AT-COLONY BEHAVIOUR OF GREAT BLACK-BACKED GULLS LARUS MARINUS FOLLOWING BREEDING FAILURE

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ABSTRACT

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Territoriality for breeding sites comes at an energetic cost—individuals actively defend the site from competitors and potential predators, thus precluding themselves from self-maintenance (e.g., foraging, preening) or offspring care. Breeding individuals are also constrained to centralplace foraging within a limited range of the territory. For these reasons, many seabirds do not spend extensive periods or make regular visits to the colony following breeding failure. To investigate behaviour following breeding failure, we studied colony and nest attendance and daily number of visits for six Great Black-backed Gulls *Larus marinus* that had failed to breed following global positioning system (GPS) tag attachment on the northeast coast of Newfoundland, Canada. Three failed breeders reduced colony and nest attendance by an average 6.32 h/d (95% confidence interval: 1.14) after the estimated date of failure. Conversely, three other failed breeders showed no decrease in attendance, and one individual increased colony attendance by 5.4 h/d. We predicted that failed breeders would be more likely to forage while attending the colony relative to active breeders (i.e., incubating or chick-rearing) due to their lack of offspring and territory to defend. During 18 two-hour nest watches of active and failed breeders, active breeders (n = 4) behaved more aggressively (e.g., predation, swooping) toward gulls at nearby sites in the colony, while failed breeders (n = 6) behaved mostly passively (e.g., maintaining breeding territory and pair bonding). Our findings also reveal that using tracking data to indicate breeding failure may be misleading and, thus, we suggest researchers also use visual confirmation of breeding failure, when possible, in future studies. Finally, we warn researchers of the negative effects of tag attachment on gull reproductive success.

Key words: breeding failure, tag effect, gulls, breeding behaviour

RÉSUMÉ

La protection d'un territoire de reproduction vient avec des coûts énergétiques, où les individus doivent défendre activement le site contre des compétiteurs et des prédateurs. Durant la défense, ils ne peuvent s'investir dans le soin d'eux-mêmes (e.g., alimentation, lissage) ou de leurs poussins. Les individus reproducteurs sont aussi restreints à l'intérieur d'une distance maximale de leur territoire lors des déplacements alimentaires (lieu central d'alimentation). Ainsi, plusieurs espèces d'oiseaux marins ne continuent pas de visiter régulièrement ou rester longtemps sur la colonie après un échec reproducteur. Nous avons étudié le comportement et la fréquence de visite de la colonie et du nid chez six goélands marins (Larus marinus) suivant le déploiement d'appareils de suivi par système mondial de positionnement (GPS) et un échec reproducteur sur la côte nord-est de Terre-Neuve, Canada. Trois des individus ont réduit la durée des visites à la colonie et au nid de 6.32 h/j en moyenne (Intervalle de confiance 95%: 1.14) à la suite de l'échec reproductif. À l'opposé, trois autres individus n'ont montré aucune réduction en durée et fréquence des visites après la date estimée d'échec et un individu a même augmenté la durée des visites à la colonie de 5.4 h/j. Nous avons prédit que les goélands avec un échec reproductif auront plus tendance à s'alimentater durant leur visites à la colonie que les goélands reproducteurs puisqu'ils n'ont pas de poussins à protéger. Durant 18 suivis des nids de 2 heures, les reproducteurs (n = 4) étaient plus agressifs (e.g., prédation, descente en piqué) vers d'autres goélands des sites voisins, alors que les goélands avec échec (n = 6) étaient plus passifs (e.g., lissage des plumes, position assise, P = 0.029). Les résultats indiquent que certains individus avec échec reproducteurs continuent de visiter la colonie, ce qui indique la présence de bénéfices (e.g., maintien du territoire de reproduction ou renforcement des liens du couple), mais aussi que les données de suivi télémétriques (i.e., taux de visites au nid ou colonie) ne sont pas toujours assez fiables pour déterminer le statut reproducteur et nous suggérons aux études futures de confirmer visuellement l'échec reproductif. Enfin, nous prévenons les chercheurs sur les effets négatifs sur la reproduction des goélands par la pose d'appareil de suivis.

Mots clés: échec reproductive, effet de déploiement, goéland, comportement de reproduction

INTRODUCTION

Breeding site territoriality comes at an energetic cost. Individuals must actively defend the breeding site from competitors and potential predators (Hinde 1956) but at the same time cannot engage in self-maintenance (e.g., foraging, preening) or offspring protection. Additionally, breeding site territoriality results in individuals being spatially limited to forage near the nest site (Orians & Pearson 1979, Krebs 2002). For most seabirds (perhaps not so much gulls; see below), the breeding season is the only time within the annual cycle when breeding adults must return to land (Gill 2006). Evolved for a life at sea, time on land can increase

their vulnerability to predators (Burger & Schreiber 2001), as well as the energetic costs of traveling to suitable foraging grounds not necessarily situated near the colony (Danchin *et al.* 2012). Although competition for nesting grounds (Kokko *et al.* 2004) and pairbonding (Stacey 1982, Spoon *et al.* 2006, Kenny *et al.* 2017) might encourage a non-breeding seabird to visit a colony, seabirds tend to reduce the frequency of visits to the colony (or land; Cubaynes *et al.* 2011, Kazama *et al.* 2013) following breeding failure (Calladine & Harris 1997).

