

SURVIVAL RATE OF THE LONG-TAILED JAEGER AT ALERT, ELLESMERE ISLAND, NUNAVUT

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Abstract. In long-lived animals, survival rate is a key demographic parameter affecting population dynamics. The objective of this study was to estimate the apparent survival rate of adult Long-tailed Jaegers (*Stercorarius longicaudus*) breeding at one of the most northerly sites on earth, northern Ellesmere Island, Canada. Because of the large temporal fluctuations in numbers of lemmings, their primary food source during the summer, we also investigated the effect of annual variations in lemming abundance on survival rate. Analysis was based on 336 individuals marked as adults over 11 years with metal and color bands and capture–mark–recapture techniques. There was strong support for a model with two age classes, as survival of newly marked birds was 18% lower than that of previously marked ones. This difference could be due to a true age effect (if a high proportion of young adults was present in our initial samples) or, perhaps more likely, to the presence of transient individuals in the population. The estimated probability of apparent annual survival of local birds (corrected for color-band loss) was 0.91, comparable to values for other seabirds, and was constant over time. We detected a weak trend for a decrease in apparent survival rate of newly marked birds in years of high lemming abundance but no effect on the survival of previously marked birds. This suggests that conditions at sea during the nonbreeding season may be more important in affecting annual survival. A new longevity record of 22 years was established for the species.

Key words: lemming, Long-tailed Jaeger, seabird, *Stercorarius longicaudus*, survival, transient, tundra.

Tasa de Supervivencia de *Stercorarius longicaudus* en Alert, Isla Ellesmere, Nunavut

Resumen. En los animales longevos, la tasa de supervivencia es una medida demográfica clave que afecta la dinámica poblacional. El objetivo de este estudio fue examinar la tasa de supervivencia aparente de los individuos adultos de *Stercorarius longicaudus* que crían en uno de los sitios más septentrionales de la tierra, el norte de la isla Ellesmere, Canadá. Debido a las grandes fluctuaciones temporales en el número de lemmings, su fuente principal de alimento durante el verano, también investigamos el efecto de las variaciones anuales en la abundancia de lemming en la tasa de supervivencia. El análisis se basó en 336 individuos marcados como adultos a lo largo de 11 años con anillos de metal y color, y técnicas de captura–marcado–recaptura. Hubo un fuerte apoyo a un modelo con dos clases de edad, ya que la supervivencia de las aves marcadas recientemente fue 18% menor que la de los individuos marcados previamente. Esta diferencia puede deberse a un verdadero efecto de la edad (si una alta proporción de jóvenes adultos estuvo presente en nuestras muestras iniciales) o, tal vez más probablemente, a la presencia de individuos en tránsito en la población. La probabilidad estimada de supervivencia anual aparente de las aves locales (corregida por la pérdida de anillos de color) fue 0.91, comparable con los valores para otras aves marinas, y fue constante en el tiempo. Detectamos una débil tendencia de disminución de la tasa de supervivencia aparente de las aves recientemente marcadas en años de alta abundancia de lemmings, pero ningún efecto en la supervivencia de las aves previamente marcadas. Esto sugiere que las condiciones en el mar durante la estación no reproductiva pueden ser más importantes en afectar la supervivencia anual. Se estableció un nuevo registro de longevidad de 22 años para esta especie.

INTRODUCTION

In long-lived species, survival of adults is one of the most important life-history traits to be considered in a study of population dynamics because slight changes in this variable can have far-reaching effects on the population's growth rate (Sæther and

Bakke 2000). Seabirds are among the longest-lived birds, and considerable efforts have been made to estimate this critical demographic parameter for seabirds adequately. Studies based on capture–recapture methods have shown that annual survival ranges from 0.80 to 0.96 in several species of the Procellariidae, Diomedidae, Laridae, and Alcidae (Jenouvrier et al. 2003,

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Sandvik et al. 2005, Crespin et al. 2006, Converse et al. 2009, Gauthier et al. 2010). Because these species have a long life span and delayed reproduction, and hence a low maximum rate of population growth (Niel and Lebreton 2005), their populations are highly sensitive to any decrease in adults' survival (Sæther and Bakke 2000) and thus subject to a high risk of extinction. For example, marked declines of several albatross populations have resulted from an increase in adult mortality caused by incidental bycatch in the long-line fishing industry (Weimerskirch et al. 1997, Véran et al. 2007).

