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Factors affecting individual variation in nest-defense intensity in colonially breeding Black-tailed Gulls (*Larus crassirostris*)

Kentaro Kazama, Yasuaki Niizuma, Kentaro Q. Sakamoto, and Yutaka Watanuki

Abstract: The physiological state of parent birds combined with the value of their clutch may affect the intensity of their nest defense. In colonially breeding birds, nest-defense intensity may also be affected by the behavior of neighbors. We investigated individual variation in the nest-defense intensity among colonial Black-tailed Gulls (*Larus crassirostris* Vieillot, 1818) over 2 years. Only 30%–40% of males attacked a decoy of an egg predator (Large-billed Crow (*Corvus macrorhynchos* Wagler, 1827)), and the other males and females rarely attacked. Males attacking the decoy had higher levels of plasma testosterone than males that did not attack. Each male's, but not female's, nest-defense intensity was consistent throughout the incubation period and also across years. The intensity was not related to egg-laying date, clutch size, or age of offspring. The intensity was likely to be higher when individuals had one or more neighbors, representing higher nest-defense intensity in the year where gulls had larger number of adjacent neighboring nests (5.23 nests), but this trend was not observed in the year where they had smaller number of the neighboring nests (3.73 nests). Thus, in addition to testosterone levels, behavior of neighbors also influences the nest-defense intensity.

Résumé : Chez les oiseaux, l'état physiologique des parents combiné à la valeur de leur portée peut affecter l'intensité de leur défense du nid. Chez les oiseaux qui se reproduisent en colonie, l'intensité de la défense du nid peut aussi être affectée par le comportement des voisins. Nous avons étudié la variation individuelle de l'intensité de la défense du nid chez des goélands à queue noire (*Larus crassirostris* Vieillot, 1818) en colonie, sur deux ans. Seulement 30 % – 40 % des mâles attaquent un leurre représentant un prédateur des œufs (corbeau à gros bec (*Corvus macrorhynchos* Wagler, 1827)) et les autres mâles et femelles attaquent rarement. Les mâles qui attaquent le leurre possèdent une plus forte concentration de testostérone dans le plasma que les mâles qui n'attaquent pas. L'intensité de défense de chaque mâle, mais non celle des femelles, se maintient durant la période d'incubation et d'une année à l'autre. L'intensité n'est pas reliée à la date de ponte des œufs, ni à la taille de la couvée, ni à l'âge des rejets. L'intensité risque aussi d'être plus élevée lorsque les individus ont un ou plusieurs voisins; il y a donc eu une intensité plus importante de défense des nids durant l'année pendant laquelle les goélands avaient un plus grand nombre de nids voisins adjacents (5,23 nids), mais la tendance n'a pas été observée l'année durant laquelle ils avaient un plus petit nombre de nids voisins (3,73 nids). Ainsi, en plus des niveaux de testostérone, le comportement des voisins affecte aussi l'intensité de la défense du nid.

[Traduit par la Rédaction]

Introduction

Among birds, defending nests against predators is fundamental to increasing reproductive success; the level of such defense is hypothesized to be an outcome of the trade-off between the increase in offspring survival and the risks of injury to the parents (reviewed by Montgomerie and Weatherhead 1988; Caro 2005). The intensity of nest defense is affected by the size and age of the clutch or brood, timing of breeding, and sex, age, or quality of the parents. Males (Reid and Montgomerie 1985), parents having a larger num-

ber of eggs or chicks (Greig-Smith 1980; Wallin 1987; Brunton 1990), and parents having good body condition (Lessells 1991) tend to engage in higher intensities of nest defense.

Nest-defense intensity may also be related to individual variation in aggressiveness (Hollander et al. 2008) that may be consistent throughout the breeding season and across years (reviewed by Groothuis and Carere 2005). Aggressiveness is moderately heritable (Drent et al. 2003; van Oers et al. 2005) and often correlates with hormonal levels (e.g., testosterone and corticosterone) (Koolhaas et al. 1997; Cockrem 2007; Kralj-Fišer et al. 2007).

