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Tide associated incubation and foraging behaviour of Saunders's Gulls *Larus saundersi*

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Various factors such as food, climate, nest predation, and phylogenetic relationships influence parental behaviour in birds. However, few studies have addressed how the tidal cycle shapes incubation behaviour in seabirds. In the intertidal zone, spatiotemporal limitations in foraging opportunities for the parents are expected to affect breeding behaviour. We studied tide-associated incubation behaviour in Saunders's Gulls *Larus saundersi*, nesting in a colony on recently reclaimed land and foraging on tidal mudflats, near Incheon in the Republic of Korea. This colony is the last remaining colony in the Republic of Korea. In May 2012, the number of non-foraging adults present in the 200 ha nesting area was monitored; also parental activity at ten nests was videotaped during the daytime, using a car black box recording system. Presence in the colony and parental activity were analysed in relation to the tidal cycle, ambient temperature, time of day, and nesting success. Our results indicated that the number of non-foraging adults staying in the nesting area was higher at high tide than at low tide, and the time that parents incubated eggs increased with higher sea level. The observed pattern was more apparent during ebb tide than during flood tide. No association of time of day, ambient temperature, and nesting success was found. We conclude that the parents regulate incubation in response to the exposure time of their foraging areas and possibly the dietary activity of benthic organisms in the mudflats.

Key words: car black box, incubation behaviour, *Larus saundersi*, mudflat, Saunders's Gull, tidal cycle

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Incubation period is one of the key reproductive stages in birds. Egg development is controlled by parental behaviour, which depends on biotic and environmental conditions such as food limitations, climate, predation risk, and phylogenetic relationships (reviewed in Deeming 2002). A comparative study in passerines suggests that (1) environments with low ambient temperatures favour high nest attendance (to maintain the physiological temperature of the eggs) and frequent foraging trips (to acquire energy for the incubating parents); (2) high risks of nest predation lower parental activity at the nests; (3) mate feeding (i.e. providing the incubating partner with food) can reduce rates of the number of trips away from the nest and/or the total time a nest is left unattended (Conway & Martin 2000). Yet, few studies have examined the breeding behaviour of birds in association with the tidal cycle (but see Castro *et al.* 2009, for an example in Charadriiformes).

Particularly, seabirds, including gulls, terns, and shorebirds in the order Charadriiformes, use distinct feeding and nesting sites in and near the intertidal zone. These tidal bird species adjust their behaviour to the spatio-temporal distribution of food resources (*sensu* Reise 1985). Indeed, many species spend more time foraging during favourable tidal conditions, i.e. when the largest area of the intertidal area and mudflats is exposed, for example cormorants (Gandini *et al.* 2005), herons (Matsunaga 2000), gulls (Sibly &

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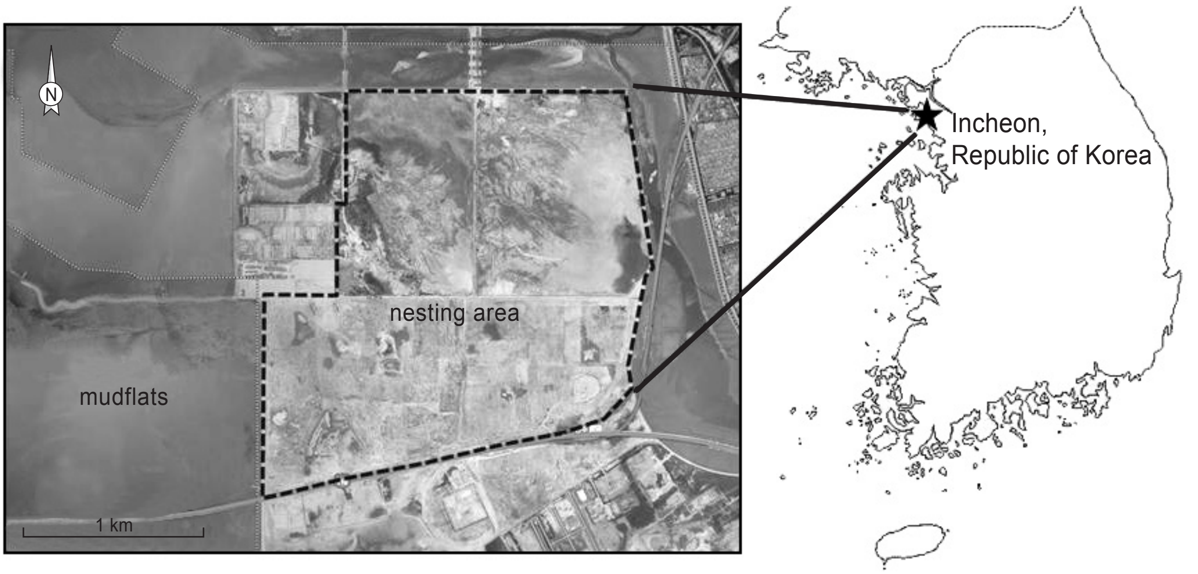

