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Intraspecific Kleptoparasitism, Attacks on Chicks and Chick Adoption in Black-tailed Gulls (*Larus crassirostris*)

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Abstract.—To understand the adaptive significance of colonial breeding, evaluating the costs and benefits that colonial breeding provides to individuals is necessary. To study some of these costs and benefits of colonial breeding, over 24,000 nest-hour observations of kleptoparasitism (stealing of food being fed to young), intraspecific attacks on and killing of chicks, and chick adoption were conducted in colonial breeding Black-tailed Gulls (*Larus crassirostris*) during two breeding seasons. Although kleptoparasitism was rarely observed (under 0.001 events/nest/observational hour), the occurrence of chick-attacks was 5-10 times higher (0.005-0.01 events/nest/observational hour) than that of kleptoparasitism, with over 10% of the attacks resulting in the death or disappearance of chicks. More than 60% of all attacks on chicks were by failed breeders and non-breeding adult floaters. The survival of attacked chicks reached 98-100% if they escaped into other nests and were accepted by “foster” adults, or if they were defended by non-parental adults. Chick adoption and non-parental defense were more likely to be observed among breeding neighbors (52-60% of chick adoptions and almost all examples of non-parental defense) than among non-neighbors. An increased chick survival rate, resulting from nesting in close to proximity to conspecific neighbors, was considered as a factor promoting colonial breeding among the Laridae. Received 20 January 2012, accepted 5 August 2012.

Key words.—altruism, chick adoption, colony, conspecific interaction, gull, kleptoparasitism, neighbor.

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Many seabird species breed in colonies. Individuals and pairs in such colonies may benefit from the presence of other colony members through early predator deterrence and group mobbing, or decreased individual predation risk because of the “dilution effect” (reviewed by Coulson 2002). However, colonial seabirds also face potential costs of conspecific interference resulting from the proximity of other colony members, including food stealing (kleptoparasitism) and attacks on chicks (Coulson 2002). The balance between the benefits and costs of behavioral interactions among colony members is believed to be one of the factors affecting the evolution and maintenance of colonial breeding (reviewed by Wittenberger and Hunt 1985; Brown and Brown 2001). In order to understand the adaptive significance of colonial breeding, it is necessary to evaluate the benefits and costs of behavioral interactions (Brown and Brown 1996).

Almost all Larid species breed colonially (Coulson 2002). Breeding Laridae display high rates of conspecific interactions, includ-

ing attacks on and killing of chicks (Hunt and Hunt 1975, 1976; Pierotti 1980; Fetterolf 1983), kleptoparasitism while parents feed their chicks (Elston and Southern 1983; Fetterolf 1983; Steele and Hockey 1995), and chick adoptions (Pierotti and Murphy 1987; Hébert 1988; Brown 1998). In order to understand the costs and benefits of colonial breeding more clearly, the causes, patterns of occurrence and consequences of interactions require detailed study. However, few studies have documented such interactions over long time periods (but see Helfenstein *et al.* 2004); furthermore, the relationship between chick adoption and the occurrence and consequences of other interactions (e.g. attacks on chicks) has not been investigated.

In this study of colonial nesting Black-tailed Gulls (*Larus crassirostris*), we conducted continuous observations of adult behavior in relation to chicks, including: attacks on and killing of chicks, chick adoption and kleptoparasitism among adults. Observations, consisting of more than 24,000 nest-hours/year, were made during two breeding sea-

sons, in order to describe the frequency, causes and consequences of such conspecific behavioral interactions. In addition, we documented parameters relating to the individuals engaging in the behavioral interactions (male, female; breeder, non-breeder; neighbor, non-neighbor) and chick age, and discuss the socio-ecological costs and benefits of those interactions.

METHODS

Study Species, Area and Observations

The Black-tailed Gull is a medium-sized (44-48 cm in length), white-headed gull found only in coastal Eastern Asia from China to northern Sakhalin and the northern Kuril Islands (Brazil 2009). The species breeds commonly around Japan, where it nests colonially on offshore islands, wherever vegetation or rocks provide moderate cover (Kazama 2007). The Black-tailed Gull's self-caught diet consists of small fish, crustaceans and mollusks, but it also scavenges and steals food from other conspecific individuals (Kazama *et al.* 2008). Pairs start forming colonies in mid-April; they lay their clutches (normally 2-3 eggs) from early May until early June, and their chicks fledge at between 35-40 days old, during early July.

