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PHILOPATRY, SITE TENACITY, MATE FIDELITY, AND ADULT SURVIVAL IN SABINE'S GULLS

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Abstract. Quantifying the dynamics of populations is fundamental to understanding life-history strategies, and essential for population modeling and conservation biology. Few details of the demography and life history of the Sabine's Gull (*Xema sabini*) are known. Uniquely color banded Sabine's Gulls breeding in East Bay, Southampton Island, Nunavut, in the eastern Canadian Arctic, were examined from 1998–2002 to quantify vital rates. Generally, birds banded as chicks first returned to the breeding area in their third year, and the earliest case of first breeding was confirmed at three years of age. Sabine's Gull pairs showed strong tenacity to their breeding site from year to year, with most pairs nesting within approximately 100 m of the previous year's site, regardless of nest success. Individuals also showed strong year-to-year fidelity to their mates. However, birds whose previous partner failed to return, or returned late, were quick to remate. On rare occasions, birds were not seen in the study area in a particular year, but seen again in later years, either because they were missed, had dispersed temporarily outside the study area, or did not return to the breeding area in some years. Standard Capture-Mark-Recapture analyses were used to calculate local resighting and survival rates. Local annual survival rate of adult Sabine's Gulls was 0.89 ± 0.03, similar to annual adult survival estimates recently reported for other small to medium-sized gulls and terns.

Key words: adult survival, life history, mate fidelity, natal philopatry, Sabine's Gull, site tenacity, Xema sabini.

Filopatría, Apego al Sitio de Nidificación, Fidelidad a la Pareja y Supervivencia de los Adultos en *Xema sabini*

Resumen. Cuantificar la dinámica de las poblaciones es fundamental para entender las estrategias de historia de vida y es esencial para la realización de modelos poblacionales y para la conservación biológica. Se conocen pocos detalles sobre la demografía e historia de vida de la gaviota *Xema sabini*. Para cuantificar sus tasas vitales, en este estudio se examinaron gaviotas anilladas que estaban criando en East Bay, Southampton Island, Nunavut (ártico canadiense) entre 1998 y 2002. Generalmente, las aves que fueron anilladas como pichones regresaron al área de cría en su tercer año, y el caso de primer apareamiento más temprano fue confirmado a los tres años de edad. Las parejas exhibieron un fuerte apego a su sitio de nidificación de año a año: la mayoría nidificaron a menos de aproximadamente 100 m del lugar en donde lo hicieron el año anterior, independientemente de su éxito de nidificación. Los individuos también mostraron gran fidelidad a sus parejas año a año. Sin embargo, las aves cuyas parejas no regresaron o lo hicieron tardíamente, encontraron nuevas parejas rápidamente. En raras ocasiones, algunas aves no fueron vistas en el área de estudio durante un año particular, pero fueron vistas en años siguientes, ya sea porque no fueron detectadas a pesar de estar presentes, porque se habían dispersado hacia afuera del área de estudio temporalmente o porque no regresaron al área de cría en algunos años. Se emplearon análisis estándar de captura, marcado y recaptura para calcular las tasas locales de reavistamiento y supervivencia. La tasa de supervivencia anual de los adultos de *X. sabini* fue 0.89 ± 0.03, un valor similar a los valores estimados de supervivencia anual de adultos documentados recientemente para gaviotines y otras gaviotas de tamaño medio.

INTRODUCTION

Quantifying the dynamics of avian populations, such as survivorship and fecundity, is fundamental to understanding their life-history strategies (Spear et al. 1987). Demography, the key to life-history theory, allows assessment of the strength of selection on life-history traits for many conditions (Stearns 1992). Clearly, it is important to establish baseline demographic information that will provide the basis for modeling population dynamics under different environmental stresses (Greenwood et al. 1993). Yet,

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to date, there has been little investigation of the demographic trends of many avian populations breeding in the Arctic. This is particularly troubling, given the extent of potential climate changes predicted for the Arctic region due to the influence of anthropogenic activities (Bengtsson 2001).