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In colonially breeding birds, nest-defense intensity may be also affected by the behavior of neighbors. Breeding neighbors in a colony are assumed to share predation risks and defense duties (Burger and Gochfeld 1991). Therefore, the costs and benefits of individuals defending their own nests should vary also with the levels of defense of the neighbors (Allaine 1991; Brown and Brown 1996). Studies of these neighbor effects during mobbing and direct attacks at predators, involving high costs and risks for parents, are scarce (but see Winkler 1994; Arroyo et al. 2001).

Black-tailed Gulls (*Larus crassirostris* Vieillot, 1818) nest colonially on gentle slopes on Rishiri Island where vegetation or rocks provide moderate cover. They lay clutches of 1–3 eggs (Kazama 2007); however, Large-billed Crows (*Corvus macrorhynchos* Wagler, 1827) take 30% of their eggs (Kazama 2007). Parent gulls typically defend their nests aggressively against the crows using intimidating actions (i.e., opening the bill and wings, body striking, or swooping) (Kazama 2007; Kazama and Watanuki 2010). There is considerable individual variation among parent gulls in this nest-defense intensity, which affect its frequency and duration (Kazama and Watanuki 2010). Factors affecting this individual variation in nest-defense intensity were examined under extremely high levels of predation risk, where attack levels by Large-billed Crows were manipulated, on average, 5–22 times normal attack rates by the placement of artificial nests containing unguarded eggs at the perimeter of the gull colony (Kazama and Watanuki 2010), but not under natural conditions.

To establish which factors affect individual variation in nest-defense intensity among parent gulls, firstly we examined whether an individual's nest-defense intensity was consistent both within and between years. Secondly, the effects of sex, size, and age of clutch, timing of egg laying, and behavior of neighbors on nest-defense intensity were examined. Finally, correlations between individual variation in nest-defense intensity and hormonal state (level of plasma testosterone) were also examined.

Materials and methods

Study area and period

The study was conducted from 20 April to 10 July 2007 and 2008 on Rishiri Island situated in the Sea of Japan (45°14'N, 141°9'E), 40 km off northern Hokkaido, Japan. A study site of 0.19 ha and including 157 nests in 2007 and 107 nests in 2008 was established in a subcolony at Oiso. Nesting microhabitat and location may affect the potential vulnerability of nests to predation (Brunton 1990; Galeotti et al. 2000), and hence, parental nest-defense behavior. In Black-tailed Gulls, nesting position (<4 m from edge of the breeding area or not) and vegetation heights surrounding the nest sites affect the risk of egg predation (Kazama 2007). Therefore, we established the study area in a small and narrow subcolony where all nests were <4 m from edge of the breeding area, and we also cut back the vegetation around the nests every 1–2 days to maintain its height <15 cm to ensure uniformity in nest potential vulnerability to predation. Nest contents were checked every 1 or 2 days. All the nests in the study site were mapped and marked with numbered stakes immediately after eggs were laid.

Identifying individuals and blood sampling

To identify sex of all individual gulls within the study site in each year (314 gulls in 2007 and 214 gulls in 2008), we observed at least once courtship feeding or copulation behavior (males courtship feed to mates and mount on mates) before egg laying for each pair in each year. Thus we could completely identify sex of all individuals within the study site. Furthermore, to facilitate individual identification of the gulls, black hair dye (Bigen hair color, containing aminophenol and stearic acid as major ingredients; Hoyu Co., Ltd., Nagoya, Japan) was used in each year. During the incubation period, dyed stones or leaves were placed in all the nest cups within the study site so that the dye would mark the breast or neck of either the male or the female parent, whichever returned to incubate the eggs first.