Unlike many seabirds, most Larids (e.g., gulls and terns) frequent land for foraging (Isaksson et al. 2016) and roosting (Schreiber 1967, Shamoun-Baranes et al. 2011), as well as breeding (Burger & Schreiber 2001). For these reasons, in the case of gulls, they may be more inclined to visit their colony even after breeding failure or during non-reproductive years than other seabird species. In fact, as a function of coloniality, the colony may become a foraging site whereby gulls depredate the chicks and eggs of other nearby seabird nests (Davis & Dunn 1976, Bukacinska et al. 1996). This behaviour is common among large gulls, including the Great Black-backed Gull Larus marinus (Stenhouse & Montevecchi 1999, Veitch et al. 2016), the largest North American gull. Like other large gulls, Great Black-backed Gulls claim territories large enough (~4-7 m spacing between nests) for their chicks to move around after 5-7 days of age and have places to hide (Good 2020). This species of gull often feeds at a higher trophic level than other gulls (Maynard & Davoren 2020), with some individuals specializing on a diet of seabird eggs or chicks (Stenhouse & Montevecchi 1999, Veitch et al. 2016). This predatory behaviour sometimes leads to lethal control or nest destruction at colonies overseen by wildlife managers (Scopel & Diamond 2017).

Following the failure of several nests targeted for tracking movements of breeding Great Black-backed Gulls, we took the opportunity to describe and compare at-colony behaviour of these failed breeders with actively incubating or chick-rearing pairs. Using tracking data, we first described colony and nest attendance of failed breeders and identified breaks (i.e., sudden changes) in daily attendance to determine the potential date of nest failure. Using nest watches, we compared behaviour of both active and failed breeders while at the colony. We hypothesized that behaviour at the nest site and colony would differ between failed and active breeders. As Great Blackbacked Gulls are known predators of seabird chicks and eggs, and failed breeders do not have offspring to protect, we predicted that failed breeders would be more likely to forage while attending the colony. We also predicted that failed breeders would exhibit more aggressive behaviour than successful breeders, including predation attempts toward gull eggs and chicks at nearby nest sites. This study informs our understanding of at-colony behaviour of gulls post-breeding failure and questions the reliability of determining breeding status using only tracking or colony attendance data.

METHODS

Study area and field work

During 2018, adult Great Black-backed Gulls were captured during incubation (n = 7, 10–11 June) and chick-rearing (n = 1, 08 July) from different nests on North Cabot Island (49°10'30.67"N, 053°21'57.57"W) on the northeast coast of Newfoundland, Canada. North Cabot Island is a small island of about 0.09 km² that supports ~10 pairs of Great Black-backed Gulls, ~100 pairs of Herring Gulls *Larus argentatus*, and a few pairs of Black Guillemot *Cepphus*

grylle (Wilhelm et al. 2015). This is the expected number of pairs for the island, and the expected ratio of Great Black-backed Gulls to Herring Gulls given the more solitary and loose coloniality of Great Black-backed Gulls (Butler & Trivelpiece 1981, Butler & Janes-Butler 1982, Good 2020). Upon capture using drop traps, gulls were fitted with a uniquely coded colour band easily readable with binoculars. Bill depth at gonys, and total head length, were recorded to allow sexing of each individual following Mawhinney & Diamond (1999). As part of a different study (Maynard et al. 2021), solar-paneled Global Positioning System (GPS) loggers (Ecotone® HARRIER-M, Ecotone Telemetry, Gdynia, Poland; ~20 g) were deployed using a leg-loop harness made of 6.5 mm Teflon tape (Mallory & Gilbert 2008). Devices weighed between 0.8%-1.3% of body mass and recorded latitude and longitude (± 18 m) at 15 min intervals. Data from tags were remotely downloaded upon return of each gull to the island via ultra-high frequency (UHF) to a base station located in the center of the colony. The coordinates and breeding status of nests of tagged individuals were recorded on the last day of the first colony visit (10–11 June) as well as on the first day of subsequent colony visits (05-09 July, 21-25 July).

To monitor the breeding performance and parental behaviour at nest sites, we performed two-hour nest watches on each day of the second and third colony visits during the morning (08h00-12h00 Newfoundland Daylight Time, NDT) and afternoon (13h00-18h00 NDT) of both members of all pairs of Great Black-backed Gulls on the island (n = 10 pairs), including nest sites of tagged individuals (total number of two-hour nest watches = 18). When possible, we confirmed the identity of each individual by the presence of a colour-band and/or GPS logger. During nest watches, the colony was scanned every 10 min. During scans, we recorded the status of each Great Black-backed Gull nest site (i.e., chick-rearing, failed). Additionally, we recorded the behaviour of solitary parents or pairs on first sight at each nest or within ~ 20 m of nest sites (i.e., instantaneous scan sample; Martin & Bateson 2007). Behaviour categories recorded for each solitary individual or individual of a pair included: aggressive behaviour towards another gull (i.e., swooping, chasing, predation events), social behaviour (i.e., preening other individuals, gathering nest material, courtship), passive behaviour (i.e., sitting, self-preening, standing), and active behaviour (i.e., walking, flying).

All procedures performed in studies involving animals were in accordance with the ethical standards of the University of Manitoba (F16-017/1/2). A master banding permit was issued to Gail Davoren (10873).