The present study was conducted from 25 April to 10 July, 2007 and 2008, on Rishiri Island (45° 14'N, 141° 09'E) about 40 km west of northernmost Hokkaido, Japan. In 2004, Kosugi *et al.* (2005) reported over 19,000 pairs of Black-tailed Gulls on the island, indicating its suitability for breeding studies. In both 2007 and 2008, we made behavioral observations in a single 0.030 ha study area within a sub-colony located on a gentle, northwestern slope of the island. The study area contained 157 nests in 2007 and 107 nests in 2008.

All nests in the study area were mapped and marked with numbered stakes immediately after eggs had been laid and checked every 1-2 days. Once chicks had hatched, we did not walk in the study area so as to avoid disturbing them. Instead, we observed nests from a blind, placed 5 m from the edge of the study area, in order to check chick numbers and survival.

The day on which the first egg was laid (elapsed days from 1 May) within the study area did not differ significantly between the two years of the study (mean \pm SD, 2007: 4.39 \pm 4.01, N = 157, 2008: 4.21 \pm 3.81, N = 107; ANOVA, $F_{1,262} = 0.15$, $P = 0.70$). Moreover, there was no significant difference in mean clutch size within the study area between years (mean \pm SD: 2007: 2.25 \pm 0.53, N = 157, 2008: 2.20 \pm 0.57, N = 107; ANOVA, $F_{1,262} = 0.73$, $P = 0.40$). Within the study area, 114 chicks hatched from 157 nests in 2007, whereas 84 chicks hatched from 107 nests in 2008.

Individual Identification

Each breeding season, we marked nesting individuals on their breasts and necks with black hair-dye (Bigen

hair color, containing aminophenol and stearic acid as major ingredients; Hoyu Co., Ltd., Nagoya, Japan), so as to facilitate individual recognition, and observed courtship feeding and copulation prior to egg laying in order to confirm gender. Marking was accomplished by placing stones or leaves coated with dye in the nests during the incubation phase, so that the dye marked individuals randomly, as they returned to the nest and settled down to incubate.

Not all individuals in the study area were breeders. Some, defined as adult floaters, were in adult plumage (Narita and Narita 2004) but did not nest within the study area (and so were not dyed). Juveniles and sub-adults three years or younger in age, were recognizable as such by their having: only some black pigmentation in their rectrices; some brownish mantle feathers; or chocolate-brown primary feathers (Narita and Narita 2004). The gender of non-breeding individuals was not determined.

Behavioral Observations

Once chicks had hatched, we conducted behavioral observations during the day from 04:00 to 20:00, on three or four days each week from 3 June to 13 July in 2007 (27,946 nest-hours) and from 30 May to 10 July in 2008 (24,075 nest-hours). We recorded all instances of attacks on chicks (and whether they resulted in chick mortality), kleptoparasitism and chick adoption.

A kleptoparasitic attack was defined as an event involving a non-parent individual landing within 0.5 m of the nest and reaching towards the food item being given to a chick by one of its parents. Successful kleptoparasitism was defined as an event in which a non-parent took the food item from a chick or its parent. The identity and gender of the kleptoparasitic individual, the nest attacked and the success of the attack, were all recorded.

Conspecific attacks on chicks were defined as events involving a non-parent pecking a chick in its nest. The identity and gender of the attacker, the nest attacked, whether a parent was present or not at the attacked nest and the behavioral responses of the attacked chicks (i.e. whether they escaped or not) were all recorded. Defense behaviors against the attacker by the attacked chicks, by the parents of the attacked chicks and by other adults (e.g. neighboring breeders) were only recorded during 2008. Defense against an attacker was defined as an event during which a chick was attacked and either one of the chick's parents attacked the intruder, or another adult threatened (by opening its bill and wings) or had body contact with the attacker.