Over the past three decades, powerful analytical tools have been developed to provide unbiased estimates of survival based on capture–recapture of marked individuals (Lebreton et al. 1992, White and Burnham 1999). Among seabirds, little attention has been paid to the demography of the arctic-nesting Stercorariidae (jaegers and skuas), particularly the Long-tailed Jaeger (*Stercorarius longicaudus*), for which no survival estimate based on robust methods is available. Jaegers are not commonly observed because their nests are widely dispersed on the arctic tundra during the summer and birds from eastern North America and Greenland migrate across the equator to winter over the South Atlantic Ocean off the African coast (Wiley and Lee 1998, Sittler et al. 2010).

During the summer, Long-tailed Jaegers completely change their diet from marine to terrestrial food sources (Dekorte and Wattel 1988, Julien 2012). Voles and especially lemmings then become their primary prey at most of their breeding sites (Maher 1970, Andersson 1976, Dekorte and Wattel 1988, Therrien et al. 2013). Across the Arctic, lemming populations typically oscillate regularly and widely at intervals of 3 to 5 years (Stenseth 1999, Krebs et al. 2002, Gilg et al. 2003, Gruyer et al. 2008). Several studies have demonstrated a strong relationship between the annual fluctuations in lemming abundance and the number of breeding Long-tailed Jaegers (Maher 1970, Andersson 1976, 1981, Gilg et al. 2006, Therrien et al. 2013). In many areas, the jaegers depend exclusively on lemmings for their reproduction, and in the absence of lemmings, the jaegers generally do not breed.

The objective of our study was to estimate the apparent survival rate of adult Long-tailed Jaegers breeding at one of the most northerly sites on earth, northern Ellesmere Island, Canada, by using robust capture–mark–recapture techniques. Because of the large temporal fluctuations in lemming numbers typical of the High Arctic, we also investigated the effect of annual variations in the abundance of lemmings on the survival and probabilities of recapture of the Long-tailed Jaeger over 11 years.

METHODS

STUDY SITE

The study site was located in the vicinity of Alert (82° 30' N, 62° 20' W), on the northeast coast of Ellesmere Island, Nunavut, Canada. Alert is a Canadian military base and an Environment Canada weather station, and it is the most northerly

settlement in the world inhabited year round. The 65-km² area is characterized by rugged terrain surrounded by hills and valleys with gentle slopes and includes five lakes. The terrain is mostly barren, consisting of frost-shattered rock, gravel, and bare clay with a sparse cover of vegetation (generally <15%; MacDonald 1953) and is thus largely a polar semi-desert. The summer climate is cold, with a mean July temperature of 3.4 °C, owing to the cooling effects of persistent sea ice along the coast. In spring, snow cover is variable though usually extensive through the end of May but typically declines rapidly after the first week of June (Davidson and Morrison 1989). An unusual feature of the area is an outfall stream where sewage from the military station has been disposed for the past 50 years (MacDonald 1953). Since the early 1990s, the discharge has included macerated food refuse, and this represents an important allochthonous source of food for several species of birds in the area, including jaegers (Julien 2012).

