowing crows to attack their nests and the probability of gulls allowing crows to depredate their eggs after attacking, logistic regression was employed. Dependent variables of attack analysis were: 1 = gulls allowed crows to attack their nests, and 0 = gulls did not allow crows to attack their nests. Dependent variables of depredation analysis were: 1 = gulls allowed crows to depredate their eggs, and 0 = gulls did not allow crows to depredate their eggs.

Variation of the ratio of the number of gulls defending to the number of the crows attacking (1, 2–5, ≥7; gulls were not attacked by six crows) was analysed by the Kruskal–Wallis H test. To detect which number of crows attacking was significantly different from others, pairwise multiple-comparisons tests were employed on certain transformed data sets. Difference in ratio of number of gulls to number of crows attacking between attacking from the air and from the ground was analysed by the Mann–Whitney U test.

To asses the effects of nesting position (peripheral or central), vegetation height and nesting density (the number of neighbour nests at the end of observation period) on egg-laying date and the interaction of those factors, egg-laying date among the three groups were compared with three-way ANOVA, where nesting position, vegetation height and nest density (within a < 1-m radius) were factors.

Effects of nesting position, vegetation height and egg-laying date of 95 nest sites; and nest density, mean egg-laying date and mean vegetation height of neighbour nests within < 1- and < 2-m radii of those nest sites on the probability of eggs being taken were examined using logistic regression. Nest density within a < 1-m radius (mean 2.07, range 1–4) was categorised as low density (one nest), medium density (two nests) and high density (three or four nests). Nest density within a < 2-m radius (mean 8.94, range 3–15) was categorised as low density (3–6 nests), medium density (7–9 nests), and high density (10–15 nests) in order to attempt to equalise the classification standard of the number of nests per unit area (< 1-m, radius 3.14 m^2; < 2-m radius, 12.57 m^2). Mean egg-laying date and mean vegetation height of neighbour nests in both spatial scales were categorised similarly to the classification of nest sites (laying date: Early, Middle, Late; vegetation height: low or high). There was no nest having neighbour nests within a < 2-m radius where eggs were laid during the Late period. Dependent variables were: 1 = nests depredated by more than one egg, or 0 = those not depredated.

To examine whether the nests closer to the edge were more likely to be depredated only in peripheral areas ($n = 68$ nests), logistic regression (logistic likelihood ratio analysis) was employed, with the distance from the edge of the colony in 0.5-m precision as the independent variable and the dependent variables being: 1 = nests depredated more than one egg, or 0 = those not depredated.

Result

The probability of gulls allowing crows to depredate their eggs

During observation, 40 of all 194 nests (21%) were depredated. Among 74 attack attempts recorded during the observation periods, crows made 35 successful attacks (47%), in which they made 20 successful predations (27%). Gull nests were attacked by 4.01 (range 1–20) crows per each attack attempt. The ratio of the number of gulls defending to the number of the crows attacking in each attack attempt was 1.5 (range 0–5).

Variations in the maximum number of crows visiting the colony were detected among Early (28.00 ± 10.58, $n = 11$ observations), Middle (18.25 ± 10.28, $n = 8$ observations; $P = 0.150$) and Late (14.00 ± 9.18, $n = 7$ observations; $H_{adj} = 6.142$, $df = 2$, $P = 0.046$) periods. Significant difference was detected between Early and Late ($P = 0.046$). The number of attack attempts per observation differed significantly by gull breeding stages ($H_{adj} = 15.814$, $df = 2$, $P < 0.001$), with significant differences detected between Early (6.20 ± 4.54, $n = 11$ observations) and Middle (1.63 ± 1.51, $n = 8$ observations; $P = 0.016$) and between Early and Late (0.29 ± 0.49, $n = 7$ observations; $P = 0.003$) periods. Variations in the numbers of crows attacking per attempt were detected among Early (4.19 ± 4.84, $n = 61$ attempts), Middle (1.27 ± 0.47, $n = 11$ attempts) and Late (13.00 ± 16.97, $n = 2$ attempts; $H_{adj} = 8.819$, $df = 2$, $P = 0.012$) periods. Significant difference was detected between Middle and Late ($P = 0.010$) periods.

The number of crows attacking from the air (3.11 ± 3.90, $n = 55$ attempts) was significantly smaller than that from the ground (7.21 ± 7.01, $n = 19$ attempts; $F = 6.408$, $df = 1, 70$, $P = 0.014$), and the number in the morning (4.17 ± 5.20, $n = 48$ attempts) was not significantly different from that in the afternoon (4.15 ± 5.20, $n = 26$ attempts; $F = 0.026$, $df = 1, 70$, $P = 0.872$). Attack tactics by time of day were not significantly different ($F = 0.615$, $df = 1, 70$, $P = 0.436$). Therefore, to eliminate correlations of independent factors, the number of crows attacking (1, 2–5, ≥7) and time of day were selected as independent variables for the logistic regression analysis on the probability of gulls allowing crows to attack their nests and the probability of gulls allowing crows to depredate their eggs after attacking. Time of day did not affect the probability of gulls allowing crows to attack their nests (Table 1). The probability of gulls allowing crows to attack their nests increased significantly as the number of crows attacking per attempt increased (1 crow 14%, 4/29; 2–5 crows 56%, 18/32; ≥7 crows 100%, 13/13) (Table 1).

