Factors affecting the egg predation in Black-tailed Gulls

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Abstract

In colonial seabirds, nesting density, egg-laying date and microhabitat of nest affect the probability of eggs to be taken by avian predators. Jungle Crows (*Corvus macrorhynchos*) are dominant predator 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 probability of eggs to be taken were studied by direct observation and egg census, respectively. The effect of vegetation heights, position in the colony and the egg-laying date and those of neighbour nests on the probability of eggs to be taken were examined at multiple spatial scales. Gull nests were depredated more easily by larger groups of the crows. The nests in peripheral areas (< 4m 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 nests synchronized highly in egg-laying within <2m radius were less likely to be depredated than less synchronized nests. The nests with tall vegetation were less likely to be depredated, though those having neighbour nests with tall vegetation were not. The number of the neighbour nests did not affect the probability of eggs to be taken. Anti-predation effects of nesting microhabitats vary with spatial scales at which the crows search and attack the nests of gulls.

Key words

Predation, Nest, Habitat selection, Spatial scale, Gull

Introduction

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

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

Eggs of ground nesting and colonial Laridae species are highly vulnerable to avian predators. They sometimes nest in heterogeneous habitat (Buckley & Buckley

1980, Schreiber & Burger 2002). Their colony often are subdivided into small groups according to their habitats in various spatial scales (Burger & Gchfeld 1981, Bosch & Sol 1998). Therefore, they are suitable for studying effects of spatial scales on predator-prey interactions.

Black-tailed Gull (*Larus crassirostris*) nests on slope with medium vegetation cover or rocks in coastal island and lay 2-3 eggs (Watanuki 1983). Jungle Crow (*Corvus macrorhynchos*) and Slaty-backed Gull (*L. schistisagus*) are known as effective avian egg predator of this species (Watanuki 1983). How do its nesting density and nest-site characteristics affect egg predation is unknown. To find out the key factor deciding the probability of gulls to allow the crow to attack their nests and to depredate their eggs, firstly I observed directly egg predation behaviour by crows and defense behaviour of gulls. Subsequently, to detect the effect of nest-site characteristics and characteristics of neighbour nests within <1m and <2 m radii on the probability of eggs to be taken of the nest-sites, I took egg-census and examined following hypotheses. First, the probability of eggs to be taken of the nests in the central areas of the colony is different from the edge areas. Second, that probability of nest-sites varies with vegetation heights of nest-sites or of neighbour nests. Third, that probability of nest-sites varies with egg-laying date of nest-sites or neighbour nests. Fourth, that probability of nest-sites varies with the number of neighbour nests.

Study area and methods

Observation of predatory behaviour of crows and defense behaviour of gulls

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

Observation of anti-predator behaviour of gulls and predatory behaviour of Jungle Crow was done at three observation areas simultaneously from 3 May to 12 June. The observations were made from the hide placed 40m from observation areas (Fig.1). Observation was done for each eight hour 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 breeding stage of gull, an observation period was divided into three stages, Early: from 3 May when observation was started to 13 May when the accumulation number of eggs laid reached 50% of all eggs, Middle: from 14 to 23 May when the accumulation number of eggs laid reached 80% of all eggs, and Late: from 24 May to 12 June when observation was ended. Total observation times were 208 h (88 h in Early, 64 h in Middle, and 56 h in Late).

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

Egg census and factors affecting probability of eggs to be taken

Nest contents were checked before and after the observations. Thus eggs depredated by the crows were distinguished from those disappeared. All the eggs were marked with the black ink. Egg-laying date was classified in three stages similarly with the observation period, Early: from 3 May to 13 May, Middle: from 14 to 23 May, and Late: from 24 May to 12 June.

Vegetation heights of 95 nest-sites in the observation areas (27, 36 and 32 nests respectively) were recorded in the end of breeding season (from 2 to 8 July) to minimize disturbance. To examine the growing patterns of vegetations, I measured vegetation heights at random points near the observation areas after the observations. Sasa bamboo (mean 11.8cm in the start of study, n=6) and the other grasses (mean 25.6cm in the start of study, n=7) grew at 3cm and 12cm respectively during observation period, and both did not grow quickly afterwards. Therefore, the heights measured at the end of breeding season could be suitable for the index of those of nest-sites throughout the study period. The mean of vegetation heights of nest-sites was 14.6cm (range 0-45, n=95). Vegetation of 0-19cm heighs that did not conceal gulls incubating were classified as short vegetation, while that of ≥20cm heights as tall vegetation. The nests within ≤4m from the edge of breeding areas was classified as peripheral nests, and the others as central nests for the sake of convenience.