Data analysis

We used the GPS tracking data to quantify daily time spent within the gull colony and at the nest site by failed and active breeders during the breeding season. GPS locations were first quantified as either on or off the breeding island and on or off the nesting site (within 20 m of nest; logger coordinate error \pm 18 m; nest coordinate error \pm 2 m) using the *intersect* function in QGIS (QGIS Development Team 2021). This allowed us to calculate h/d each tracked gull spent within the gull colony on the island (colony attendance) as well as within 20 m of the nest (nest attendance). To identify the date of nest failure, we detected breakpoints (i.e., abrupt changes in attendance; Ponchon *et al.* 2017) in colony and nest attendances for each tagged individual using the package "strucchange" in R (Zeileis *et al.* 2002). We also calculated the number of colony and nest site visits per day during the breeding season. When a breakpoint was identified, we compared mean attendance and number of visits before and after the breakpoint. We considered a significant difference between means if 95% confidence intervals did not overlap. We did not compare attendance and visits per day between failed and active breeders given the small sample size of active breeders (n = 2), but we used these metrics to compare with other studies.

Using data from the nest watches, we used a *t*-test to compare the number of individuals per pair present at nest sites between failed and active breeders. To evaluate whether nest site behaviour differed with breeding status, we summed the number of times an individual exhibited a behaviour in each of the four behavioural categories (i.e., aggressive, social, passive, active) at each nest site as the four response variables and conducted a MANOVA, where the predictor variables were breeding status and nest ID. When a predictor was significant, we used univariate ANOVAs to determine the contribution of predictors to each of the four response variables. All analyses were performed in R version 3.6.0 (R Core Development Team 2021). Results are presented as mean \pm confidence interval.

RESULTS

GPS loggers were deployed on six male (LMG01–LMG05; LMG08) and two female Great Black-backed Gulls (LMG06, LMG07) from independent pairs. Loggers recorded data for 6–66 d during the period 10 June–15 August. Nest fate was determined on 05 July, the first day of the second colony visit, indicating that nest failure had occurred for six of the initial seven tracked individuals between 08 June and 05 July (Table 1). The tracked individual with a successful nest had two chicks on 05 July but had lost its GPS logger after 10 days (LMG07). The GPS logger deployed on 08 July (LMG02) was lost after five days during which the nest site had two chicks (Fig. 1). Therefore, GPS loggers from breeding individuals (i.e., LMG02, LMG07) recorded for 6–13 d and from failed breeders for 14–66 d (Table 1). Additionally, we observed two untagged, undisturbed pairs of Great Black-backed Gulls during nest watches that successfully raised four chicks in total.

We identified breakpoints in colony attendance for four failed breeders (LMG04, LMG05, LMG06, LMG08; Fig. 1A, Table 1). LMG05 also had a sudden decline in colony and nest attendance after 20 June (Fig. 1), but it was not identified as a breakpoint in the model; colony attendance and number of visits were higher after the identified breakpoint than before (Table 1, Fig. 1). For the other three individuals (LMG04, LMG06, LMG08), colony attendance and visits were significantly lower after the breakpoint date than before (mean difference 6.8 ± 1.7 h/d; Table 1, Fig. 1). For nest attendance, two breakpoints were identified for LMG04 and LMG06 (Fig. 1) at the same date as colony attendance (Table 1). For both birds, nest attendance (mean difference 5.65 ± 0.76 h/d) and number of visits to nest (mean difference: 1.25 ± 0.21 visits/d) were significantly lower after the date of breakpoint than before (Table 1). In particular, LMG08 spent < 5 h/d at the nest throughout the study period, generally had the lowest mean colony and nest attendance relative to other birds and was observed a few times ~35 m west of its original nest site during the nest watches.

We completed 18 two-hour nest watches for a total of 36 h on all 10 Great Black-backed Gull nests on the study island. Based on these nest watches, the number of individuals per pair remaining at and nearby their nest sites did not differ between failed (1.0 ± 0.1 individuals) and active breeders (1.1 ± 0.1 individuals; $t_{155} = 1.47$, P = 0.14). A MANOVA revealed that active and failed breeders exhibited different behaviour when present at the colony ($F_{4,158} = 2.76$, P = 0.029). Active breeders were slightly more active (i.e., flying, walking; 0.42 ± 0.17 events/watch) than failed breeders (0.26 ± 0.15 events/watch; Fig. 2), but this was not significant (ANOVA: $F_{1,158} = 1.8$, P = 0.18). Observations of aggressive behaviours differed between active and failed breeders (ANOVA: $F_{1,158} = 7.43$, P = 0.007), whereby failed breeders did not exhibit

 TABLE 1

 Mean and breakpoint date in colony and nest attendance and visits per day for eight tagged Great Black-backed Gulls Larus marinus

Individual	Breeding status	Colony ^a						Nest ^a						
		BP date ^b	Attendance ± CI (h/d)		No. visits/d ± CI		%	BP	Attendance ± CI (h/d)		No. visits/d ± CI		%	No. tracking
			Before BP	After BP	Before BP	After BP	days ^c	date ^b	Before BP	After BP	Before BP	After BP	days ^c	days
LMG02 ^d	Chicks	-	12.3 ± 3.6		3.7 ± 1.3		100	-	9.0 ± 3.9		3.2 ± 1.4		100	6
LMG07	Chicks	-	15.4 ± 2.5		5.0 ± 1.2		100	-	13.3 ± 2.3		4.4 ± 1.3		100	13
LMG01	Failed	No BP	11.2 ± 1.46		2.9 ± 0.5		93.8	No BP	9.5 ± 1.3		2.4 ± 0.4		92.2	64
LMG03	Failed	No BP	16.8 ± 2.5		4.0 ± 1.2		100	No BP	13.27 ± 2.7		3.4 ± 0.9		100	14
LMG04	Failed	04 Jul	16.7 ± 1.7	12.0 ± 2.2	3.6 ± 0.5	3.3 ± 0.7	93.9	03 Jul	13.5 ± 2.0	8.4 ± 2.2	3.4 ± 0.5	2.3 ± 0.4	92.4	66
LMG05	Failed	03 Jul	12.6 ± 3.6	18.0 ± 1.4	2.5 ± 0.9	5.2 ± 0.7	90.9	No BP	12.6	± 1.5	3.7 ±	± 0.5	90.9	66
LMG06	Failed	17 Jun	12.4 ± 3.7	4.1 ± 1.4	4.3 ± 1.0	2.5 ± 0.4	86.2	17 Jun	9.1 ± 2.8	2.9 ± 1.2	3.6 ± 0.7	2.2 ± 0.4	75.9	58
LMG08	Failed	17 Jun	11.0 ± 3.3	3.3 ± 1.6	3.0 ± 0.9	1.4 ± 0.3	40.0	No BP	1.0 ± 0.8 1.3 ± 0.3		20	60		