Time of day did not affect the probability of gulls allowing crows to depredate their eggs after attacking (Table 1). If gulls were attacked by crows in a large group, crows had a significantly higher probability of depredating the eggs after attacking (≥7 crows 85%, 11/13) than in single (40%, 2/5) and in small group (2–5 crows 29%, 5/17) (Table 1). Ratio of number of gulls defending to number of crows attacking from the ground in each attack attempt (0.44 ± 0.54, $n = 19$) was significantly smaller than for attacks from the air (1.29 ± 1.37, $n = 55$; $U = 333.50$, $z = -2.339$, $P = 0.019$). The ratio of number of gulls defending to number of crows attacking for each attack attempt differed significantly by the number of crows attacking ($H_{adj} = 8.324$, $df = 2$, $P = 0.016$), with significant differences detected between 1 crow (1.69 ± 1.58, $n = 29$) and 2–5 crows (0.80 ± 0.89, $n = 32$; $P = 0.0156$) and between 1 crow and ≥7 crows (0.38 ± 0.54, $n = 13$; $P = 0.006$).

Characteristics of nest sites and predation risks

Gulls of 95 nest sites in the analysis of relationship between nesting habitats and the probability of eggs being taken laid 1.73 ± 0.66 eggs on average in each of their nests, and their mean egg-laying date was 11.36 ± 7.14. Thesegulls took 2.216 days ($n = 95$) on average to form their clutch. Egg-laying date at the central nests (13.11 ± 6.82, $n = 27$) was not significantly different from peripheral nests (10.66 ± 7.19, $n = 68$; $F = 2.786$, $df = 1, 83$, $P = 0.099$). Egg-laying date in nests in short vegetation (10.52 ± 7.37, $n = 65$) also was not significantly different from that in tall vegetation (13.17 ± 1.16, $n = 30$; $F = 0.411$, $df = 1, 83$, $P = 0.521$). Egg-laying date also did not differ significantly by nest density within a < 1-m radius (low 12.17 ± 7.05, $n = 30$; medium 8.69 ± 6.12, $n = 36$; high 13.83 ± 7.52, $n = 29$; $F = 1.657$, $df = 1, 83$, $P = 0.197$). The interaction of

Table 1 Logistic regression model of the factors affecting on the probability of Black-tailed Gulls allowing the Jungle Crows to attack their nests and the probability of gulls allowing the crows to depredate their eggs after attacking

	Factor	Degrees of freedom (df)	Chi-square (χ^2)	P value
Gulls allow the crows to attack ($n = 74$)	No. of crows attacking	2	36.369	< 0.001
	Time of day	1	1.530	0.216
Gulls allow the crows to depredate after attacking ($n = 35$)	No. of crows attacking	2	10.823	0.005
	Time of day	1	0.372	0.542

those three factors was not significant ($P > 0.05$). Therefore, nesting position, vegetation height, nest density and egg-laying date were independent of each other.

Twenty-two (23%) 95 nests in which the analysis of relationship between nesting habitats and the probability of eggs being taken were depredated. Nesting position, vegetation height and egg-laying date of nest sites, and the mean egg-laying date of neighbour nests within a <2-m radius affected the probability of eggs being taken (Table 2). Nest density within both radii, mean egg-laying date of neighbour nests within a <1-m radius, and mean vegetation height of neighbour nests within both radii did not affect the probability of eggs being taken (Table 2). Peripheral nests were significantly more likely to be depredated (32%, 22/68) than were central nests (0%, 0/27). Nests with short vegetation cover were more likely to be depredated (31%, 20/65) than were those with tall vegetation cover (7%, 2/30). Nests where eggs were laid in the Early period were significantly more likely to be depredated (40%, 21/52) than were those in the Middle (3%, 1/32) and Late (0%, 0/11) periods. Nests highly synchronised in egg laying within a <2-m radius (the absolute value of the difference between their egg-laying date and the mean laying date of neighbours was smaller than 2.216 days) were significantly less likely to be depredated (5%, 1/22) than were less synchronised nests (another nests 29%, 21/73). In peripheral areas ony, the distance from the edge of the colony in 0.5-m precision did not affect the probability of eggs being taken (logistic likelihood ratio analysis $\chi^2 = 0.781$, $df = 1$, $P = 0.3769$).