To identify individuals from year to year, 34 males (22% of all the males within the study site) in 2007 were captured by box- or line-trap, and these birds were banded with numbered plastic and metal rings. In 2008, 26 of all the males captured and banded in 2007 returned and nested at the same nest site in 2007 (the rate of return was 76.4%). Although nest site and mate fidelity of larids across years would be high (Blokpoel and Courtney 1980; Naves et al. 2006), all gulls without rings were regarded as different individuals between years, even if they returned to the nest sites where they nested the previous year. In 2008, 30 males were captured (26 out of 30 males were recaptured). Head lengths of all captured males were measured to the nearest 0.02 mm with calipers (D30TN, Mitutoyo Co., Ltd., Kawasaki, Japan) following the procedure described in Bosch (1996).

As levels of plasma testosterone in male Black-tailed Gulls change with the elapsed day from first egg laying (Kazama et al. 2008), 1.0 mL blood was taken from the brachial wing veins of 24 males in 2007 and 12 males in 2008 captured within 4–6 days after the first egg-laying date (blood was taken with an EDTA-rinsed syringe within 2 min of capture). The mean total handling time (from capture to release) of bled gulls was 9 min ($N = 36$). After centrifugation at 2000g for 10 min, plasma was stored at -30°C .

No behavioral changes resulting from color marking, such as an increase in susceptibility of marked birds to predation or territorial attack by other birds, were observed. No marked birds abandoned their nests and no marked pairs stopped incubating their clutches during the study periods. Thus, neither handling nor manipulation harmed the gulls.

Nest-defense intensity

To control for the proximity and approach speed of predators to nests, as well as weather and wind conditions, all of which may influence the defense response (Gilchrist et al. 1998), we exposed individual gulls to a model predator, i.e., a crow decoy (a plastic hunting decoy painted to resemble an American Crow (*Corvus brachyrhynchos* Brehm, 1822); Carry-Lite Inc., Fort Smith, Arkansas, USA) from 1300 to 1700 on clear and calm days. The decoy was placed at ground level 1.5 m from the nearest nest to the decoy and covered with a cloth for more than 30 min before beginning the presentation to allow the gulls to calm down following their disturbance by the researchers. The decoy was exposed to the gulls for 2 min by pulling on a line attached to the cloth to remove it. No more than four presentations were

conducted per day for nests within 10 m of one another. The decoy was exposed to gulls for more than 3-day intervals if the decoy was exposed repeatedly to the same gull within a year. During each presentation, gulls were incubating and their mates were away from their nests (single gull stayed at each nest). During decoy presentations, no Large-billed Crows attacked gull nests within the study site.

Because distance between the gulls and the predator did not affect the defense response of Black-tailed Gulls (Kazama and Watanuki 2010), we recorded responses of 3–6 gulls nesting within <2.5 m radius of the decoy at once in a decoy presentation from a blind located 5 m from the study site. During the decoy presentation, all the gulls within <2.5 m radius of the decoy stopped incubating, stood up, and gave alert calls; several of them attacked the decoy, striking it with their bodies or legs. Because all gulls within <2.5 m radius of the decoy responded to the decoy (i.e., stopped incubation and stood up), all the gulls could be stimulated by the decoy. The responses of individual gulls to the crow decoy were similar to those made by gulls to live Large-billed Crows (Kazama and Watanuki 2010). During natural egg predation by crows, the first gull to attack the crow drove it away effectively and quickly (within several seconds); we refer to this gull as a “first defender”. Although only rarely (<1% of all defenses) did other gulls join in the nest defense against the Large-billed Crow (Kazama and Watanuki 2010), sometimes two or three gulls defended against our decoy because the decoy remained on the ground during the 2 min decoy presentation; we also refer to the second and (or) third gulls as first defenders.

In 2007, we collected 151 records of nest-defense intensity from 58 males (including 34 captured males) and 39 females. In a total of 39 decoy presentations, the nest-defense intensities (the first defender or not) were measured once each for 17 males and 20 females, twice each for 35 males and 12 females, three times each for 6 males and 6 females, and four times each for 1 female. In 2008, we collected 177 records of nest-defense intensity from 58 males (including 26 recaptured males) and 46 females. In a total of 46 decoy presentations, the nest-defense intensities were measured once each for 30 males and 25 females, twice each for 18 males and 14 females, three times each for 7 males and 4 females, four times each for 3 males and 2 females, and five times each for 1 female. For 26 recaptured males, nest-defense intensity was measured repeatedly in both 2007 and 2008.