^a Abbreviations: BP = breakpoint; CI = confidence interval.

^b 'No BP' indicates that a break point could not be detected. Bold font indicates significant differences in means before and after the breakpoint.

^c Percent tracking days (% days) indicates number of days with at least one colony or nest visit over the number of tracking days.

^d Captured during chick-rearing on 08 July.

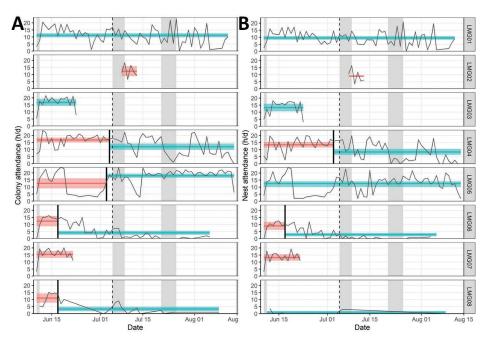


Fig. 1. Daily colony (A) and nest (B) attendance by tagged individual Great Black-backed Gulls *Larus marinus* (red: active breeders, blue: failed breeders) between 10 June 2018 and 15 August 2018 on North Cabot Island, Newfoundland, Canada. Solid vertical lines indicate identified breakpoints in attendance whereas coloured horizontal lines indicate mean attendance with 95% confidence intervals (shading). The dashed line represents the date when breeding failure was confirmed. The grey areas represent colony visits by researchers.

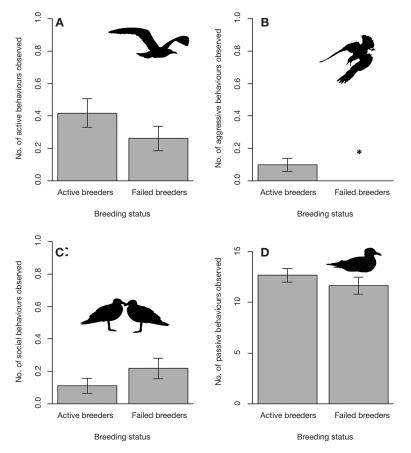


Fig. 2. Number of active (A), aggressive (B), social (C), and passive (D) behaviours in active (n = 4) compared to failed (n = 6) breeding Great Black-backed Gulls *Larus marinus* observed during 18 two-hour nest watches on North Cabot Island, Newfoundland, Canada. Note that the y-axis is different for (D) passive behaviour. Asterisk indicates a significant difference between active and failed breeders.

aggressive behaviour (0 \pm 0 events/watch) while active breeders exhibited aggressive behaviour toward other gulls (0.09 \pm 0.07 events/watch; Fig. 2), including one predation event on a Herring Gull chick. Observations of social behaviour (i.e., preening, gathering nest material; ANOVA: $F_{1,158} = 1.66$, P = 0.19) and passive behaviour (ANOVA: $F_{1,158} = 0.82$, P = 0.37) did not differ between active breeders (social: 0.11 \pm 0.09 events/watch, passive: 12.68 \pm 1.29 events/watch) and failed breeders (social: 0.22 \pm 0.12 events/watch, passive: 11.66 \pm 1.67 events/watch; Fig. 2).

DISCUSSION

Failed breeders continuously visited the colony throughout the breeding season. Visits to the colony, however, were not limited to nest sites. Half of the failed breeders showed lower attendance and visits after the estimated nest failure date (date of breakpoint), but three individuals showed either an absence of breakpoint or an increase in attendance after the breakpoint. Failed breeders also exhibited mostly passive, social behaviours with few interactions with other gull adults or chicks relative to active breeders. Additionally, the high breeding failure of tagged individuals (n = 6) relative to undisturbed breeding pairs (n = 2) or tagged individuals who were able to quickly remove their loggers (n = 2)raised the possibility that tagging may impact breeding success, as suggested previously (Maynard & Davoren 2018, Maynard & Ronconi 2018); therefore, tagging effects should be considered in future studies. Overall, our results indicate that failed breeders may benefit from continuing to visit the colony (e.g., known roosting sites, maintaining breeding territory) and the nest site after a failed breeding attempt.