Arctic-breeding birds tend to be characterized as having high adult survival rates, delayed age of first breeding, and generally low and variable annual reproductive output (Tuck 1961, Birkhead and Harris 1985). These traits have likely evolved as a response to the harsh and variable breeding conditions encountered each year by these birds (Freuchen and Salomonsen 1958). At high latitudes, where the breeding season is short, site tenacity could be high as it may reduce time spent searching for a previous mate (Bried and Jouventin 2002). Mate fidelity between years could also be comparatively high, due to the limited time available for assessment of new partners (Flynn et al. 1999).

The Sabine's Gull (*Xema sabini*) is a transequatorial migrant that breeds at high latitudes. It winters at coastal upwelling zones off western South America and southern Africa, and breeds in coastal areas of Arctic and Subarctic regions in North America, Greenland, and Russia (Day et al. 2001). It generally breeds in dense colonies on small coastal islands (Forchhammer and Maagaard 1991) or solitarily at the edges of shallow ponds in coastal wetland areas (Abraham 1986). The Sabine's Gull is considered unusual within the gull family (*Laridae*) and is recognized as phylogenetically distinct (Chu 1998), as well as atypical in several aspects of its behavior (Brown et al. 1967) and reproductive biology (Stenhouse et al. 2001). Yet, few details are known regarding its demography and life history. For example, Sabine's Gulls are assumed to first breed at two years of age (Day et al. 2001), based on the fact that they acquire mature adult plumage in their second spring molt (Grant 1986). However, this has never been confirmed.

Stenhouse et al. (2001) provided information on the breeding biology of Sabine's Gulls, including fecundity, and compared it with other gulls. This study attempts to fill some of the remaining gaps in our knowledge, and presents results on the demographic and life-history traits of Sabine's Gulls, specifically natal philopatry, age at first breeding, nest-site tenacity, and mate fidelity. Adult survival is estimated and compared to other small to medium-sized, northern-breeding gulls.

METHODS

STUDY AREA

Field work was conducted from late May to mid-August 1998–2002 in the East Bay Migratory Bird Sanctuary (64°01′N, 81°47′W), Southampton Island, Nunavut, in the eastern Canadian Arctic (see Stenhouse et al. 2001 for map). The East Bay sanctuary encompasses an area of approximately 1200 km^2. Although Southampton Island lies principally in the Southern Arctic ecozone, the eastern coast falls within the Northern Arctic ecozone, being influenced in its ecological and physical characteristics by the deep, cold waters of the Foxe Channel to the northeast (Ecological Stratification Working Group 1995). Mean summer temperature in this ecoregion is around 2°C, and land-fast sea ice can remain in East Bay well into July. The study plot is a 2 × 2.5-km block of low-lying, coastal wetland tundra typical of the area, with a complex of brackish and freshwater ponds. Within the plot, subhabitats are few and distinct, with wetland areas characterized by mosses, sedges, and grasses, and drier areas dominated by dwarf shrubs (*Salix* spp.) and mountain avens (*Dryas integrifolia*). High-salinity areas close to shore are colonized by few plants, and characterized by bare, sandy, or rocky substrate sparsely broken up by small patches of sedges and mosses. In summer, the area supports a diverse avian community typical of Arctic coastal wetlands (Abraham and Ankney 1986).

DATA COLLECTION

Breeding adult Sabine's Gulls were caught at the nest during incubation using a simple wire-mesh 'fall trap' (Bub 1991). Chicks were caught by hand at, or near, the nest. In this area, Sabine's Gulls nest solitarily, so there was no chance of confusion over which nest a chick came from. Chick captures had to be carefully timed, however, as there is only a very short window of opportunity before the entire family leaves the nest area completely (~24 hr after last chick hatched), after which it is extremely difficult to find or get close to chicks. Throughout this study, adults were given a numbered metal band and marked with individual combinations of 3 color bands, while chicks were given a num-

TABLE 1. Number of Sabine's Gulls banded at East Bay, Southampton Island, Nunavut, Canada, and resighted at the same location in subsequent years in relation to age.