Chick displacement was considered to have occurred when a chick approached within 0.5 m of a non-natal nest, and chick adoption occurred when a chick away from its natal nest was not attacked (i.e. neither bitten nor struck), but was fed or incubated for more than 2 min by the parents of the nest it had entered (termed the foster nest). The identity (nest number) of the displaced chick, the cause of the chick's departure from its natal nest (attracted by food, caught in a territorial fight or escaping from conspecific attack), the identity

of the foster parents, the behavior (feeding or defense) of the foster parents at the nest and the consequence of chick displacement (i.e. adoption or rejection), were all recorded. Also recorded were the behavioral patterns of displaced chicks if they were rejected from other nests. Because chicks were not individually marked or identifiable, the consequences of adoption (i.e. whether they fledged from the foster nest or not) were not recorded.

Data Analysis

The sample sizes of several conspecific interactions, such as kleptoparasitism, were small but similar in occurrence in both years of the study, thus data from the 2007 and 2008 breeding seasons were pooled for all statistical tests. The differences in all proportion data (e.g. proportion of occurrence, chick mortality rate or adoption rate.) were examined using chi-square tests. All analyses were conducted using PASW Statistics ver. 18.0.0 (SPSS Inc. 2009).

RESULTS

Kleptoparasitism

Although kleptoparasitism was only rarely observed (Table 1), compared with attacks on chicks (Table 2), or chick displacement (Table 4), 80-90% of kleptoparasitic attacks were successful (Table 1). All attackers were adults, and adult males initiated such attacks significantly more frequently than did adult females ($\chi^2_1 = 72.25$, $P < 0.001$, Table 1; attackers that could not be categorized were excluded from the analysis). One particular individual male made five out of twelve kleptoparasitic attacks in

2007, and eight out of 28 in 2008. Kleptoparasitic attacks were initiated significantly more frequently by non-neighbors than by neighbors ($\chi^2_1 = 42.25$, $P < 0.001$, Table 1).

Attacks on Chicks

All observed attacks on chicks were made by conspecifics. Adult gulls attacked chicks from two to ten times more frequently (Table 2) than they engaged in kleptoparasitism (Table 1) or chick displacement (Table 4). Failed breeders and adult floaters attempted attacks on chicks more frequently than did breeders ($\chi^2_1 = 4.91$, $P = 0.027$, Table 2), and adult males attempted to attack chicks significantly more frequently than did adult females ($\chi^2_1 = 15.80$, $P < 0.001$, unsexed non-breeders were excluded from the analysis, Table 2). Non-neighbors were significantly more likely to initiate attacks on chicks than neighbors ($\chi^2_1 = 13.35$, $P < 0.001$, Table 2). Attackers (adults, subadults and juveniles) tended to attack chicks that were 10-25 days-old more frequently than younger or older chicks (Fig. 1).

Of the chicks that were attacked, 44% (2007) and 64% (2008) remained in their natal nests after the attack (Table 3). Some chicks fled their nest following an attack and their fates varied. Some of them, 17% in 2007, and 11% in 2008 escaped, hid tem-

Table 1. Summary of the patterns of occurrence and outcomes of kleptoparasitism in breeding Black-tailed Gulls during 2007 and 2008.

		Year	
		2007	2008
Frequency of kleptoparasitic attacks ^a		15 (0.0005)	29 (0.0012)
Type of kleptoparasite	Breeder ^c	12	28
	Unknown	3	1
Sex of kleptoparasite ^{b,*}	Male	83.3 (10)	96.4 (27)
	Female	16.7 (2)	3.6 (1)
Relationship between attacker and the attacked nest ^{b,*}	Neighbor ^d	41.7 (5)	7.1 (2)
	Non-neighbor	58.3 (7)	92.9 (26)
Consequence of kleptoparasitism ^b	Success	80.0 (12)	93.1 (27)
	Fail	20.0 (3)	6.9 (2)

^aNumber of attacks per nest per hour of observation are shown in parenthesis.

^bShown as the proportion (%), with the frequency in parenthesis.

^cIndividuals nesting within the study area.

^dWithin <1.5 m radius of adjacent nests.

*An unknown attacker was excluded from the value.

Table 2. Summary of the pattern of occurrence of conspecific attacks on chick in breeding Black-tailed Gulls during 2007 and 2008.