Figure 1. The monitored nesting area of Saunders's Gulls in May 2012 in a reclaimed wetland area that was surrounded by large mudflats in Songdo, Incheon, Republic of Korea.

McCleery 1983, Yorio *et al.* 2004), plovers (Burger *et al.* 1977, Pienkowski 1981, Castro *et al.* 2009), and sandpipers (Goss-Custard *et al.* 1977, Dominguez 2002). This foraging pattern is known to be influenced by the dietary activity of benthic organisms which is higher during low tide (Masson *et al.* 1995, Bradshaw & Scoffin 1999, Gibson 2003). Here, we present a study on tide-related incubation behaviour in the Saunders's Gull *Larus saundersi*, a coastal species, breeding in the intertidal zone.

Saunders's Gulls are biparental; both parents incubate and provide food to their young. They breed in the coastal areas of eastern China, and sporadically on the west coast of South Korea. They winter in the southern coastal areas of the Korean peninsula, Hong Kong, Taiwan, and Japan (IUCN 2012). The species, which belongs to the Charadriiformes, an order with many tidal flat obligates, is globally threatened due to the loss of foraging and nesting habitats (IUCN 2012). We investigated this species in the coastal area of Incheon, Republic of Korea during the breeding season of 2012. The ground colony is situated in a large reclamation area of former wetlands, reclaimed for the purpose of economical development. The gulls breed near mudflats, where they primarily feed on lugworms and crabs, but also on smaller unidentified prey items (H.W. Park, unpubl. data). Because the availability of food is determined by the tidal cycle, the allocation of time during the reproductive phase to the various fitness-related activities, such as incubating eggs, providing post-hatching chicks with food, and defending nests or chicks against predators (and even conspecific adults), is expected to be driven by the tidal cycle. This study examines the degree to which the tide influences the presence of breeding pairs of Saunders's Gulls at the nest. We predict that the trade-off between time spend on incubation and on foraging will vary with the tidal cycle. We will discuss how efficiently the parents allocate time to feed themselves, incubate eggs, and defend nest sites.

METHODS

The nesting site of Saunders's Gulls is currently located in the northern portion (37°24'N, 126°36'E) of a recently reclaimed wetland area and is surrounded by a wide range of mudflats (Figure 1). The area is a part of the Incheon Free Economic Zone in Songdo, Incheon, Republic of Korea. The climate in this region is a transitional type of continental and oceanic climate, with an annual average temperature of 11.7°C, which is warm relative to the central inland region of the Korean peninsula. Recently, this area has received international attention because of habitat loss for breeding seabirds, and waterbirds in general, due to ongoing wetland and tidal flat land reclamation and subsequent urbanization (Park 2003, Kwon & Chung 2009, Park 2010). The global population estimate of the Saunders's Gull reaches 21,000 to 22,000 individuals (e.g. 14,400 mature adults; IUCN 2012). The approximate size of the breeding population in the Republic of Korea

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(2011–2012) was estimated to be 200–300 pairs. Our study colony, with an area of 400 ha, is the only one extant colony that has remained in the Republic of Korea. The proportion of mature individuals in our study area is estimated to be 1.4–2.1% of the global population (Yoon *et al.*, pers. obs.). In our study area (Figure 1), the foraging sites of Saunders's Gulls included mainly non-reclaimed mudflats near the nesting site.