Attendance and at-colony behaviour

All failed breeders that were tracked continuously visited the colony throughout the breeding season. Visiting the colony after breeding failure has previously been observed for Great Black-backed Gulls in the western North Atlantic but was often followed by multi-day foraging trips outside the foraging range of the colony (Maynard & Davoren 2018, Maynard & Ronconi 2018). Continued and high daily nest and colony attendance is somewhat surprising because we expected lower attendance and/or visit rates to the nesting territory as seen in failed or sabbatical breeders in other seabird studies (Kazama et al. 2013, Ponchon et al. 2015). For instance, Bukacinska et al. (1996) found that failed breeders of Herring Gulls travelled away from the colony more frequently and for longer periods relative to successful pairs. Another study at a nearby colony in Newfoundland found that tagged Great Black-backed Gulls that failed to breed exhibited prolonged absences from the colony and multi-day, long distance foraging trips south (up to 2 300 km). However, these trips occurred several weeks following breeding failure and coincided with prey hotspots in southeastern Newfoundland (Maynard & Davoren 2018). Birds, however, may benefit from foraging within a restricted range around the colony despite a lack of breeding due to increased familiarity with the area, leading to reduced chances of nest failure in future years (Calladine & Harris 1997). Indeed, larids can increase spatial knowledge of prey resources by staying within range of the colony during non-breeding periods (Irons 1998, Bijleveld et al. 2010, Kazama et al. 2013). Alternatively, high colony attendance might prevent other gulls from taking over an established nesting site from the pair (Ainley & Boekelheide 1990, Kokko et al. 2004). Overall, the duration and frequency of visits to the colony after breeding failure may be influenced by competition for nesting sites and favorable local foraging conditions, which may vary from year to year or across space. Depending on the foraging opportunities in the region, tracking data could thus be a weak indicator of breeding failure in some years but a stronger indicator in other years.

Half of the failed breeders showed lower attendance and visits after the estimated nest failure date (date of breakpoint), but three individuals showed either the absence of a breakpoint or increase in attendance after the breakpoint. In our study, most of the failed breeders spent a substantial amount of time at the colony (15%-80% of their day) and at their nest site (15%-45%) even after the date of breakpoint, which contradicts findings of some other seabird studies (Bukacinska et al. 1996, Zangmeister et al. 2009, Ponchon et al. 2017). Nest attendance of failed breeders, however, varied on a day-to-day basis during the summer season, with some individuals spending < 5 h/d at the nest site; we expected that active breeders would have attended the nest for 30%-60% of the day (about 8–14 h/d). This consistent occurrence of low nest attendance might indicate a failure to breed (Bukacinska et al. 1996, Ponchon et al. 2017). A breakpoint in colony attendance paired with lower attendance after the date of breakpoint could indicate the date of failure (Ponchon et al. 2017). Interestingly, breakpoints detected for LMG04 and LMG05 were 03-04 July, which coincided with our second colony visit (05–09 July) when we visually confirmed breeding failure. Additionally, although we confirmed breeding failure, LMG05 attended the colony longer after the breakpoint than prior. Although it is possible that these breakpoints indicate the dates of nest failure, they may also indicate a change in attendance related to additional stress from our presence at the colony, as observed in other studies (Hunt 1972, Frid & Dill 2002). Two other failed breeders (LMG01 and LMG03) showed no change in attendance patterns throughout the tracking period that were indicative of date of failure. The lack of a breakpoint for LMG03 could be due to the limited tracking period (~14 d of tracking, 10-23 June), but LMG01 was tracked for ~8 weeks and consistently spent around 65% of its day at the colony and 30% at the nest with no indication of failure except for visual confirmation on the first day of our second colony visit.. Therefore, although colony and/or nest attendance could be used as indicators of breeding failure, high attendance after failure was observed in several failed breeders, and visual monitoring of breeding status was necessary to confirm failure for these birds.

We did not find evidence that failed breeders use the colony as a foraging site, indicating that other reasons such as nesting competition or pair bonding might be the reasons for the visits. Because large gulls are known to depredate the offspring of other gulls (Bukacinska et al. 1996), and the study colony is also a Herring Gull colony (Wilhelm et al. 2015), the presence of failed Great Black-backed Gulls at the colony throughout the season was hypothesized to be related to foraging opportunities. Aggressive behaviour towards other adult gulls and attempts to depredate eggs and chicks, however, were only exhibited by actively breeding Great Black-backed Gulls. Therefore, we suggest that foraging is unlikely the primary reason for continued colony presence of failed breeders. Instead, failed breeders exhibited passive behaviour while at the colony, whereby individuals mostly sat and preened near their respective nesting territory, sometimes with a mate. These observations match previous reports of colony visits of failed Great Black-backed Gulls, whereby 45% of the time at the colony was spent roosting (Maynard & Davoren 2018). Failed breeders also exhibited as much social behaviour (i.e., calling, gathering nesting material, allopreening) as active breeders. Social behaviours tighten the bond between mates and the nesting ground, and further increase the chances of success in future breeding attempts (Stacey 1982, Spoon et al. 2006, Kenny et al. 2017). Continuous visits may also prevent other gulls from establishing nesting territory in close proximity (Butler & Trivelpiece 1981, Butler & Janes-Butler 1982, Kokko et al. 2004), therefore maintaining the nesting territory for future years. In this regard, Black-legged Kittiwakes Rissa tridactyla visit their colony after breeding failure to prospect for new nesting sites for future reproductive years (Ponchon et al. 2017). Failed breeders may also use the colony as a roosting site, whereby the presence of other gulls can reduce their risk of depredation by other species, such as Bald Eagles Haliaeetus leucocephalus (Dominguez et al. 2003) or terrestrial predators. Thus, our results suggest that continuous presence at the nesting colony reflects territoriality and social behaviour that may increase future chances of survival and higher reproductive output.