		Year	
		2007	2008
Frequency of conspecific attacks on chicks ^a		145 (0.0052)	271 (0.0112)
Type of chick-attacker ^b	Breeder ^c	39.3 (57)	37.3 (101)
	Failed breeder	27.6 (40)	15.1 (41)
	Adult floater ^d	33.1 (48)	43.9 (119)
	Juvenile or sub-adult ^e	0 (0)	3.7 (10)
Sex of chick-attacker ^{b,*}	Male	79.4 (77)	63.4 (90)
	Female	20.6 (20)	36.6 (52)
Relationship between attacker and attacked chick ^b	Neighbor ^f	33.8 (49)	30.6 (83)
	Non-neighbor	66.2 (96)	69.4 (188)

^aNumber of attacks per nest per hour of observation are shown in parenthesis.
^bShown as the proportion (%), with the frequency in parenthesis.
^cIndividuals nesting within the study area.
^dIndividuals in adult plumage but not nesting within the study area.
^eIndividuals not in adult plumage.
^fWithin <1.5 m radius of adjacent nests.
^{*}Adult floaters, juveniles, and sub-adults were excluded from the values.

porarily in bushes nearby, then returned to the natal nest later (Table 3). Other chicks, 27% in 2007 and 15% in 2008, escaped into foster nests. The remaining chicks (12% in 2007 and 10% in 2008) were killed during the attack or disappeared from the study area (Table 3). Of those killed, 90% (nine chicks) were killed by adult males. With the exception of one chick that was killed when 35 days old, all other chicks were ten days old or younger when killed. Of all the chicks that hatched within the study area, 15.8% (18/114 chicks in 2007) and 32.1% (27/84 in 2008) disappeared or were killed after conspecific attacks during our observa-

tions. Although chicks were killed by their attackers, none were observed to be eaten by their attackers in either year of observation.

Most attacks on chicks 97% [140/145 attacks] in 2007 and 95% [257/271] in 2008) were made while parents were absent. The attacked chicks defended themselves if they were older than 15 days old, but such defense was rare (2.3% [6/257 attacks]). In 23% (58/257) of attacks, neighboring breeders defended the chicks, while in 1.6% (4/257) non-neighboring breeders defended the chicks. In 155 cases, attacked chicks were not defended in any way; 57 (37%) of them escaped temporarily, disappeared, or were killed. In contrast, all chicks (100%; 6/6) that defended themselves survived, as did 98% (61/62) of those defended by non-parents. Thus, it appears that defense by neighbors and non-neighbors may increase the survival of chicks that are attacked.

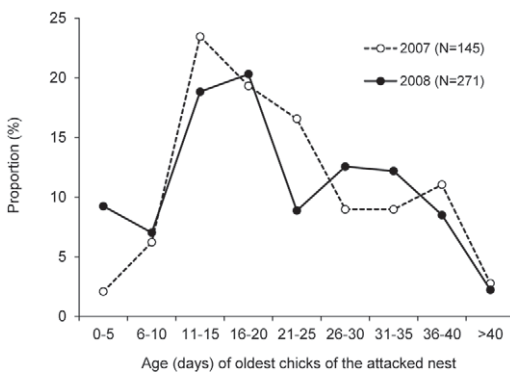


Fig. 1. Attacks on chicks (%), in relation to the age of the oldest chick in the attacked nest, in Black-tailed Gulls.

Chick Displacement and Adoption

Displacement of chicks from their natal territories was rare (Table 4). More than half of displaced chicks approached a neighbor's nest (Table 4). In general, chicks younger than ten days old were more likely than older chicks to be displaced from their natal nests; and all displaced chicks, regard-

Table 3. Fates (% [N]) of Black-tailed Gull chicks attacked by conspecifics during 2007 and 2008.

Year	Disappeared	Killed	Temporarily escaped, hid nearby, then returned to the natal nest later	Escaped to another nest	Remained at the natal nest
2007	11.0 (16)	1.4 (2)	16.6 (24)	26.8 (39)	44.1 (64)
2008	7.0 (19)	3.0 (8)	11.4 (31)	15.1 (41)	63.5 (172)

less of their age, were more likely to move to nests that contained chicks younger than ten days old than to nests containing older chicks (Fig. 2). Three chicks in 2007 and five in 2008 approached nests containing eggs that had not yet hatched (Fig. 2).