To compare the number of non-foraging adults remaining in the nesting area at the time of minimum and maximum sea levels (hereafter *low tide* and *high tide*), we conducted a 5-min count survey (14 surveys by two observers twice a week from April–May 2012) in a 200 ha area in the southern part of the nesting area (as shown in Figure 1). This southern area has sparse vegetation (e.g. a Reed bed of genus *Phragmites*) which allowed us to detect variation in the number of gulls in relation to tidal conditions. We also monitored the breeding stages of the nests found in this area during April–May 2011 (Yoon *et al.* 2013) and April–May 2012: the average clutch size was 2.8 (n = 78 nests in 2011) and 2.7 (n = 61 nests in 2012) eggs per nest (mode = 3 eggs) at clutch completion, ranging from one to four eggs per nest. In 2011–2012, 64% of all monitored nests had at least one fledgling, as determined by the fledging behaviour of the semi-precocial chicks; nesting failure was mostly (43%) caused by nest predation (e.g. disappeared or broken eggs in the nest) during the incubation period (Yoon *et al.*, in preparation). A preliminary study (Park 2003) reported a list of egg predators, including Black-tailed Gulls *Larus crassirostris*, Grey Herons *Ardea cinerea*, Raccoon Dogs *Nyctereutes procyonoidaes*, feral dogs *Canis domesticus*, feral cats *Felis catus*, weasels *Mustela sibirica*, rats (family Muridae), and snakes (family Colubridae). However, during our study period we did not observe predators or their tracks, except frequent visits of Black-tailed Gulls, that were chased by flocks of adult Saunders's Gulls.

We randomly selected ten nests in the study area in May 2012 (a peak time for incubation) to document incubation behaviour of the Saunders's Gull, using a car black box recording system (P200 Season 2, Provia Inc., Seoul, Republic of Korea). The black box and battery pack were placed near the nests (Figure 2). This device generated a video file (2.0 mega pixel; Audio Video Interleave, AVI, format) with imbedded time stamps at 2-min intervals. This recording method allowed us to observe parental activity at nests for a long period (i.e. continuous recording without gaps between video files for more than 20 hours) with minimal disturbance of the birds. After installing the recording equipment, we made sure that parents had returned and remained at the nests for at least 10 minutes to prevent nest abandonment. The recorded AVI files were