	Year banded	Number banded	Total banded	Year resighted			
				1999	2000	2001	2002
Adults	1998	26	26	21	20	17	12
	1999	13	39	–	12	9	5
	2000	0	39	–	–	–	–
	2001	4	43	–	–	–	2
Chicks	1998	35	35	0	1	3	3
	1999	13	48	–	0	0	3
	2000	37	85	–	–	0	1
	2001	23	108	–	–	–	0

bered metal band and marked with a single color band indicating the year of hatching. However, some chicks were so small at day 2–3 after hatching that they lost their metal band (which were found at the nest site), but all retained their color bands.

All adult Sabine's Gulls observed within the study area, and farther afield in East Bay, were checked for leg bands by two dedicated observers working in the study area in each year (except in 2002, where researchers involved in other projects observed Sabine's Gulls whenever possible). Color band combinations, or partial combinations, were recorded whenever conditions allowed. It was rare, however, to even glimpse bands of airborne birds, and confirmation required birds to land within 80–100 m of observers. However, observations were frequent as Sabine's Gulls at East Bay spent much of their time on the ground, searching for terrestrial invertebrates that they feed on during the breeding season (IJS, pers. obs.).

Nests were located by searching on foot, and adults at each nest were examined for leg bands at every visit. Due to their habit of communal mobbing, it often took several visits to confirm which adults were associated with a particular nest. Nests were generally visited daily until the clutch was completed, on average every three days during incubation, and daily during the hatching period, allowing assessment of reproductive success for each nest. Eggs that disappeared from a nest prior to their projected hatching dates (21–22 days after laying; Stenhouse et al. 2001) were assumed depredated.

STATISTICAL ANALYSES

To calculate local survival rates (ϕ) and resighting rates (p), standard Capture-Mark-Recapture analyses (CMR; Pollock et al. 1990, Lebreton et al. 1992) were carried out in the program MARK (White and Burnham 1999). Only birds captured as adults were used in this analysis. Encounter histories were created based on initial captures and subsequent resighting of adult birds in following years. The global model included time variation in survival and resighting rates (ϕ_t, p_t), while the candidate model set included models with constant survival and resighting rates. Additionally, it was expected *a priori* that resighting rates would be lower in the final year of the study, as effort to resight birds was considerably lower, so we also constructed models with a constant resighting rate for 1999–2001, but a different rate for 2002. Akaike Information Criterion, corrected for small sample size (AIC_c), was used to choose the best-fitting model among candidate models ($n = 6$) and model likelihoods were used to assess the relative fit of each model (Burnham and Anderson 1998). Goodness-of-fit was assessed with the program RELEASE (Burnham et al. 1987). In addition, the variance inflation factor ($\hat{c}$) was calculated based on the global model, with the parametric bootstrap, using 100 simulations and taking the ratio of the observed deviance to the expected deviance (Cooch and White 2001). Mean adult life expectancy was calculated using the equation $1-\ln^{-1}(\phi)$.

RESULTS

RETURN OF BANDED BIRDS

A total of 43 adults and 108 chicks were banded at East Bay (Table 1). Of the 26 adults banded in 1998, 81% returned to the study area in the following year, but this was reduced to 46% by the fourth year (2002). Of the 13 adults banded

in 1999, 92% returned in the following year, but this was reduced to 38% by the third year (2002; Table 1).

In 1999, five breeding birds were banded at a similar site 8 km east of the study area, but none of these individuals were ever observed in the study area in subsequent years.

NATAL PHILOPATRY

One bird (3%) banded as a chick in 1998 returned to the study area in 2000, although it did not appear to pair successfully and did not breed in that year. Three (9%) birds banded as chicks in 1998 returned to the study area in 2001 and in 2002, one of which was confirmed breeding in the study area in 2001, its third year.