Chicks left their natal nests for several reasons. Primarily, they did so as a result of being attacked by a conspecific adult gull (83% [39/47 cases] in 2007; 65% [41/63 cases] in 2008). Chicks also left because they were attracted by neighboring parents feeding their own chicks (8.5% [4/47 cases] in 2007; 18% [11/63 cases] in 2008); or because they were disturbed during a territorial fight between adults (8.5% [4/47 cases] in 2007; 18% [11/63 cases] in 2008).

There were a number of different outcomes of chick displacement. Approximately 70% of displaced chicks (47 chicks in 2007 and 63 in 2008) were adopted by foster parents (Table 4). The proportion of parents that adopted another chick at least once during our observation was surprisingly high, with 18% of study pairs (28/157 pairs) adopting in 2007, and 28% (30/107) in 2008. The adoption rate (the number of chicks adopted / displaced chicks) was similar among neighboring nests (74% [14/19 cases] in 2007; 60% [18/30] in 2008) and non-neighboring nests (75% [21/28] in 2007; 76% [25/33] in 2008) ($\chi^2_1 = 0.73$, $P = 0.39$). The adoption rate was also similar for male and female foster parents (males 60% [9/15 cases] in 2007 and 70% [26/37] in 2008; fe-

males 75% [9/12] in 2007 and 67% [16/24] in 2008) ($\chi^2_1 = 0.03$, $P = 0.85$, foster parents of unknown sex were excluded). The rate of adoption was not dependent on the age-class of the displaced chicks (0-5 days-old 71% [24/34 cases]; 6-10 days-old 59% [16/27]; 11-15 days-old 82% [9/11]; 16-20 days-old 67% [2/3]) ($\chi^2_3 = 4.06$, $P = 0.26$). However, the rate of adoption was significant higher when the oldest chick in the foster nest was 0-10 days old (Fig. 3, $\chi^2_5 = 15.79$, $P < 0.01$).

When displaced chicks were rejected by foster parents, 67% (8/12 chicks) in 2007, and 35% (7/20) in 2008 returned to their own nests, while the remainder were attacked and killed by the foster parents (17% [2/12 chicks] in 2007; 30% [6/20] in 2008) or disappeared from the study area (17% [2/10] in 2007; 35% [7/20] in 2008).

DISCUSSION

Attacks on chicks by conspecific adults represent a significant threat to chick survival because more than 10% of chicks attacked disappeared or were killed. Chicks that were 10-20 days old were more likely to be attacked than younger or older chicks. Gulls protect their offspring against thermal stress (reviewed by Schreiber 2002). Black-tailed Gull parents are particularly attentive when their chicks are young; they brood their very small (<10 day-old) chicks, which have poor thermoregulatory abilities, and only thereafter reduce their levels of nest attentive-

Table 4. Frequency of chick displacement from the natal nest, rate of displaced chick adoption, and likelihood of chick adoptions among neighbors, in breeding Black-tailed Gulls during 2007 and 2008.

Year	Frequency of chick displacement from the natal nest*	rate (%) of adoption of displaced chicks (N)	proportion (%) of occurrence of chick adoptions among neighbors (N)
2007	47 (0.0019)	74.5 (35/47)	59.6 (28/47)
2008	63 (0.0026)	68.3 (43/63)	52.4 (33/63)

*Number of displaced chicks per nest per hour of observation in parenthesis.

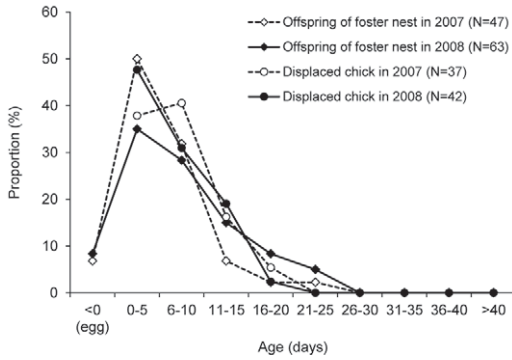


Fig. 2. Chick adoption (%), in relation to the age of the oldest chick in the foster nest, and the age of the displaced chick, in Black-tailed Gulls.

ness (K. Kazama unpublished data). Thus, the risk of attacks on chicks is lowest when they are less than ten days old, and seems to increase thereafter. Once chicks are 20 days old, their risk of being attacked declines further, presumably because by then they are better able to defend themselves.