Testosterone assay

Levels of plasma testosterone were measured by enzyme immunoassay using a commercial kit (Correlate-EIA, Assay Designs Ltd., Miami, Florida, USA). The cross-reactivity of this kit with 19-hydroxytestosterone and dihydrotestosterone was 14.46% and <0.001%, respectively (provided by Assay Designs Ltd.). The minimum detectable level of plasma testosterone was 0.0029 ng/mL, and the standard curve range was 0.008–2.0 ng/mL. For each plasma sample, 100 μ L was assayed in duplicate. The samples collected in 2007 and 2008 were assayed in separate series. The intra-assay coefficients of variation were 1.1% in 2007 and 2.3% in 2008, and the cumulative interassay coefficients of variation were 2.2% in 2007 and 4.4% in 2008.

Statistical analysis

Between-year differences in the first egg-laying date, clutch size, and the number of neighbor nests (the number of adjacent neighbor nests within <1.5 m radius) were examined using linear mixed models (LMM) where year was included as a fixed effect. As 26 recaptured males were observed repeatedly in 2007 and 2008, nest identity was included as a random effect in the models to avoid pseudoreplication.

To examine individual consistency of nest-defense intensity within a year and between years, the repeatability (r) of the intensity was estimated. Repeatability is calculated as $r = S_A^2 / (S^2 + S_A^2)$, where S_A^2 is the variance among individuals and S^2 is the variance within individuals over time (Lesells and Boag 1987), and was calculated for binomial data following Nakagawa and Schielzeth (2010). Standard error and statistical significance of repeatability was calculated following Becker (1984) and Nakagawa and Schielzeth (2010), respectively. Within-year repeatability was calculated for gulls where nest-defense intensity was measured more than twice within a year (41 males and 18 females in 2007 and 28 males in 2008). The repeatability for females in 2008 could not be calculated because no females, of which the nest-defense intensity was measured more than twice within the year (21 females), became the first defender. Males that were first defenders at least once in each year were defined as “aggressive defenders” and the others were called “non-aggressive defenders”. Between-year repeatability was calculated based on whether the male was consistently an aggressive or nonaggressive defender across years, and calculated for 26 recaptured males.

We examined factors affecting nest-defense intensity using generalized linear mixed models (GLMM) with binomial distributions for nest-defense intensity of individual gulls in each decoy presentation (the first defender or not) for each year separately. The models contained sex, clutch size, first egg-laying date, clutch size, age of first egg (elapsed days from first egg-laying date), and the nest-defense intensity by neighbors, which is a 0 or 1 value (gulls having at least one first-defender neighbor in the decoy presentation had a value of 1, whereas the others had a value of 0) as fixed effects, and individual identity as a random effect. We used the 151 records of nest-defense intensity from 2007 and the 177 records from 2008 in the analyses.

The effect of levels of plasma testosterone on the nest-defense intensity was examined in males (16 in 2007 and 8 in 2008) using GLMM with binomial distribution, where aggressive (1) or nonaggressive (0) defender was a dependent variable, level of plasma testosterone and year were fixed effects, and individual identity was a random effect. To normalize the levels of plasma testosterone measured using different series of assays, we applied Z-score transformations in each year. To examine the effects of body size (relative head length (mm; measured size – mean size) on the nest-defense intensity in males, we fitted generalized linear models (GLMs) with binomial distributions including body size and year as independent variables. Among larids, skeletal size is considered suitable as an index of body size because individual variation in skeletal size is greater than in other parts of the body (such as wing length) (Croxall 1995). Because the above two analyses included data from different years, year was included as an independent variable to control for the effect of year.