CAPTURE AND MARKING OF BIRDS

We captured most Long-tailed Jaegers with rocket nets at the sewage outfall of the military base, where the birds concentrate to feed, especially early in the season (mid-June to mid-July). Jaegers were captured and marked from 1987 to 2008, but because captures were too sparse before 1998, we retained data for only the last 11 years for our analysis of annual survival. During this period, we captured between 1 and 141 individuals annually (number of individuals captured per attempt with the rocket net ranged from 1 to 15). We also captured a smaller number of birds incubating on their nest by using a small “pull net” (Hicklin et al. 1989). All jaegers were marked with a standard U.S. Fish and Wildlife Service metal band when first captured ($n = 336$ different birds between 1998 and 2008, 315 with rocket nets and 21 on their nest). Their sexes were unknown because there are no reliable criteria for sexing Long-tailed Jaegers externally and all were adults (≥ 1 year old). We made 54 recaptures of previously marked individuals. Starting in 2001, captured birds ($n = 240$) were also marked with a unique combination of three colored plastic bands to allow identification of individuals at a distance and thus increase the probability of encounters. Since then, we have observed at the sewage outfall by spotting scope and noted all color-banded individuals ($n = 257$ observations, excluding multiple observations within a year).

LEMMING ABUNDANCE

At Alert, the only species of small mammal is the collared lemming (*Dicrostonyx groenlandicus*). To identify peak years, we assessed its abundance qualitatively each year by the number of lemmings encountered during normal field activities. Because of the very strong variations of lemming populations between years of high and intermediate/low abundance, this index should be sufficient to identify peaks (Lecomte et al. 2008). Years of high lemming abundance at Alert were 2000, 2003 and 2006, with abundance greatest in 2003 (R. I. G. Morrison, pers. obs.), as also indicated by the presence of Snowy Owls (*Bubo scandiacus*)

that year, an unusual species at Alert. Summer presence and reproduction of Snowy Owls is closely tied to local peaks in lemming abundance (Gauthier et al. 2004, Therrien et al. 2013).

STATISTICAL ANALYSES

We applied the Cormack–Jolly–Seber capture–mark–recapture model (Lebreton et al. 1992), implemented in the software MARK, to estimate probabilities of survival and resighting (White and Burnham 1999). To determine whether this model fitted the data well, we used the goodness-of-fit tests of the software U-CARE (Choquet et al. 2009), which tests for permanent or temporary heterogeneity in re-encounters for each cohort. Permanent effects are generally associated with heterogeneity in survival probability, which can be caused by an age effect or because of the presence of transient individuals in the population. Temporary effects are generally associated with heterogeneity in capture probability and can be caused by trap-dependence (trap-shyness or trap-happiness). To select models, we used Akaike's information criterion corrected for small sample size (AIC_c) and AIC weights (w_i , which measures the relative likelihood of a given model among a set of models fitted; Burnham and Anderson 2002). We corrected AIC_c values for the overdispersion coefficient (\hat{c}) on the basis of goodness-of-fit tests ($\hat{c} = \chi^2/df$).

We considered temporal effects on probabilities of both survival and re-encounter. Because we expected differences in encounter probability between individuals marked with metal bands only (1998–2000) and those marked with color bands (2001–2008), we defined two groups (group 1: metal band only; group 2: metal and color bands). We assumed that survival (S) of the two groups would be similar but that capture probability (p) would differ. Furthermore, because in 2005 and 2006 we made no captures but did record resightings, we fixed p at 0 for group 1 (metal) in those 2 years. Nineteen individuals originally captured and marked with a metal band only before 2001 were recaptured and marked with additional color bands between 2001 and 2008. For these individuals, we censored their encounter history in the first group upon their second marking and started a new encounter history in group 2 at this time. We tested for a possible effect of years of high lemming abundance on both S and p by contrasting years of peak abundance (coded 1) with other years (coded 0) as a covariate.