Discussion

When gulls were attacked by large groups of crows, a relatively small number of gulls defended against the crows, and hence gulls allowed the crows to attack their nests and to depredate their eggs easily. Some seabird species attacked by large groups of avian egg predators allow predators to more easily attack their nests than when they are attacked bysingle predator or by small groups of predators (Montevecchi 1979).

Table 2 Logistic regression model of characteristics of Black-tailed-Gull nest sites and of neighbour nests within <1- and <2-m radii affecting the probability of eggs being taken by a Jungle Crow ($n = 95$)

Spatial scales	Characteristics	Degrees of freedom (df)	Chi-square (χ^2)	P value
Nest site	Nesting position	1	14.142	<0.001
	Vegetation height	1	4.099	0.043
	Egg-laying date	2	26.466	<0.001
<1-m radius	Nest density	2	2.516	0.284
	Vegetation height	1	0.225	0.635
	Egg-laying date	2	2.647	0.266
<2-m radius	Nest density	2	4.961	0.084
	Vegetation height	1	0.339	0.560
	Egg-laying date	1	9.145	0.003

Peripheral nests were more likely to be depredated because peripheral areas were more likely to be attacked by predators hopping or walking on the ground, as shown for other seabirds (Tinbergen et al. 1967; Gaston and Elliot 1996; Massaro et al. 2001). A smaller number of gulls defended against crows walking on the ground than those attacking from the air. It might be more difficult for gulls incubating to notice crows hopping or walking from the outside areas of the colony where vegetation grows thick than those attacking from the air. On the other hand, Coulson (1968) suggested the birds nesting in the periphery of the colony are younger and have less body condition than are birds in the central area. In this study, gulls nesting in peripheral areas might be inexperienced and have less ability to defend against crows than are birds in the central area. Only in peripheral areas, however, were nests closer to the edge less likely to be depredated. Gull nests in peripheral areas were attacked frequently by large groups of crows in large scale; therefore, nesting position might affect the scale by several meters.

Gull nests where eggs were laid in the Early period were more likely to be depredated because more crows visited the colony in the Early than the Middle and Late period. The Early period of gull breeding season almost matched the chick-rearing stage of crows (K. Kazama, personal observation). Gull eggs laid in the Early period might be highly available prey for crows feeding chicks. Nests highly synchronised in egg laying within a <2-m radius, however, were less likely to be depredated than were less synchronised nests. In colonial breeding Common Murre *Uria aalge*, while the birds incubate and their mates defend vigorously against avian predators, some birds that have not yet laid the first egg fly away when the avian predators attack (Murphy and Schauer 1996). Thus, in Common Murre the nests with neighbours breeding synchronously in the scale of several metres have a lower risk of egg predation because such neighbours simultaneously mob up against predators (Murphy and Schauer 1996). Also in gulls, the synchronisation in egg laying seemed to affect the probability of eggs being taken under a similar mechanism. Egg-laying date of neighbour nests within a <1-m radius, however, did not affect the probability of eggs being taken. Since gull nests were attacked often by large groups of crows in this study, group defence not at a small scale (<1 m) but at a large scale (<2 m) might effectively prevent attack by large group of crows in the Early period, though the spatial scale at which group defence is functioning was unknown in this study.

Nest density at both <1- and <2-m scales did not affect the probability of eggs being taken in this study, although in seabird species mobbing against predators, high nesting density is advantageous for group defense (Wittenberger and Hunt 1985; Gilchrist and Gaston 1997; Massaro et al. 2001). The nesting density was measured at the end of the breeding season. The number of gulls incubating and their mates staying in their territory when crows attacked might directly influence the effect of group defense and not depend on the number of nests at the end of the breeding season.

In ground-nesting seabirds, vegetation density or height effectively protect the nest contents against being found or accessed by predators (Buckley and Buckley 1980; Burger and Gochfeld 1981; Pierotti 1982; Kim and Monaghan 2005). In this study, eggs in the nests in tall vegetation had lower probability of being taken than did those in short vegetation only in nest-site scale. Vegetation height of neighbour nests, however, did not affect the predation risk in large spatial scales (< 1, 2 m). In tree-nesting bird species, the effects of vegetation coverage in large spatial scales (several meters surrounding nest-sites) on search images of predators and those in small spatial scales (nest sites) on predator access were indicated (Tarvin and Garvin 2002). In this study, vegetation coverage seemed to affect search image of crows in large spatial scales less strongly than did nesting position but seemed to function as a defensive obstacle in small spatial scale after crows had landed.

In summary, not only position in the colony, egg-laying date and vegetation height of the nest-sites but also egg-laying date of neighbour nests within a < 2-m radius of colonial breeding Black-tailed Gulls affected egg predation risks by Jungle Crows. These variations of antipredation effects of nesting microhabitats with spatial scales were determined by the crows searching or accessing the nests.

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