Table 1. (a) Within-year repeatability and (b) between-year repeatability of the nest-defense intensity in Black-tailed Gulls (*Larus crassirostris*).

(a) Within-year repeatability.					
Year	Sex	Proportion of consistent individuals in defense (%) [*]	Mean (\pm SE) repeatability (r)	p	$N_{(2, 3, 4)}^{\dagger}$
2007	Male	78.0	0.34 \pm 0.13	0.004	35, 6, 0
	Female	61.1	0.00 \pm 0.18	0.99	11, 6, 1
2008	Male	89.3	0.77 \pm 0.06	<0.001	18, 7, 3
	Female	—	—	—	—
(b) Between-year repeatability. [‡]					
Year	Sex	Proportion of consistent individuals in defense (%) [§]	Mean (\pm SE) repeatability (r)	p	N
2007–2008	Male	92.3	0.83 \pm 0.06	<0.001	26

^{*}Proportion of individuals being the first defender in every decoy presentation or never being the first defender within a season.

[†] $N_{(2, 3, 4)}$ indicates the numbers of individuals for which the nest-defense intensity was measured twice, three times, and four times in a year.

[‡]Calculation of the repeatability of whether a gull was an aggressive or nonaggressive defender across years.

[§]Proportion of individuals being an aggressive defender or nonaggressive defender in both years.

All analyses in this study were performed using R version 2.12.0 (R Development Core Team 2010).

Results

Breeding biology in 2007 and 2008

The mean (\pm SD) first egg-laying date (elapsed days from 1 May) in 2007 (4.39 \pm 4.01 days, N = 157) did not differ significantly from that in 2008 (4.21 \pm 3.81 days, N = 107; LMM, t = -0.85, p = 0.40). The mean (\pm SD) clutch size in 2007 (2.25 \pm 0.53 eggs, N = 157) also did not differ significantly from that in 2008 (2.20 \pm 0.57 eggs, N = 107; LMM, t = -0.78, p = 0.44). However, the mean (\pm SD) number of neighbor nests (the number of adjacent neighboring nests within <1.5 m radius) in 2007 (5.23 \pm 2.00 nests, N = 157) was significantly greater than in 2008 (3.73 \pm 1.66 nests, N = 107; LMM, t = -6.67, p < 0.001).

Repeatability of nest-defense intensity

The nest-defense intensity of males was highly repeatable within a year in both 2007 and 2008, but not so for females (Table 1a). In 2007, 34% of males (20/58 individuals) and 5% of females (2/39 individuals) were categorized as aggressive defenders; in 2008, 41.4% of males (24/58 individuals) and 8.7% of females (4/46 individuals) were categorized as aggressive defenders. Whether males were aggressive or non-aggressive defenders was highly repeatable between years (Table 1b).

Factors affecting variation in nest-defense intensity

Males were more likely to be the first defender than females in both years (Tables 2, 3). When the decoy was exposed, gulls with first defenders among their neighbors were more likely to be a first defender than those without such neighbors in 2007; this was not the case in 2008 (Table 3, Fig. 1). Neither first egg-laying date, clutch size, nor age of first egg affected the nest-defense intensity in both years (Table 3).

Effect of plasma-testosterone levels and body size

The mean (\pm SE) level of male plasma testosterone was 0.162 \pm 0.02 ng/mL (range = 0.06–0.37 ng/mL, N = 24) in

2007 and 0.187 \pm 0.06 ng/mL (range = 0.06–0.67 ng/mL, N = 12) in 2008. Males having higher levels of normalized plasma testosterone were more likely to be aggressive defenders (GLMM, estimate \pm SE = 1.38 \pm 0.66, Z = 2.10, p = 0.036, N = 24) without year effect (estimate \pm SE = -0.09 \pm 1.12, Z = -0.08, p = 0.933, N = 24). Relative head length, a measure of body size, did not significantly correlate with male aggressiveness (aggressive or nonaggressive defenders; GLMs, estimate \pm SE = 0.26 \pm 0.19, Z = 1.41, p = 0.16, N = 40) without year effect (estimate \pm SE = -0.38 \pm 0.93, Z = -0.41, p = 0.68, N = 40).