Plastic color bands wear out and can break over the years, rendering identification of individuals impossible. This problem can be especially severe in long-lived birds such as the Long-tailed Jaeger. Loss of auxiliary markers will bias survival downward because these individuals will no longer be observable. However, because we had physical recaptures during which we could ascertain the presence or absence of plastic bands (as all birds also received a metal band), we could calculate a band-retention rate to correct the survival estimates a posteriori. For a few birds that were recaptured more than once, we retained only the latest date of recapture

to ensure independence of the data. We used the approach of Gauthier et al. (2001) to estimate annual probability of retaining a color band (θ_j), defined as the probability that a bird alive with its color band at time j retains its color band from j to $j+1$, given that the bird also survives. Among N birds released and recaptured k years after marking, the expected number of individuals (E) still wearing a full color-band combination (T_k) is estimated by the general model

$$E[T_k] = N \prod_{j=1}^k \theta_j.$$

We modeled annual probability of color-band retention as a function of color-band age rather than calendar year because we believed that the principal cause of color-band loss was aging of the plastic. We also tested a reduced model in which we considered the annual retention rate constant (i.e., independent of color-band age). We used the program SURVIV (White 1983) for this analysis and selected the best model by the AIC_c . We divided survival-rate estimates by rate of color-band retention to correct for band loss and computed SE by the delta method (Powell 2007).

RESULTS

GOODNESS-OF-FIT TESTS

The result of the overall goodness-of-fit test for the two groups (metal band only and metal + color bands) was not significant ($\chi^2_{21} = 28.6$, $P = 0.12$). However, when the test components are considered, component 3Sr (which tests for permanent heterogeneity) approached significance for color-banded individuals (group 2, Table 1) and the directional z -statistic was significant ($z = 2.22$, $P = 0.03$). This indicates that newly marked individuals were recaptured less than previously marked ones. This could be due to a negative effect of marking on survival, a high proportion of young with low survival among newly marked birds, or the presence of transients (see Discussion). We corrected for this potential source of heterogeneity by adjusting a model with two age classes on survival rate (first year after marking vs. all other years; Pradel et al. 1997).

TABLE 1. Goodness-of-fit tests of the Cormack–Jolly–Seber model for two groups (group 1 = metal band only; group 2 = metal and color bands) of Long-tailed Jaegers marked and re-encountered at Alert, Nunavut, Canada, 1998–2008.

Test component	Group 1			Group 2		
	χ^2	df	P	χ^2	df	P
3Sr	0.66	1	0.415	8.60	4	0.072
3Sm	0.00	2	1.000	3.84	3	0.279
2Ct	0.00	1	1.000	12.97	5	0.023
2Cl	0.56	1	0.450	2.01	4	0.733
Sum	1.22	5	0.943	27.42	16	0.037

The component 2Ct (which tests for temporary heterogeneity) was significant for color-banded birds (group 2; Table 1), and the directional z -statistic was negative ($z = -3.12$, $P < 0.001$), indicating trap-happiness (Choquet et al. 2005). We corrected for this overdispersion with a correction factor (\hat{c}) calculated from the residual goodness-of-fit test (i.e., excluding component 3Sr because we accounted for the presence of transients in our model). This correction factor was quite low ($\hat{c} = 19.38/16 = 1.211$).

RATE OF COLOR-BAND RETENTION

We recaptured 24 color-banded birds up to 7 years after they were marked initially, among which 7 had lost at least one color band. A model in which band-retention rate was constant was preferred over one where retention varied according to age of the band ($\Delta\text{QAIC}_c = 10.8$). Annual retention rate was estimated at 0.89 ± 0.04 (95% CI = 0.82–0.97).

SURVIVAL RATE

There was strong support for a model of survival with two age classes, as 10 of the 11 top models retained this effect (sum of $w_i = 0.99$; Table 2). We found weak support for an effect of years of high lemming abundance on survival, as this effect was only retained in the second, third and fifth best models. The sum of w_i of models with a lemming effect was 0.39 for the first age class and 0.26 for the second age class. However, high lemming abundance tended to have a negative effect on the survival rate of the first age class (possibly a mixture of transients and local birds; $\beta = -0.85$, SE = 0.63, model 2) but a positive effect on that of the second age class (local birds only; $\beta = 0.27$, SE = 1.08, model 5), although the 95% confidence interval for both of these slope parameters included zero. We found no evidence for other temporal variation in survival rate (Table 2).