Potential causes of breeding failure

During our tracking study, we tagged eight Great Black-backed Gulls from different nesting pairs, six of which resulted in nesting failures. Tracked gulls that raised chicks successfully either lost or removed their loggers within 11 d. While we observed the predation of one nest shortly after tag deployment while the nest was left unattended, all other tagged individuals still had eggs on the last day of tag deployment, and birds were observed returning to the nest shortly following tag deployment. Recent tracking studies of Great Black-backed Gulls in Atlantic Canada (but led by different field teams) have also shown high nest failure of tagged birds (Maynard & Ronconi 2018, Maynard & Davoren 2018). In contrast, several studies that involve capturing individuals without tagging do not report breeding failure (Butler & Trivelpiece 1981, Helberg et al. 2005). Therefore, device attachment may be the primary factor influencing breeding success. Tagging in this study, however, followed a similar protocol to other Great Black-backed Gull (Borrmann et al. 2019) and larid studies (Thaxter et al. 2014, Shlepr et al. 2021) in which breeding success/failure was not reported. Other factors might also have increased the chances of breeding failure in tagged gulls, such as a later hatching date which is known to reduce probability of success (Spear & Nur 1994), low breeding experience (Brown et al. 1997), and human disturbance (Hunt 1972, Frid & Dill 2002, Krüger 2002). Gulls in this study could also have inferior dominance and/or were unexperienced breeders, causing them to be more likely to fail in their breeding attempts (Calladine & Harris 1997). The breeding colony also has nesting Herring Gulls (Wilhelm et al. 2015), the presence of which can negatively affect breeding success through increasing inter- and intraspecific interference (Butler & Trivelpiece 1981). Although the breeding failure in our study was likely related to the presence of tracking devices, the gulls targeted in our study might also have been susceptible to breeding failure due to some of the aforementioned factors. We caution against tracking Great Black-backed Gulls and other larids without careful consideration of the potential negative reproductive consequences of using tracking devices. We invite future studies to assess capture and device attachment methods for Great Black-backed Gulls to reduce tag effects for this and other seabird species.

CONCLUSIONS

Our findings indicate high colony and nest attendance (i.e., elevated hours/day and number of visits) of Great Black-backed Gulls after

breeding failure compared with other seabird studies. Therefore, we caution that tracking data alone might not be reliable for monitoring breeding status or identifying the date of failure in Great Blackbacked Gulls, as some individuals exhibit no changes in behaviour following nest failure when measured by this method. We also showed that the presence of failed breeders at the colony is likely not related to foraging opportunities at the colony, but rather to increased pair-bonding with mates and defense of nesting sites, or reduced predation risk by roosting at a known safe location. The continuous presence of failed breeders near their nesting sites in our study also suggests that destruction of gull nests, a common management practice used to protect other seabirds (such as alcids and terns) from gull predation (Scopel & Diamond 2017), may not effectively reduce predation. Exploring tag effects on Great Black-backed Gulls that would otherwise be targeted for nest destruction would provide an opportunity to better understand the causes of breeding failure associated with tagging, and it would provide increased knowledge of gull foraging behaviour and nest site attendance. Given the negative tag effects demonstrated in our study, future tracking research on this species should be carefully considered to balance the value of these data relative to possible negative population-level impacts.

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REFERENCES

- AINLEY, D.G. & BOEKELHEIDE R. J. 1990. Seabirds of the Farallon Islands: Ecology, Structure and Dynamics of an Upwelling System Community. Palo Alto, USA: Stanford University Press.
- BIJLEVELD, A.I., EGAS, M., VAN GILS, J.A. & PIERSMA, T. 2010. Beyond the information centre hypothesis: Communal roosting for information on food, predators, travel companions and mates? *Oikos* 119: 277–285. doi:10.1111/j.1600-0706.2009.17892.x
- BORRMANN, R.M., PHILLIPS, R.A., CLAY, T.A. & GARTHE, S. 2019. High foraging site fidelity and spatial segregation among individual Great Black-backed Gulls. *Journal of Avian Biology* 50: jav.02156. doi:10.1111/jav.02156
- BROWN, J.L., BROWN, E.R., SEDRANSK, J. & RITTER, S. 1997. Dominance, age, and reproductive success in a complex society: A long-term study of the Mexican Jay. *The Auk* 114: 279–286. doi:10.2307/4089168
- BUKACINSKA, M., BUKACINSKI, D. & SPAANS, A. 1996. Attendance and diet in relation to breeding success in Herring Gulls (*Larus argentatus*). *The Auk* 113: 300–309. doi:10.2307/4088896