The chance of seeing birds banded as chicks in 1999 return to the study site was considerably limited because of the low number of chicks that hatched and were banded in that year. Of these, up to three were seen for the first time in 2002 (their third year), although none were confirmed breeding in that year. One bird banded as a chick in 2000 was seen in the study area in 2002, but also did not breed in that year (Table 1).

SITE TENACITY

Throughout this study, Sabine's Gulls showed strong tenacity to their breeding site from year to year. Of 13 pairs banded in 1998, two pairs reused the same nest cup in 1999 as they had in the previous year, 9 pairs nested nearby (approximately 100 m), and only two pairs nested >200 m from their previous nest sites. The pair that moved furthest (410 m) had failed at their previous site due to predation of their entire clutch early in the breeding season. Movements of nesting pairs from year to year were similar in all years (1998–2002) to those observed between 1998 and 1999.

Combining all years, and only examining movements of pairs where both birds were banded (n = 21), median distance moved between years for those pairs which successfully hatched a clutch was 44 m (n = 11, range = 27–880 m), while median distance moved after predation or abandonment of a clutch was 65 m (n = 10, range = 30–1190 m). Overall, most pairs nested close to the previous year's nest site, whether successful or otherwise (Mann-Whitney U-test, z = 0.42, P = 0.67).

MATE FIDELITY

Sabine's Gulls showed strong fidelity to their mates between years, with an overall annual mate retention rate of 65% (1st year = 80%–88%, 2nd year = 63%–75%, 3rd year = 20%–33%). Of nine pairs banded in 1998, eight reunited in 1999, five in 2000, and one in 2001 and again in 2002. Of the five pairs banded in 1999, four reunited in 2000, three in 2001, and one in 2002.

Birds paired in one year may not have reunited in the following year for a variety of reasons. Throughout this study, however, there were only two confirmed cases where both members of a pair returned to the study area but did not breed together: in one case, both were confirmed breeding with new mates; and in the other case, only one was confirmed breeding with a new mate, while the original partner, although present, did not appear to breed. In most cases of re-mating (12% of all pair-years), the original partners were not seen in the study area again, and it is impossible to know whether they did not return because they died during the preceding winter or because they emigrated out of the area to breed elsewhere.

ADULT SURVIVAL

Based on the ratio of observed to expected deviances, $\hat{c}$ = 0.49 ± 0.01, considerably less than 1.0, suggesting that the data set may show underdispersion (i.e., less variation than expected by chance). Similarly, the program RELEASE did not detect any sources of heterogeneity, (TEST 2 and TEST 3 combined χ^2_5 = 0.00, P = 1.00), also indicating evidence of underdispersion. It is not clear whether to adjust $\hat{c}$ when it is less than 1.0 (Cooch and White 2001), thus no adjustment was made and the data were assumed to be distributed with a binomial error structure.

Based on AIC_c weights and model likelihoods, a model with a constant survival rate and resight rates pooled from 1999–2001, with a separate rate for 2002, was 4.8 times better supported than a model with time variation in survival rates (Table 2). Local annual survival rate for this model was 0.89 ± 0.03 (95% profile likelihood intervals: 0.80–0.94), which compares well with adult annual survival estimates for other small to medium-sized larid species (Table 3). Based on this survival estimate, mean (± SE) adult life expectancy for Sabine's Gulls

TABLE 2. Model selection results for Sabine's Gulls breeding at East Bay, Southampton Island, Nunavut, Canada, 1998–2002. The survival rate (ϕ) and the resighting rate (p) subscripted with time (t) indicate that the rates were allowed to vary annually, while the subscript 1999–2001, 2002 in resighting rate indicates that 2002 was estimated as a separate rate. Deviance is an index of model fit, while AIC_c (Akaike's Information Criterion corrected for small sample size) is a measure of the models ability to explain the data. ΔAIC_c is simply the AIC_c difference between the best (lowest AIC_c) model and the model in question, while the AIC_c weight is the relative support of each model compared to all others in the model set.