Statistical analysis

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

Variations of maximum number of crows visiting the colony, number of attack attempts per observation and number of crows attacking per attempt among the breeding stages of gulls (Early, Middle, Late) were analyzed by 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 time of the day (morning or afternoon) on number of crows attacking and interaction of those factors, I compared number of crows attacking between the two groups with two-way ANOVA, where attack tactics and time of the day were factors.

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

The variation of ratio of number of gulls defending to number of the crows attacking among the number of crows attacking (1, 2-5, $\geq$7; gulls were not attacked by 6 crows) was analyzed by Kruskal-Wallis H test. To detect which the 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 the crows attacking between attacking form the air and from the ground was analyzed by Mann-Whitney U-test.

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

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

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

Result

The probability of gulls allowing the crows to depredate their eggs

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

The variations of 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; p=0.150), and Late (14.00 ±9.18, n=7; H_{adj}=6.142, df=2, p=0.046). Significant difference was detected between Early and Late (p=0.046). Number of attack attempts per observation was differed significantly by the breeding stages of gulls (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; p=0.016), and between Early and Late (0.29 ±0.49, n=7; p=0.003). The variations of numbers of crows attacking per attempt were detected among Early (4.19 ±4.84, n=61 attempts), Middle (1.27 ±0.47, n=11), and Late

(13.00 $\pm$16.97, n=2; H_{adj}=8.819, df=2, p=0.012). Significant difference was detected between Middle and Late (p=0.010).

Number of crows attacking from the air (3.11 $\pm$3.90, n=55) was significantly smaller than that from the ground (7.21 $\pm$7.01, n=19; F=6.408, df=1, 70, p=0.014), and that of attempt in the morning (4.17 $\pm$5.20, n=48) was not significantly different from that in the afternoon (4.15 $\pm$5.20, n=26; F=0.026, df=1, 70, p=0.872). Attack tactics-by-time of the day interaction was not significant (F=0.615, df=1, 70, p=0.436). Therefore, to eliminate correlations of independent factors, the number of crows attacking (1, 2-5, $\geq$7) and time of the day were selected as the independent variables of the logistic regression analysis on the probability of gulls allowing the crow to attack their nests and the probability of gulls allowing the crow to depredate their eggs after attacking.

Time of the day did not affect the probability of gulls allowing the crow to attack their nests (Table 1). The probability of gulls allowing the crow 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; $\geq$7 crows: 100%, 13/13)(Table 1).

Time of the day did not affect the probability of gulls allowing the crow to depredate their eggs after attacking (Table 1). If gulls were attacked by the crow in large group, they had significantly higher probability to depredate their eggs after attacking ($\geq$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 the crows attacking from the ground in each attack attempt (0.44 ±0.54, n=19) was significantly smaller than those 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 the crows attacking of 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 1crow and ≥7 crows (0.38 ±0.54, n=13; p=0.006).

Characteristics of nest-sites and predation risks

Gulls of 95 nest-sites that employed into analysis of relationship between nesting habitats and the probability of eggs to be taken, laid 1.73 ±0.66 eggs on average in their nests and their mean egg-laying date was 11.36 ±7.14. Those gulls of 95 nests took 2.216 days (n=95) on average to form their clutch. Egg-laying date of 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). That date of the nests with short vegetation (10.52 ±7.37, n=65) also was not significantly different from tall vegetation (13.17 ±1.16, n=30; F=0.411, df=1, 83, p=0.521). That date also did not differ significantly by nest density within <1m (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 interactions of those three factors were not significant (p>0.05). Therefore, nesting position, vegetation heights, nest density and egg-laying date were independent each other.

Twenty-two (23%) of 95 nests employed into analysis of relationship between nesting habitats and the probability of eggs to be taken were depredated by the crows. Nesting position, vegetation heights and egg-laying date of nest-sites, and the mean egg-laying date of neghbour nests within <2m radius affected the probability of eggs to be taken (Table 2). Nest density within both radii, the mean egg-laying date of neighbour nests within <1m radius, and the mean vegetation heights of neighbour nests within both radii did not affect probability of eggs to be taken (Table 2). Peripheral nests were significantly more likely to be depredated (32%, 22/68) than central nests (0%, 0/27). The nests with short vegetation cover were more likely to be depredated (31%, 20/65) than those with tall (7%, 2/30). The nests where eggs were laid in Early were significantly more likely to be depredated (40%, 21/52) than those in Middle (3%, 1/32) and Late (0%, 0/11). The nests synchronized highly in egg-laying within <2m 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 less synchronized nests (another nests; 29%, 21/73). Only in peripheral areas, the distance from the edge of the colony in 0.5m precision did not affect the probability of eggs to be taken (logistic likelihood ratio analysis: χ^2=0.781, df=1, p=0.3769).