- BURGER, J. & SCHREIBER, E.A. (Eds.) 2001. Biology of Marine Birds. Boca Raton, USA: CRC Press. doi:10.1201/9781420036305
- BUTLER, R.G. & JANES-BUTLER, S. 1982. Territoriality and behavioral correlates of reproductive success of Great Blackbacked Gulls. *The Auk* 99: 58–66. doi:10.2307/4086021
- BUTLER, R.G. & TRIVELPIECE, W. 1981. Nest spacing, reproductive success, and behavior of the Great Black-Backed Gull (*Larus marinus*). *The Auk* 98: 99–107.
- CALLADINE, J. & HARRIS, M.P. 1997. Intermittent breeding in the Herring Gull *Larus argentatus* and the Lesser Blackbacked Gull *Larus fuscus*. *Ibis* 139: 259–263. doi:10.1111/ j.1474-919X.1997.tb04623.x
- CUBAYNES, S., DOHERTY, P.F., SCHREIBER, E.A. & GIMENEZ, O. 2011. To breed or not to breed: A seabird's response to extreme climatic events. *Biology Letters* 7: 303–306. doi:10.1098/rsbl.2010.0778
- DANCHIN, É., GIRALDEAU, L.-A. & CÉZILLY, F. 2012. *Écologie Comportementale*. Paris, France: Dunod.
- DAVIS, J.W.F. & DUNN, E.K. 1976. Intraspecific predation and colonial breeding in Lesser Black-backed Gulls *Larus fuscus*. *Ibis* 118: 65–77. doi:10.1111/j.1474-919X.1976.tb02011.x
- DOMINGUEZ, L., MONTEVECCHI, W.A., BURGESS, N.M., BRAZIL, J. & HOBSON, K.A. 2003. Reproductive success, environmental contaminants, and trophic status of nesting Bald Eagles in eastern Newfoundland, Canada. *Journal of Raptor Research* 37: 209–218.
- DRENT, R.H. 1970. Functional aspects of incubation in the Herring Gull. *Behavior* 17: 1–132.
- FRID, A. & DILL, L. 2002. Human-caused disturbance stimuli as a form of predation risk. *Ecology and Society* 6: 11. doi:10.5751/es-00404-060111
- GILL, F.B. 2006. Ornithology, 3rd Edition. New York, USA: Freeman & Co.
- GOOD, T.P. 2020. Great Black-backed Gull (*Larus marinus*), version 1.0. In BILLERMAN, S.M. (Ed.) *Birds of the World*. Ithaca, USA: Cornell Lab of Ornithology. doi: 10.2173/bow. gbbgul.01
- HELBERG, M., BUSTNES, J.O., ERIKSTAD, K.E., KRISTIANSEN, K.O. & SKAARE, J.U. 2005. Relationships between reproductive performance and organochlorine contaminants in Great Black-backed Gulls (*Larus marinus*). *Environmental Pollution* 134: 475–483. doi:10.1016/j. envpol.2004.09.006
- HINDE, A. 1956. The biological significance of the territories of birds. *Ibis* 98: 340–369. doi:10.1111/j.1474-919X.1956. tb01419.x
- HUNT, G.L., JR. 1972. Influence of food distribution and human disturbance on the reproductive success of Herring Gulls. *Ecology* 53: 1051–1061.
- IGUAL, J.M., ORO, D. & TAVECCHIA, G. 2013. The biparental pattern of incubation and its relationship to food availability in the Yellow-legged Gull *Larus michahellis*. *Ardeola* 60: 365–370. doi:10.13157/arla.60.2.2013.365
- IRONS, D.B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology* 79: 647–655. doi:10.1890/0012-9658(1998)079[0647:FAFOIS]2 .0.CO;2
- ISAKSSON, N., EVANS, T.J., SHAMOUN-BARANES, J. & ÅKESSON, S. 2016. Land or sea? Foraging area choice during breeding by an omnivorous gull. *Movement Ecology* 4: 11. doi:10.1186/s40462-016-0078-5

- JUVASTE, R., ARRIERO, E., GAGLIARDO, A. ET AL. 2017. Satellite tracking of red-listed nominate Lesser Blackbacked Gulls (*Larus f. fuscus*): Habitat specialisation in foraging movements raises novel conservation needs. *Global Ecology and Conservation* 10: 220–230. doi:10.1016/j. gecco.2017.03.009
- KAZAMA, K., HIRATA, K., YAMAMOTO, T. ET AL. 2013. Movements and activities of male Black-tailed Gulls in breeding and sabbatical years. *Journal of Avian Biology* 44: 603–608. doi:10.1111/j.1600-048X.2013.00103.x
- KENNY, E., BIRKHEAD, T.R. & GREEN, J.P. 2017. Allopreening in birds is associated with parental cooperation over offspring care and stable pair bonds across years. *Behavioral Ecology* 28: 1142–1148. doi:10.1093/beheco/arx078
- KOKKO, H., HARRIS, M.P. & WANLESS, S. 2004. Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the Common Guillemot Uria aalge. Journal of Animal Ecology 73: 367–376. doi:10.1111/j.0021-8790.2004.00813.x
- KREBS, J.R. 2002. Optimal foraging, predation risk and territory defence. Ardea 55: 83–90. doi:10.5253/arde.v68.p83
- KRÜGER, O. 2002. Analysis of nest occupancy and nest reproduction in two sympatric raptors: Common Buzzard *Buteo buteo* and goshawk Accipiter gentilis. Ecography 25: 523–532. doi:10.1034/j.1600-0587.2002.250502.x
- MALLORY, M.L. & GILBERT, C.D. 2008. Leg-loop harness design for attaching external transmitters to seabirds. *Marine Ornithology* 36: 183–188.
- MARTIN, P. & BATESON, P. 2007. *Measuring Behaviour: An Introductory Guide. 3rd Edition*. Cambridge, UK: Cambridge University Press.
- MASELLO, J.F., WIKELSKI, M., VOIGT, C.C. & QUILLFELDT, P. 2013. Distribution patterns predict individual specialization in the diet of Dolphin Gulls. *PLoS One* 8: e67714. doi:10.1371/ journal.pone.0067714
- MAWHINNEY, K. & DIAMOND, T. 1999. Sex determination of Great Black-backed Gulls using morphometric characters. *Journal of Field Ornithology* 70: 206–210.
- MAYNARD, L.D. & DAVOREN, G.K. 2018. Sea ice influence habitat type use by Great Black-backed Gulls (*Larus marinus*) in coastal Newfoundland, Canada. *Waterbirds* 41: 449–456.
- MAYNARD, L.S., & DAVOREN, G.K. 2020. Inter-colony and interspecific differences in the isotopic niche of two sympatric gull species. *Marine Ornithology* 48: 103–109.
- MAYNARD, L.D., GULKA, J., JENKINS, E. & DAVOREN, G.K. 2021. Different individual-level responses of Great Black-backed Gulls (*Larus marinus*) to shifting local prey availability. *PLoS One* 16: e0252561. doi:10.1371/journal. pone.0252561
- MAYNARD, L.D. & RONCONI, R.A. 2018. Foraging behaviour of Great Black-backed Gull *Larus marinus* near an urban center in Atlantic Canada: Evidence of individual specialization from GPS tracking. *Marine Ornithology* 46: 27–32.
- ORIANS, G.H. & PEARSON, N.E. 1979. On the theory of central place foraging. In: HORN, D., MITCHELL, R. & STRAITS, G. (Eds.) Analysis of Ecological Systems. Athens, USA: Ohio University Press.
- PONCHON, A., CHAMBERT, T., LOBATO, E., TVERAA, T., GRÉMILLET, D. & BOULINIER, T. 2015. Breeding failure induces large scale prospecting movements in the Blacklegged Kittiwake. *Journal of Experimental Marine Biology* and Ecology 473: 138–145. doi:10.1016/j.jembe.2015.08.013