Black-tailed Gulls are sexually dimorphic with males averaging larger and heavier than females (Chochi *et al.* 2002). Further, males are more aggressive towards conspecifics than are females (Kazama *et al.* 2011; Kazama *et al.* 2012). In this study, males were also found to be significantly more likely than females to attack chicks. Their greater size and heightened intraspecific aggression mean that

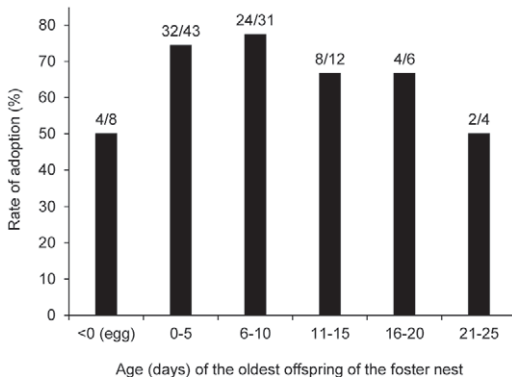


Fig. 3. Age of oldest offspring in the foster nest and rate of adoption of displaced chicks (%) in Black-tailed Gulls. Numbers above the bars indicate the number of chicks adopted / the number of chicks displaced into the nest.

males may be more physically capable of successfully attacking chicks or repelling other birds' attacks than are females. The majority of attacks on chicks were attempted by failed breeders and non-breeding adult floaters, perhaps indicating that the risks of such attacks are higher when breeding success is low. Nest failure was higher in the study colony in 2008 than in 2007 (K. Kazama, personal observation), which might explain why twice as many attacks were recorded in 2008 than in 2007.

The reason why failed breeders and non-breeding adult floaters attacked conspecific chicks was unclear. Among birds, adults may kill conspecific chicks in order to eat them (e.g. cannibalism), or to reduce competition and increase access to limited resources (Mock 1984). While chick cannibalism by conspecific adults has frequently been observed in several large-sized (>60cm total body length) gull species (Parsons 1971; Watanuki 1988) and sometimes in medium-sized species (Brown and Lang 1996), it was not observed during this study. In making attacks, failed breeders and non-breeding adult floaters might, perhaps, be attempting to deprive the parents of attacked chicks of their breeding territory, thus compromising their future breeding opportunities. Among colonial breeding gulls, individuals that have failed to breed in a given year are, when compared with successful breeders, less likely to return to the failed nest site in subsequent years (Danchin *et al.* 1998; Naves *et al.* 2006).

In contrast to attacks on chicks, which were quite common, kleptoparasitism was rarely observed. Although those adult gulls that attempted to steal food were highly successful, the frequency of kleptoparasitism was very low when the provisioning rate of Black-tailed Gulls (0.10 feeds per nest per observational hour) is considered (Kazama *et al.* 2012). Thus kleptoparasitism is considered not to have a large effect on chick survival in this species. Kleptoparasitism is a common foraging strategy in several gull species (Elston and Southern 1983; Steele and Hockey 1995); however, kleptoparasitism can sometimes involve great energy expenditure and high risk of injury (Furness 1987; Sirot 2000). Among seabirds, kleptoparasitism may be beneficial to individuals only under certain ecological conditions,

such as when hosts feed on large visible food items (Brockmann and Barnard 1979) and during periods of food shortage (Oro 1996; Sirot 2000). Kleptoparasitism might not be a profitable foraging strategy for adult Black-tailed Gulls provisioning small food items invisibly (i.e. by regurgitation) to their chicks (Kazama *et al.* 2008; Kazama *et al.* 2012), although food availability was unknown in this study.