TABLE 2. Modeling of various effects on the probabilities of survival (ϕ) and re-encounter (p) of Long-tailed Jaegers marked at Alert, Nunavut, Canada (1998–2008), corrected for over-dispersion ($\hat{c} = 1.211$). ΔQAIC_c = difference between this model and the lowest QAIC_c model, K = number of parameters, t = time effect, g = group effect (metal vs. metal + color band), $2a$ = two age classes, a_1 = first age class (newly marked birds), a_2 = second age class (previously marked birds), lem = high lemming abundance, $.$ = constant effect, \times = interaction, $+$ = additive effect.

Model	ϕ	p	ΔQAIC_c	w_i	K	QDeviance
1	2a	$g + t$	0.00	0.287	13	194.89
2	$a_1 + \text{lem}, a_2$	$g + t$	0.47	0.227	14	193.20
3	$2a + \text{lem}$	$g + t$	1.16	0.161	14	193.89
4	$2a + t$	$g + \text{lem}$	2.01	0.105	14	194.74
5	$a_1, a_2 + \text{lem}$	$g + t$	2.09	0.101	14	194.82
6	$a_1 \times t, a_2$	$g + \text{lem}$	3.14	0.060	12	200.18
7	$a_1 \times t, a_2$	$g + t$	4.25	0.034	20	183.77
8	2a	$g \times t$	6.85	0.009	17	193.03
9	$2a + t$	$g + t$	7.53	0.007	22	182.55
10	.	$g \times t$	8.69	0.004	16	197.06
11	$a_1 \times t, a_2$	$g \times t$	10.57	0.001	24	181.02

Mean apparent survival probability averaged across the top three models (i.e., those that differed by < 2 in terms of QAIC_c) was 0.65 ± 0.06 (95% CI = 0.31–0.80) and 0.81 ± 0.04 (95% CI = 0.67–0.89) for newly marked and previously marked birds, respectively (Appendix 1). When corrected for the estimated rate of color-band retention, survival probability became 0.72 ± 0.06 (SE) and 0.91 ± 0.04 , respectively. Even though our survival estimate was based on a combination of metal band only and metal + color band birds, there was no evidence that applying an overall correction for color-band loss inflated the survival rate (Appendix 2). If we assume that newly marked birds (i.e., first age class) were actually a heterogeneous sample of (1) transients that we never re-encountered (thus apparent survival = 0) and (2) local birds with the same survival as that of previously marked birds, we can estimate the proportion of transients by $1 - \phi_{a1}/\phi_{a2}$ (Pradel et al. 1997). On the basis of this assumption, up to 18% of newly marked Long-tailed Jaegers at Alert may have been transients (see Discussion).

ENCOUNTER RATE

As expected, the probability of re-encounter of the two types of markers differed (all models in Table 2 retained this effect) and varied temporally in parallel (i.e., additive effect) in the two groups (sum of w_i for time = 0.83). The large annual variation in re-encounter probability is not surprising because observation effort varied by year. There was little evidence that years of high lemming abundance influenced re-encounter probability (sum of w_i = 0.17). In the best model, annual recapture probability averaged 0.17 ± 0.06 for birds marked with a metal band only, while the probability of resighting was 0.61 ± 0.05 for those marked with a combination of metal and color bands.

DISCUSSION

Our study presents the first estimate of the Long-tailed Jaeger's apparent annual survival rate calculated with modern capture–recapture methods. However, this estimate was derived from birds at the species' most northerly breeding site in the world and thus may not be representative of its whole breeding range. Nonetheless, the Long-tailed Jaeger is known to be well adapted to the High Arctic environment and may not be unduly stressed by this northerly location (Dekorte 1984, Dekorte and Wattel 1988, Wiley and Lee 1998). Moreover, the availability of anthropogenic food is thought to increase the jaegers' ability to breed at Alert in low lemming years (Julien 2012), but whether this could also affect the survival rate is unknown.