- PONCHON, A., ILISZKO, L., GRÉMILLET, D., TVERAA, T. & BOULINIER, T. 2017. Intense prospecting movements of failed breeders nesting in an unsuccessful breeding subcolony. *Animal Behaviour* 124: 183–191. doi:10.1016/J.ANBEHAV.2016.12.017
- QGIS DEVELOPMENT TEAM. 2021. *QGIS Geographic Information System*. Open Source Geospatial Foundation Project.
- R DEVELOPMENT CORE TEAM 2018. *R: A language and environment for statistical computing*. Vienna, Austria: The R Foundation for Statistical Computing.
- SCHREIBER, R.W. 1967. Roosting behavior of the Herring Gull in central Maine. *The Wilson Bulletin* 79: 421–431.
- SCOPEL, L.C. & DIAMOND, A.W. 2017. The case for lethal control of gulls on seabird colonies. *Journal of Wildlife Management* 81: 1–9. doi:10.1002/jwmg.21233
- SHAMOUN-BARANES, J., BOUTEN, W., CAMPHUYSEN, C.J. & BAAIJ, E. 2011. Riding the tide: Intriguing observations of gulls resting at sea during breeding. *Ibis* 153: 411–415. doi:10.1111/j.1474-919
- SHLEPR, K.R., RONCONI, R.A., HAYDEN, B., ALLARD, K.A. & DIAMOND, A.W. 2021. Estimating the relative use of anthropogenic resources by Herring Gull (*Larus argentatus*) in the Bay of Fundy, Canada. Avian Conservation and Ecology 16: 2. doi:10.5751/ace-01739-160102
- SPEAR, L, & NUR, N. 1994. Brood size, hatching order and hatching date : Effects on four life-history stages from hatching to recruitment in Western Gulls. *Journal of Animal Ecology* 63: 283–298.
- SPOON, T.R., MILLAM, J.R. & OWINGS, D.H. 2006. The importance of mate behavioural compatibility in parenting and reproductive success by Cockatiels, *Nymphicus hollandicus*. *Animal Behaviour* 71: 315–326. doi:10.1016/j.anbehav.2005.03.034

- STACEY, P.B. 1982. Female promiscuity and male reproductive success in social birds and mammals. *The American Naturalist* 120: 51–64.
- STENHOUSE, I.J. & MONTEVECCHI, W.A. 1999. Indirect effects of the availability of capelin and fishery discards: Gull predation on breeding storm-petrels. *Marine Ecology Progress Series* 184: 303–307. doi:10.3354/meps184303
- THAXTER, C.B., ROSS-SMITH, V.H., CLARK, J.A. ET AL. 2014. A trial of three harness attachment methods and their suitability for long-term use on Lesser Black-backed Gulls and Great Skuas. *Ringing & Migration* 29: 65–76. doi:10.1080/030 78698.2014.995546
- VEITCH, B.G., ROBERTSON, G.J., JONES, I.L. & BOND, L. 2016. Great Black-backed Gull (*Larus marinus*) predation on seabird populations at two colonies in Eastern Canada. *Waterbirds* 39: 235–245. doi:10.1675/063.039.sp121
- WILHELM, S.I., MAILHIOT, J., ARANY, J., CHARDINE, J.W., ROBERTSON, G.J. & RYAN, P.C. 2015. Update and trends of three important seabird populations in the Western North Atlantic using a Geographic Information System approach. *Marine Ornithology* 43: 211–222.
- ZANGMEISTER, J.L, HAUSSMAN, M.F., CERCHIARA, J. & MAUCK, R.A. 2009. Incubation failure and nest abandonment by Leach's Storm-Petrels detected using PIT tags and temperature loggers. *Journal of Field Ornithology* 80: 373–379. doi:10.1111/j.1557-9263.2009.00243.x
- ZEILIS, A., LEISCH, F., HORNIK, K., KLEIBER, C. & KLEIBER, K.H.A. 2002. strucchange: An R package for testing for structural change in linear regression models. *Journal of Statistical Software* 7: 1–38.