Of the nests we observed, 18% in 2007 and 28% in 2008 contained at least one adopted chick. The observed proportion of Black-tailed Gull pairs adopting chicks was similar to rates reported previously in other gull species: 8-13% in Western Gulls (*L. occidentalis*) (Hunt and Hunt 1975; Pierotti and Murphy 1987), 5-35% in Herring Gulls (*L. argentatus*) (Graves and Whiten 1980; Holley 1981, 1984; Pierotti and Murphy 1987), 10-38% in Ring-billed Gulls (*L. delawarensis*) (Brown *et al.* 1995) and 19-48% in Audouin's Gulls (*L. audouinii*) (Oro and Genovart 1999). While the age of the displaced chicks was not related to the rate of adoption, parents with younger chicks were more likely to adopt displaced chicks than parents with older chicks. Gull parents are suspected of being able to discriminate between their chicks and unrelated chicks based on their vocalizations (Beer 1969, 1979; Miller and Emlen 1975; Chung *et al.* 2004), an ability that becomes established in adult Black-tailed Gulls when the chicks are between 4-7 days-old (Chung *et al.* 2004; Kazama *et al.* 2009). Once parents have learned the vocal properties of their own chicks they are able to reject displaced chicks moving into their nest.

The main reason for chicks leaving their natal nests was to escape attacks by adults. Displacement of chicks is costly, with 34% in 2007 and 65% in 2008 of displaced chicks being killed by attackers or disappearing if rejected by foster parents. Chick adoption therefore increases the survival rate of chicks that have been attacked by conspecific adults, with foster nests acting as temporary refuge shelters. The cost to foster parents of failing to discriminate between their own and other chicks was not clear in this study, although the costs seem to be relatively small in other gull species (Brown 1998).

Only a few cases of interference interactions (7-42% of kleptoparasitism and 31-34%

of conspecific attacks on chicks) occurred among neighbors. In comparison, there were many cases of beneficial interactions (52-60% of chick adoption and 94% of non-parental guarding of chicks) among neighbors. Thus, individuals might gain socio-ecological benefits, rather than suffer costs, from their neighbors. The beneficial interactions among neighbors might be interpreted as reciprocation. For instance, conspecific-intruders might repeatedly attack the same area during the chick-rearing period (K. Kazama personal observation). In areas that are more intensively attacked, chick adoption and defense might be more common than in areas that are attacked by conspecifics less often. Therefore, individuals in the areas of high risk might be more likely to cooperate with their neighbors (i.e. defend or adopt chicks) in expectation of reciprocation if their own chicks were threatened in the future. In a few species of colonially breeding seabirds, small neighborhoods may be comprised of kin groups (Friesen *et al.* 1996; Bukacinski *et al.* 2000; Ibaruchi *et al.* 2011). Therefore, further research is required to examine the kin relationships among neighbors, as well as reciprocal altruism, in Black-tailed Gulls.

In attempting to understand the evolution and maintenance of colonial breeding, many researchers have attempted to explain how nesting in close proximity to numerous other conspecifics may benefit individuals (reviewed by Wittenberger and Hunt 1985; Brown and Brown 2001; Krause and Ruxton 2002). Empirical evidence of such benefits, however, seems to be scarce (reviewed by Danchin and Wagner 1997). Among colonially breeding Black-tailed Gulls, the risk of egg predation during the incubation period can be reduced by the defense behavior of breeding neighbors toward avian egg-predators (Kazama and Watanuki 2010). The present study has indicated that chick survival during the chick-rearing period was increased through the interactions among neighboring breeders. The increase in offspring survival during the breeding season, owing to nesting close to other conspecifics, may be implicated as one of the factors promoting colonial breeding in gull species.

Populations of colonial breeding gull species have dramatically increased, or

decreased, in recent decades in Europe, North America, Australia and Asia (Blokpoel and Spaans 1991; Furness *et al.* 1992; Pons 1992; Smith and Carlile 1993; Osa and Watanuki 2002) necessitating population management in some instances (Bosch *et al.* 2000). Increased chick survival resulting from the proximity of neighboring breeders in this study indicates that the presence or absence of active (successful) breeding neighbors could be one of the factors contributing to gull population dynamics. Our results suggest that controlling social conditions among neighbors needs to be taken into consideration when undertaking population management and/or conservation measures for gull species.

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