TRANSIENT BIRDS

The lower apparent survival of newly marked birds could be due to several factors. First, this effect could be due to mortality induced by the marking process, thereby leading to reduced

short-term survival. However, this is unlikely because individuals were never injured by the rocket-net and dead birds were never found at the study site following release. Second, our samples of newly marked birds could have been dominated by immature or first-time breeders, whose survival may be lower than that of older birds (i.e., a true age effect). Lower survival of immature birds (>1 year old) or first-time breeders has been reported in some seabirds (Bradley et al. 1989, Ratcliffe et al. 2002) but not in others (Aebischer and Coulson 1990, Weimerskirch 1992, Harris et al. 1994, Frederiksen and Bregnballe 2000, Jenouvrier et al. 2008). Even when such an effect is detected, however, survival of immature birds >1 year old is often only slightly reduced from that of adults. In our study, the difference in apparent survival between newly marked and previously marked birds (18%) appears too large to be due solely to a true age effect.

An alternative, and perhaps more plausible, explanation is that samples of newly banded birds included individuals that were not part of the local breeding population, i.e., transients that were temporary visitors to the site and never came back (e.g., Pradel et al. 1995). Parmelee and MacDonald (1960) reported that at Eureka, also on Ellesmere Island, many new jaegers visited the site throughout the summer. Similarly, Maher (1970) observed transient, nonbreeding birds at Lake Hazen, also on Ellesmere Island. The Long-tailed Jaeger is a long-lived bird and becomes sexually mature only after three or four years (Andersson 1976). As in other seabirds (Boulinier et al. 1996, Jenouvrier et al. 2008), immature individuals are thought to spend only a short period of time on land during the summer to forage and prospect for future breeding sites before returning to the sea (Dekorte 1984). Consequently, transient individuals could be either nonreproductive individuals prospecting for future breeding sites or failed breeders taking advantage of the food available from the sewage outfall of the military station, where most of the captures took place. Therefore, presence of these transients may have contributed to bias low the survival of newly marked birds.

LEMMING EFFECT

The hypothesis that the Long-tailed Jaeger's survival depended on variation in lemming abundance received little support. Although our estimate of lemming abundance was coarse, we are confident that we would have detected strong effects of lemming peaks on the jaeger's survival if present. However, we can not exclude the possibility of more subtle effects of rodent population cycles. Although the Long-tailed Jaeger's reproduction depends on lemming abundance, the jaeger is considered a semi-generalist predator because of its ability to eat a wide variety of alternative prey (bird eggs, young birds, fishes, and invertebrates; Maher 1970, Andersson 1976, Dekorte and Wattel 1988, Julien 2012). The jaeger's ability to find other food sources for its needs in low lemming years can buffer it from annual variations in lemming

abundance. At Alert, we observed jaegers feeding on invertebrates on the tundra, and the presence of an anthropogenic food source easily accessible from the sewage outfall of the military base (Julien 2012) is another factor that may explain why lemming abundance had a negligible effect on survival. Furthermore, we estimated survival on an annual basis, and the time the jaeger spends on the tundra during the summer represents only a short period (~3 months) of its annual life cycle. For most of the year, jaegers have a marine life and depend on completely different food resources.

Nonetheless, lemming abundance tended to have a weak, negative effect on apparent survival of birds in the first year after marking (i.e., first age class), which is surprising. This negative effect could be explained by the presence of transient individuals within the population of newly marked birds. Indeed, if more transients are attracted to the site in years of high lemming abundance than in other years, this could bias downward the apparent survival rate of the first age class. According to this hypothesis, the decline in apparent survival of newly marked individuals does not reflect a real decline in survival but an increase in permanent emigration due to the capture of a larger number of transients in high lemming years.