Model	Number of parameters	Deviance	AIC_c	ΔAIC_c	AIC_c weight
ϕ, $p_{1999–2001,2002}$	3	8.34	149.32	0.00	0.57
ϕ_t, $p_{1999–2001,2002}$	5	7.16	152.45	3.13	0.12
ϕ_t, p	5	7.16	152.45	3.13	0.12
ϕ, p_t	5	7.40	152.70	3.37	0.11
ϕ, p	2	14.94	153.82	4.50	0.06
ϕ_t, p_t	7	6.48	156.25	6.92	0.02

at East Bay was 8.2 ± 2.1 years. Resighting rates were high for 1999–2001 (0.94 ± 0.03) and dropped to 0.67 ± 0.11 in 2002.

DISCUSSION

The return of birds banded as chicks to the study area shows that Sabine's Gulls exhibit some natal philopatry. The relatively low rate of natal philopatry that we observed, however, may be due to 1) high juvenile mortality during the first few years, 2) reproductive maturation beyond the second year, 3) the short temporal scale of this study, or 4) low detectability due to band loss. Although a few birds banded as chicks returned to the breeding area in their second year, these individuals did not establish territories. Instead, they often joined feeding flocks of failed breeders that built up over the course of the season each year, and did not appear to associate with a particular area. Despite our small sample size, it appears that breeding at two years of age is unlikely or uncommon in Sabine's Gulls. Our earliest (and only) confirmed first breeding was a bird at three years of age.

Most birds in this study nested close to the site of their nest in the previous year. This site tenacity probably facilitates a reuniting of the pair, and could enhance reproductive success through familiarity with the breeding site (Greenwood and Harvey 1982). Interestingly, Sabine's Gull pairs usually returned to a breeding area despite their nest fate in the previous year (Haas 1998). This might suggest that 1) there were no suitable alternative sites, which

TABLE 3. Adult annual survival rate of Sabine's Gulls breeding at East Bay, Southampton Island, Nunavut, Canada, 1998–2002, compared with recent estimates of adult survival for other small to medium-sized, northern-breeding gulls and terns. For each study, values are presented as mean ± SE or with 95% confidence intervals. Estimation method based on the Cormack-Jolly-Seber models (CJS; see Pollack et al. [1990] and Lebreton et al. [1992] for the general approach), unless otherwise indicated.

Species	Survival Rate	Estimation Method	Source
Sabine's Gull (*Xema sabini*)	0.89 ± 0.03	Resighting	This study
Ivory Gull (*Pagophila eburnea*)	0.86 ± 0.04	Recovery[a]	Stenhouse et al. (2004)
Black-legged Kittiwake (*Rissa tridactyla*)	0.88 ± 0.02	Resighting	Harris et al. (2000)
	0.80 ± 0.03	Recapture	Oro and Furness (2002)
Black-headed Gull (*Larus ridibundus*)	0.90 (0.86–0.92)	Resighting	Prévot-Julliard et al. (1998)
Mew Gull (*Larus canus*)	0.90 ± 0.01[b]	Resighting and recapture	Rattiste and Lilleleht (1995)
Common Tern (*Sterna hirundo*)	0.88 ± 0.04	Recapture	Nisbet and Cam (2002)
Least Tern (*Sterna antillarum*)	0.85 ± 0.06	Resighting	Renken and Smith (1995)

[a] Estimation method was derived from recovery data.
[b] In normal winters.

seems unlikely, or 2) that breeding failure is usually associated with some aspect of environmental stochasticity (e.g., predation, weather), rather than the specific characteristics of a particular nest site. Broad scale environmental events, such as a late snow melt, severe storms, or exceptional precipitation and flooding, tend to affect all nests in a given year, despite their location. In marginal years, however, familiarity with a breeding area may be of considerable importance in reproductive success.

Like most seabirds, Sabine's Gulls are socially monogamous and relatively long-lived (Day et al. 2001). As such, members of a pair are likely to benefit by reuniting in successive breeding seasons. Mate fidelity may 1) promote early breeding, by saving time required to find a new mate each year, and 2) enhance reproductive success, by increasing cooperation and coordination in parental activities (Hamer et al. 2002).