Discussions

Previous studies have predicted that nest-defense intensity (i.e., frequency and duration) should be regulated in relation to the size and age of the clutch and the timing of egg laying (Montgomerie and Weatherhead 1988; Caro 2005). In Black-tailed Gulls, however, the nest-defense intensity of males was highly repeatable over time within a year and between years, and was related to levels of plasma testosterone rather than to the size and age of the clutch, the timing of egg laying, or body size (head length). Furthermore, females rarely defended their nests. These suggest that the level of plasma testosterone is a dominant factor constraining the nest-defense intensity in Black-tailed Gulls. In larids during breeding season, levels of plasma testosterone in males are 2–15 times higher than those in females (Wingfield and Farner 1993).

In birds, genetic or maternal effects and age or social status are assumed to control individual variation in levels of plasma testosterone (Kempnaers et al. 2008). In male Black-tailed Gulls, nonaggressive defenders rarely became aggressive defenders in the next year (Table 1b), indicating that the level of plasma testosterone and the nest-defense intensity were controlled by certain long-term (at least over 2 years) consistent factors, such as genetic or maternal effects. Because age of males was unknown in our study, we also could not rule out the age effect on the level of plasma testosterone and the nest-defense intensity in long-lived Black-tailed Gulls (over 20 years maximum; Narita and Narita 2004).

Parents of colonially breeding Montagu's Harriers (*Circus*

Table 2. Probability (%) of being the first defender of an individual Black-tailed Gull (*Larus crassirostris*) during a decoy presentation in 2007 and 2008.

Year	Males	Females
2007	28.1 (89)	14.5 (62)
2008	37.4 (99)	5.1 (78)

Note: The number in parentheses is the number of records of the nest-defense intensity.

Table 3. Factors affecting the nest-defense intensity of Black-tailed Gulls (*Larus crassirostris*) to an egg-predator decoy in 2007 and 2008.

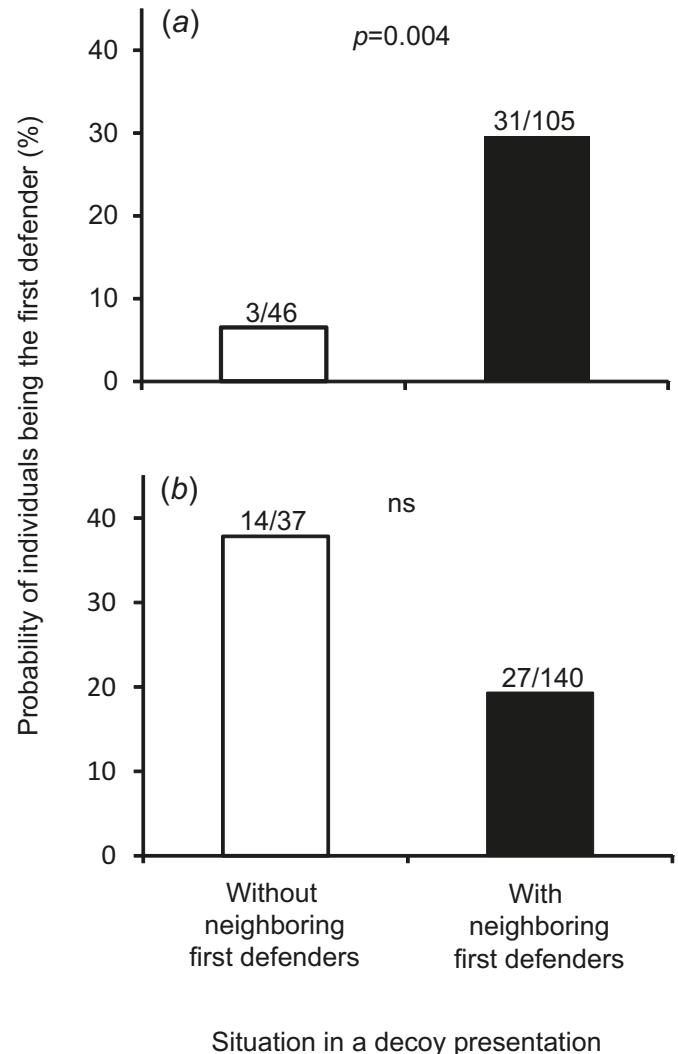
Fixed effects	Estimate	SE	Z	p
2007 (N = 151)				
Sex	-1.429	0.537	-2.66	0.008
Clutch size	0.302	0.496	0.61	0.54
First egg-laying date	-0.079	0.083	-0.95	0.34
Age of first egg	0.063	0.043	1.48	0.14
Neighbor's behavior*	2.113	0.742	2.85	0.004
2008 (N = 177)				
Sex	-3.186	0.952	-3.35	0.001
Clutch size	0.337	0.689	0.49	0.62
First egg-laying date	-0.114	0.123	-0.93	0.35
Age of first egg	0.039	0.087	0.45	0.65
Neighbor's behavior*	-0.898	0.681	-1.32	0.19