There was no evidence that lemming abundance affected encounter probability. Because Long-tailed Jaeger reproduction is strongly influenced by fluctuations in lemming abundance (Andersson 1981, Gilg et al. 2006, Therrien et al. 2013), we expected an increase in temporary emigration from the site due to individuals not breeding in years of low lemming abundance, and thus a decrease in capture probability. Three hypotheses could explain the absence of this effect. First, it could be due to the anthropogenic food (sewage outfall), which reduces the effect of annual variations in lemming abundance on the probability of breeding at Alert from that at other sites (Julien 2012). Second, the majority of birds were captured and observed at the sewage outfall and not at the nest. Even if there were more nonbreeders in low lemming years than in peak years, these individuals could stay at the site to take advantage of this anthropogenic food source, which is abundant and stable, and thus explain the absence of an effect of lemmings on re-encounter probability. Third, jaegers are believed to be faithful to their breeding sites, returning to the same area from year to year (Andersson 1981). At Alert, these birds may occupy territories even in years when they do not breed owing to low lemming densities (R. I. G. Morrison, unpubl. obs.), rendering them observable in both high and low lemming years.

SURVIVAL AND POSSIBLE CAUSES OF MORTALITY

The lack of temporal variability in adults' survival is not surprising considering that seabird populations are commonly rather stable (Furness and Monaghan 1987, Weimerskirch et al. 1987), with catastrophic mortality of adults being rare

(Cairns 1987). Indeed, because change in adults' survival has a strong effect on population growth in long-lived vertebrates, we expect this trait to be canalized (i.e., its variability reduced) via natural selection (Gibson and Wagner 2000, Gaillard and Yoccoz 2003). The only other estimate of survival rate available for the Long-tailed Jaeger is that of Andersson (1976), who estimated an annual rate between 0.84 and 0.91 from a small sample size and return rate (i.e., he did not account for capture probability), a method that usually underestimates survival (Lebreton et al. 1992). Although our estimate of annual survival probability (0.91) is still confounded by permanent emigration of local birds, it is likely low because of jaegers' high site fidelity (Andersson 1976, Parmelee and Pietz 1987, Pietz and Parmelee 1994, Davis et al. 2005). Survival rates are available for other species of *Stercorarius* such as the Parasitic Jaeger (*S. parasiticus*) in Scotland, where Furness (1987) estimated annual survival at 0.89 and Phillips and Furness (1998) estimated it at 0.90 (both estimates based on return rates only). Ratcliffe et al. (2002) reported survival probabilities between 0.81 and 0.96 for several species of skuas and gulls, and Jenouvrier et al. (2005) reported a value of 0.94 for the Snow Petrel (*Pagodroma nivea*), a seabird nesting in Antarctica. Since all these values are comparable to those of Long-tailed Jaegers at Alert, it suggests that the harshness of the climate, the low productivity of the habitat, and the long migration associated with this very northerly breeding site have no negative effect on adults' survival.

The longevity record currently reported for the Long-tailed Jaeger is about 8 years (Clapp et al. 1982). During our study, we recaptured one adult jaeger banded in 1987 in summer 2008, which means it was a minimum of 22 years old, a longevity similar to that reported for many species of gulls (Clapp et al. 1982).

At Alert, over the past 25 years, no adult Long-tailed Jaeger has been found dead naturally or killed by a predator during the breeding period (R. I. G. Morrison, pers. obs.), even though the arctic fox (*Vulpes lagopus*), a potential predator, is present. This suggests that mortality of adults during the summer may be lower than during other phases of the annual cycle such as the migration or winter. The lack of clear differences in survival between low and high lemming years also suggests that much of the annual mortality may take place away from the nesting grounds. Food availability during winter appears to be an important factor affecting annual survival of seabirds (Hüppop and Wurm 2000, Furness et al. 2006). Little is known, however, about the Long-tailed Jaeger's winter range and even less about food availability there. In contrast to some other seabirds (Weimerskirch et al. 1997, Véran et al. 2007), including skuas (Brothers et al. 2010), there is no evidence that human activity is a source of offshore mortality for the Long-tailed Jaeger. Nevertheless, there is a need for additional studies of jaeger survival linked to large-scale oceanographic and climatic variations during the nonbreeding period.

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