As is common among seabird species (Wood 1971, Mills 1973, Ollason and Dunnett 1978, Bradley et al. 1990), Sabine's Gulls do not appear to maintain pair bonds throughout the year and members of a pair are believed to disperse separately and reunite at the beginning of each breeding season (Day et al. 2001). In this study, returning birds, whose previous partner failed to return, or perhaps returned late, were quick to remate. Once remated, birds were found to reunite with their new mates in successive years, even if their original partner returned to the study area in later years. Given strong mate fidelity and site tenacity, the fact that some birds were not seen in the study area in a specific year, but seen again in later years, suggests that individuals were present, but not seen, or dispersed temporarily outside the study area. However, these explanations seem unlikely, given the extensive coverage of the study area and beyond in each year, and the relatively short distance moved between nesting attempts. A third possibility is that individuals of this species will forego breeding and not return to the area in some years, perhaps because of unsuitable body condition prior to spring migration (Forchhammer and Maagaard 1991).

Due to high resighting rates, averaging 0.94 in all but the last year, we calculated a survival rate of 0.89, in spite of having only 43 adult birds for the analysis. Although few individuals were available for this analysis, we had high-quality data, as many were resighted multiple times, leading to a relatively precise single estimate of annual local survival. Whether this survival rate is representative of Sabine's Gull populations in general will require studies at other sites and over different time spans.

Due to the difficulties of identifying emigration and band loss, both of which appeared as mortality in this analysis, the survival rate presented should be considered a minimum estimate. Although the best model indicated a constant survival rate, true survival rate is not necessarily constant in this, or any, population. In studies with a relatively small number of individuals, and only five occasions, reduced parameter models are generally more strongly supported (Anderson et al. 1994). Random-effect models show promise to incorporate process (or annual) variation and residual sampling variation in one estimate with appropriate error that can be decomposed into both sources (Burnham and White 2002). However, for this study, with only three estimates of survival, calculating a random-effects model is not recommended (Burnham and White 2002). Even so, a random-effects model did produce a similar estimate (0.89 ± 0.03) to the one obtained from the constant survival-rate model.

It is unusual for resighting data to show evidence of underdispersion, while overdispersion is common in many data sets (Prévot-Julliard et al. 1998, Franklin et al. 2002). Underdispersion likely reflects both the high survival and resighting rates obtained in this study. When rates are high, most of the birds survive and are seen from one occasion to the next, leaving little opportunity for many birds to show radically different encounter histories. The relatively short duration of this study likely exacerbates this problem. Additionally, some of the birds in this study were paired, and, although it is unlikely that pairs remain together throughout the entire nonbreeding season and suffer the same mortality source (Coulson and Wooller 1976, Spear et al. 1987), they may disperse from the study areas with equal frequency (either as a pair, or, if one fails to return, the surviving member may disperse). This statistical dependence among pairs could contribute to the observed underdispersion. Further, all birds captured in this study were breeding adults. With a longer study period and eventual inclusion of younger breeding birds, the evidence of underdispersion would

likely diminish. Fortunately, underdispersion is not likely to bias the estimate of survival rate, and the estimates of error that we present assume a binomial distribution of random errors.

Prior to this study, few details of the demography of Sabine's Gulls were known (Day et al. 2001), which has until recently prevented meaningful comparisons with other gull species. Such comparisons could help to determine whether or not species considered closely related share important demographic characteristics. The survival rate presented here compares well with recent estimates of adult survival in other small to medium-sized, northern-breeding gulls, among which percent survival estimates are typically high (Table 3). Furthermore, in spite of displaying some aberrant behavior (Brown et al. 1967, Abraham 1986, Stenhouse et al. 2001), Sabine's Gulls show typical larid life history patterns, including natal philopatry, nest site tenacity, and mate fidelity. Age at first breeding remains an open question, due to a small sample size, although this study found no evidence to support the assumption that Sabine's Gulls breed at two years of age.

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