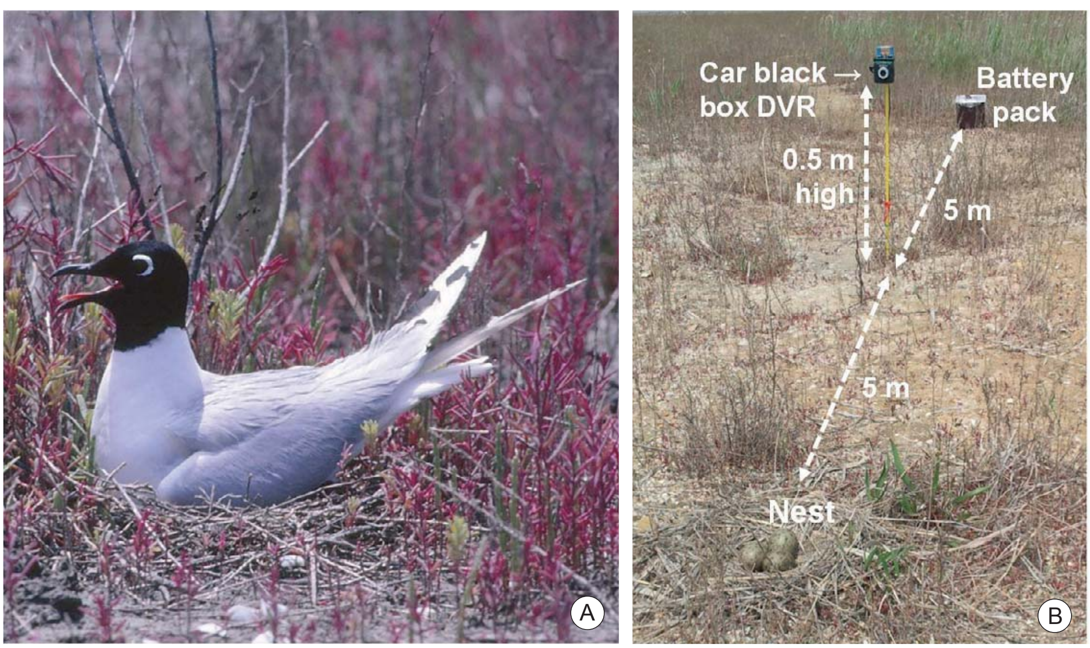

Figure 2. An incubating Saunders's Gull at the nest (A; photograph by Moo-Boo Yoon) and a digital video recording (DVR) system using a commercial car black box with a hand-made battery pack to record daily parental activity at a Saunders's Gull nest during the incubation period (B).

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We defined two response variables, nest attentiveness and hourly trips away from the nest. Nest attentiveness was defined as the percentage of daylight spent on the nest to incubate eggs (*sensu* Kendeigh 1952), and we calculated the percentage in intervals of 90 minutes (i.e. the numbers of minutes at the nest per 90-min session) during the daytime (04:30 to 19:30 KST with visibility). The second variable, hourly trips away from the nest was calculated and rescaled as the number of times the incubating parent went away from the nest per hour at the 90-min interval. The sex of the incubating parent was not verified because we did not mark individuals.

We related the above defined response variables to temporal variation in the tidal cycle, ambient temperature, and nesting success as explanatory variables. We obtained hourly tide- and ambient temperature data for the Incheon region from the tidal and climate forecast services at the Korea Hydrographic and Oceanographic Administration and the Korea Meteorological Administration. We divided the tidal cycle into two periods: *ebb tide* from highest to lowest sea level versus *flood tide* from lowest to highest sea level. Each period was rescaled to the percentage of maximum tide height ranging from 0 to 1 (hereafter *percentage of sea level*) during the same interval of 90 minutes as used for the behavioural data. Nesting success variable (i.e. fledged or depredated) was taken from our nest check data (see above).

The number of non-foraging adults present in a particular nesting area was compared between low and high tide using a two-sample *t*-test. A general linear mixed model was used to predict nest attentiveness (or hourly nest trips) as a function of tide type, percentage of sea level, the two-way interaction (tide type × sea level), time of the day (90-min intervals from 4:30 to 19:30), nesting success, and ambient temperature (°C). In the model, a nest ID was included as a random effect to control for repeated measures of same nests. All statistics were performed in SPSS version 16.0 (SPSS Inc. 2007). We did not need to transform any variables to meet model assumptions. All means are presented with ± 1 SE.

RESULTS

The number of non-foraging Saunders's Gulls staying in the 200 ha nesting site was lower at low tide (217 ± 11 individuals; n = 8 observations) than at high tide (371 ± 42 individuals; n = 6 observations; t-test: $t_{5.8}$ = –3.56, $P < 0.05$). Regarding nest attentiveness, parents incubated eggs at a high rate during the daytime (95.3 ± 0.4%; n = 10 nests; Figure 3A). Nest attentiveness and number of trips away from the nest was not related to time of the day, ambient temperature, and nest success (all $P > 0.10$). Without the three non-significant variables in the model, mean nest attentiveness did not vary with tide type: 96.2 ± 0.8% during the ebb tide period versus 93.7 ± 1.1% during the flood tide period (mixed model: tide type $F_{1,68.0} = 0.01$, $P = 0.94$; sea level $F_{1,68.0} = 5.37$, $P < 0.05$; tide type × sea level $F_{1,68.0} = 0.48$, $P = 0.49$). However, nest attentiveness increased with sea level (slope estimate = 7.8% of daylight time ± 3.2%). In particular, nest attentiveness increased significantly with sea level during the ebb tide period (sea level $F_{1,43.0} = 8.92$, $P < 0.01$) whereas it did not vary significantly with sea level during the flood tide period (sea level $F_{1,18.3} = 0.53$, $P = 0.48$; Figure 3A). Overall, parents made trips away from the nests at a rate of 3.1 ± 0.5 trips per hour during the daytime (n = 10 nests; Figure 3B). Hourly nest trips varied with tidal patterns in a different way than nest attentiveness. Variation in hourly nest trips was only explained by the two-way interaction between tide type and sea level, but was not explained by tide type or sea level independently (mixed model: tide type $F_{1,43.0}$ = 1.15, $P = 0.29$; sea level $F_{1,50.5} = 1.81$, $P = 0.19$; tide type × sea level $F_{1,42.9} = 5.51$, $P < 0.05$). This means that hourly nest trips did not differ by tide type: 4.1 ± 0.6 trips per hour during the ebb tide period versus 6.2 ± 0.6 trips per hour during the flood tide period; it marginally decreased with increasing sea level during the ebb tide period (sea level $F_{1,29.0} = 3.04$, $P = 0.09$), but not during flood tide (sea level $\mathrm{F}_{1,14.8} = 3.09$, $P = 0.10$; Figure 3B).