Discussion

When gulls were attacked by large groups of crows, 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. In some seabird species when they are attacked by large groups of avian egg predators, they allow the predators more easily to attack their nests than when they are attacked by those in single or small groups (Montevecchi 1979).

Peripheral nests were more likely to be depredated because peripheral areas were more likely to be attacked by hopping or walking from the ground as shown for other seabirds (Tinbergen et al. 1967, Gaston & Elliot 1996, Massaro et al. 2001). Smaller number of gulls defended against the crows walking from the ground than those attacking from the air. It might be more difficult for gulls incubating to notice the crows hopping or walking from the outside areas of the colony where vegetation grew thick than those attacking from the air. On the other hand, Coulson (1968) suggested the birds nesting in the peripheral of the colony are younger and have less body condition than central. Gulls nesting in peripheral areas might be inexperienced and have less ability to defend against the crows than central in this study. Only in peripheral areas, however, the nests that were closer to the edge were not more likely to be depredated. Gull nests in peripheral areas were attacked frequently by large groups of crows in some large scale, therefore, nesting position might affect in the scale of several meters.

Gull nests where eggs were laid in Early were more likely to be depredated, because more crows visited the colony in Early than Middle and Late stage. Early stage of gull breeding season was nearly matched chick-rearing stage of crows (Kazama, pers. obs.). Gull eggs laid in Early might be highly available prey for crows feeding chicks. The nests synchronized highly in egg-laying within <2m radius, however, were less likely to be depredated than less synchronized nests. In colonial breeding Common

Murre *Uria aalge*, while the birds incubating and their mates defend vigorously against avian predators, some birds that have not yet laid first egg fly away when the avian predators attack (Murphy & Schauer 1996). Thus in Common Murre the nests with neighbours breeding synchronously in the scale of several meters had lower risks of egg predation because such neighbours mob against predators simultaneously (Murphy & Schauer 1996). Also in gulls, the synchronization in egg-laying seemed to affect the probability of eggs to be taken under the similar mechanism. Egg-laying date of neighbour nests within <1m radius, however, did not affect the probability of eggs to be taken. Since gull nests were attacked often by large groups of the crows in this study, group defense at not small scale (<1m) but some large scale (<2m) might prevent attacking by large group of crows effectively in Early, though spatial scale at which group defense is functioning was unknown in this study.

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

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

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

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

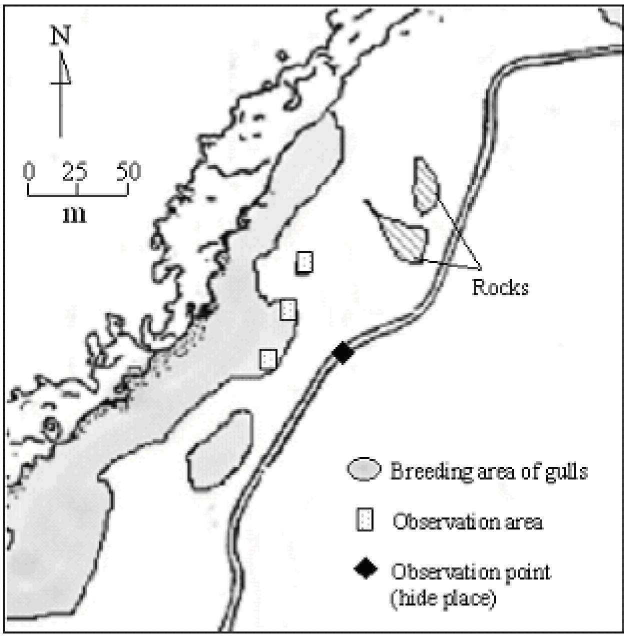

Table 1. Logistic regression model of the factors affecting on the probability of Black-tailed Gulls allowing the Jungle Crows to attack their nests and the probability of gulls allowing the crows to depredate their eggs after attacking.

	Factor	*df*	χ^2	*P*
Gulls allow the crows to attack (n=74)	No. of crows attacking	2	36.369	<0.001
	Time of the 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 the day	1	0.372	0.542

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

Spatial scales	Characteristics	*df*	χ^2	*P*
Nest-site	Nesting position	1	14.142	<0.001
	Vegetation heights	1	4.099	0.043
	Egg-laying date	2	26.466	<0.001
<1m radius	Nest density	2	2.516	0.284
	Vegetation heights	1	0.225	0.635
	Egg-laying date	2	2.647	0.266
<2m radius	Nest density	2	4.961	0.084
	Vegetation heights	1	0.339	0.560
	Egg-laying date	1	9.145	0.003