*Whether an individual had one or more neighboring first defenders or not when the decoy was presented.

pygargus (L., 1758)) reduce the nest-defense intensity if their neighbors participate in group defense (Arroyo et al. 2001). In contrast, parent Black-tailed Gulls with neighbors showing higher levels of defense defended their nests more intensively. One possible explanation for our results is the "responsive amplifier" (Winkler 1994). In another colonial species, the Tree Swallow (*Tachycineta bicolor* (Vieillot, 1808)), parents use the nest-defense intensity of close neighbors as a reliable indicator of the threat of a predator to their own nest and the nest-defense intensity increases if an individual has neighbors showing higher levels of defense (Winkler 1994). Another possible explanation is reciprocation. An egg predator, such as the Large-billed Crow, may attack the same area repeatedly during the incubation period at a gull colony (Kazama 2007; Kazama and Watanuki 2010). Therefore, neighbors of a first defender were likely to cooperate as a first defender (really a "second defender") in expectation of reciprocation if their own nests were subsequently threatened. In 2008, however, the nest-defense intensity among Black-tailed Gulls did not correlate with that of their neighbors. Among Tree Swallows, the probability of parents participating in group defense was higher when neighboring nests were more closely adjacent (Winkler 1994). In this study of gulls, the number of adjacent neighbour nests was smaller in 2008 than in 2007.

Only about 30%–40% of male Black-tailed Gulls showed aggressive defense consistently over time. Among birds, anti-predator defense is associated with time and energy costs, as well as injury risks (Dugatkin and Godin 1992). High levels of testosterone can cause an immunosuppressive effect (Bese-

Fig. 1. Comparisons of the probabilities of individual Black-tailed Gulls (*Larus crassirostris*) being a first defender between those having neighboring first defenders and those without, when an egg-predator decoy was presented in (a) 2007 and (b) 2008. Numbers above the bars indicate the number of records. Significant *p* values were obtained from GLMM (see Table 3).



dovsky and del Rey 1996), decrease survival (Nolan et al. 1992), and reduce parental care (Ketterson et al. 1992, Alonso-Alvarez 2001). Furthermore, aggressive defenders reduce the risk of egg predation for their neighbors' nests as well as their own (Kazama and Watanuki 2010). Hence, aggressive defenders partly support an increase in the reproductive success of their potential competitors. These suggest that the balance between the costs and the benefits of antipredator nest defense would differ between aggressive and nonaggressive defenders. Further study into the reproductive advantages of aggressive defenders is necessary to examine the adaptive significance of aggressive nest defense in Black-tailed Gulls.

In conclusion, the nest-defense intensity by Black-tailed Gulls was not regulated based on size and age of clutch, timing of egg laying, or body size, but it may be affected by the nest-defense intensity of their neighbors in addition to their levels of plasma testosterone.

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