DISCUSSION

We examined the degree to which the tide influenced the presence of breeding pairs of Saunders's Gulls at the nest. As predicted, parents seemed to spend less time incubating eggs and/or make more foraging trips when the exposed surface of the mudflats allowed them to forage on benthic prey during low tide (i.e. this would mean that during low tide birds would favour more often foraging over incubating). Our results indicated that Saunders's Gulls attended nests to incubate for most of the day (95%), but the small variation in their incubation behaviour was partially explained by the effect of sea level and tide type: more adults on the

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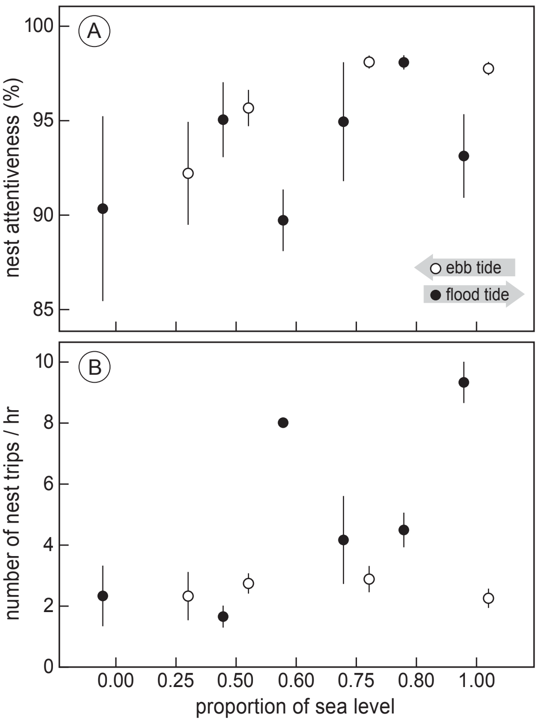

Figure 3. Incubation behaviour of Saunders's Gulls during daytime, in relation to tide type and sea level: (A) nest attentiveness (percentage of time at the nest); (B) hourly trips away from the nest. Grey arrows indicate tidal movement toward lowest or highest sea level (ebb versus flood tide). Proportion of sea level shows height changes in the ocean's surface, ranging from the lowest (0) to highest (1) level. Error bars denote ± 1 SE.

nesting ground during high tide and increasing nest attentiveness with increasing sea level. This incubation pattern is congruent with foraging behaviour of other seabirds breeding near the intertidal areas and mudflats (Matsunaga 2000, Dominguez 2002, Yorio *et al.* 2004, Gandini *et al.* 2005).

The patterns of tide-related incubation behaviour in Saunders's Gulls appeared to be most strongly related to changing sea level during ebb tide. The foraging activity in other seabirds also tends to be more related with the progress of ebb tide compared to that of flood tide (Matsunaga 2000, Gandini *et al.* 2005). The foraging activity of some intertidal benthic organisms that are prey items for seabirds may be higher during the ebb tide period than during the flood tide period. This would mean that the foraging time of intertidal benthic prey species and avian foragers is synchronized. However, other benthic organisms may hide deeper in the mud during low tide to survive from seabirds. The major prey items of Saunders's Gulls are lugworms and crabs (Park 2003). Feeding activity of polychaetes, including lugworms, decreases during low tide because the physical and chemical conditions (e.g. high temperature, high desiccation, and low oxygen content) of the mud flat sediments during this tidal period can cause mortality or migration of polychaetes (Masson *et al.* 1995). Additionally, Soldier Crabs *Dotilla myctiroides* favour the period of ebb tide for feeding, managing burrows, and mating, resulting in higher activity during the shorter time of tidal exposure of the sand flats (Bradshaw & Scoffin 1999). Thus, the ebb tide period may provide favourable conditions for foraging not only by benthic organisms but also by seabirds in the intertidal areas and mudflats, suggesting a reduced rate of incubation in seabirds nesting near those areas.

Few studies have examined habitat use and sex roles while providing parental care in the family Laridae, which generally exhibits biparental care (Fasola & Saino 1995, Stenhouse *et al.* 2004, Watson *et al.* 2012). In Kentish Plovers *Charadrius alexandrinus* during the breeding season, both sexes concentrate their feeding activity during the peak hours of low tide, but the sexes allocate different amounts of time to foraging (i.e. 2 hours less in females than in males; Castro *et al.* 2009). Although we did not quantify sex differences in incubation behaviour of Saunders's Gulls, males and females may take turns in incubating eggs and foraging. Since the nests are sometimes unattended during high tide, we cannot exclude the possibility that both parents visit alternative feeding areas such as inland freshwater near the nest (see Park 2003). In this study, we conclude that Saunders's gull parents regulate incubation in response to the exposure time of their foraging areas and possibly the feeding activity of benthic organisms in the mudflats. To understand the foraging and breeding ecology of the species in a better resolution, future studies should monitor individually marked breeding birds, to relate nest attendance and foraging to the relative use of different habitats, and to assess the role of sex in parental care throughout the tidal cycle. This might also help plan any future conservation acts on the habitat management for this endangered species.

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SAMENVATTING

Er zijn verschillende factoren die de variatie in ouderlijk gedrag van broedvogels kunnen beïnvloeden, zoals voedsel, klimaat, nestpredatie en fylogenetische verwantschap. Er zijn betrekkelijk weinig studies verricht naar de invloed van het getij op het broedgedrag van zee- en kustvogels. In een getijdengebied kunnen vogels niet altijd en overal foerageren. De verwachting is dan ook dat deze beperking van invloed is op het broedgedrag. De auteurs bestudeerden in een waddengebied nabij Incheon, Zuid-Korea, in hoeverre het getij van invloed is op het broedgedrag van de bedreigde Saunders' Meeuw (ook wel Chinese Kokmeeuw genoemd) *Larus saundersi*. De Saunders' Meeuwen in deze enige overgebleven kolonie in Zuid-Korea nestelen op ingepolderde delen van het wad en foerageren op de omliggende wadplaten. In 2012 werd in het broedareaal van 200 ha op 14 afzonderlijke dagen elke vijf minuten het aantal aanwezige volwassen vogels geteld. Daarnaast werd bij tien nesten de aanwezigheid en de activiteit van de oudervogels vastgelegd met een digitaal videosysteem. Het aantal aanwezige vogels in de kolonie en het gedrag bij het nest werden geanalyseerd in relatie tot getij, temperatuur, tijd van de dag en uiteindelijk broedsucces (wel of geen uitgevlogen jongen). Uit de resultaten blijkt dat er tijdens hoogwater meer meeuwen in de kolonie aanwezig waren dan tijdens laagwater. De tijd die de ouders aan het bebroeden van de eieren besteedden, nam toe met de waterhoogte. Bij afgaand getij werd bij eenzelfde waterhoogte door meer vogels gebroed dan met opkomend getij. Er werd geen relatie met temperatuur, tijd van de dag en broedsucces gevonden. De auteurs concluderen dat de vogels de tijd dat zij de eieren bebroeden, afstemmen op het droogvallen van de foerageergebieden. De sterkere reactie op waterhoogte met afgaand tij is mogelijk een aanpassing aan de activiteitspatronen van de bodemdieren in het wad (moeilijker te vangen dan met opkomend getij). (YIV)

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