Testing for Geographic Variation in Survival of Spectacled Eider (*Somateria fischeri*) Populations in Chukotka, Russia and the Yukon-Kuskokwim Delta, Alaska

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(Received 8 July 2016; accepted in revised form 4 April 2017)

ABSTRACT. Information on variation in survival among geographically distinct breeding populations can produce valuable insights about the population dynamics of a species. The Yukon-Kuskokwim Delta sub-population of Spectacled Eiders in Alaska decreased precipitously between the 1950s and 1990s. Causes for this decline are unknown but may be attributed to low female survival due to predation and lead exposure on the breeding grounds. From 2014 to 2015, we compared annual survival probabilities of Spectacled Eiders on Kigigak Island in the Yukon-Kuskokwim Delta, Alaska, and Ayopechan Island in the Chaun Delta, Chukotka, where similar field protocols were implemented. A Cormack-Jolly-Seber maximum likelihood approach was used to estimate apparent survival (φ) and recapture probability (p) from mark-resight data. We tested a) whether Russian and Alaskan sub-populations differed in their survival rates, b) whether survival varied annually, and c) whether survival followed an increasing or decreasing trend over time at either site. We found no evidence for differing survival between the two breeding areas when mean survival across years was compared, and we did not find strong evidence for a linear trend in survival over time at either site. Furthermore, our data supported models with annually varying survival at Kigigak Island and constant survival at Ayopechan Island. Sample size constraints precluded estimates of annual survival at Ayopechan Island. Our finding of no difference in mean survival between sites lends support to the idea that survival may be a function of conditions on the wintering grounds.

Key words: Spectacled Eider; Somateria fischeri; Kigigak Island; Ayopechan Island; annual survival rate; recapture probabilities

RÉSUMÉ. Les données en matière de variations de survie chez des populations nicheuses géographiquement distinctes peuvent donner un précieux aperçu de la dynamique des populations d'une espèce. La sous-population d'eiders à lunettes du delta Yukon-Kuskokwim, en Alaska, a chuté abruptement entre les années 1950 et les années 1990. Nul ne connaît les causes de ce déclin, mais elles pourraient être attribuables au faible taux de survie des femelles en lien avec la prédation et l'exposition au plomb dans les aires de reproduction. De 2014 à 2015, nous avons comparé les probabilités de survie annuelle des eiders à lunettes sur l'île Kigigak, dans le delta Yukon-Kuskokwim, en Alaska, et sur l'île Ayopechan, dans le delta Chaun, au Tchoukotcha, où des protocoles d'étude similaires sur le terrain ont été adoptés. La méthode du maximum de vraisemblance Cormack-Jolly-Seber a servi à estimer la survie apparente (φ) et la probabilité de recapture (p) à partir de données de marquage et de relocalisation. Nous avons tenté de déterminer a) si les sous-populations de la Russie et de l'Alaska avaient des taux de survie différents, b) si les taux de survie variaient d'une année à l'autre et c) si le taux de survie affichait une tendance à la hausse ou à la baisse au fil des ans à l'un ou l'autre des sites. Nous n'avons trouvé aucune preuve justifiant le taux de survie différent aux deux aires de reproduction au moyen de la comparaison des moyennes de survie au fil des ans, et nous n'avons pas trouvé de preuve importante permettant de déceler une tendance linéaire au fil des ans en matière de survie à l'un ou l'autre des deux sites. De plus, nos données ont permis d'étayer des modèles ayant des taux de survie annuels variables à l'île Kigigak et des taux de survie constants à l'île Ayopechan. Des contraintes en matière de taille d'échantillons ont empêché de faire l'estimation des taux de survie annuels à l'île Ayopechan. Le fait que nous n'ayons pas trouvé de différence entre les moyennes de survie des deux sites soutient l'idée selon laquelle la survie peut être tributaire des conditions des aires d'hivernage.

Mots clés : eider à lunettes; Somateria fischeri; île Kigigak; île Ayopechan; taux de survie annuel; probabilités de recapture

Traduit pour la revue Arctic par Nicole Giguère.

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РЕЗЮМЕ. Данные об изменении выживаемости в географически обособленных гнездовых популяциях позволяют понять тенденции динамики популяций рассматриваемого вида. В период с 1950-х по 1990-е гг. наблюдалось резкое снижение численности гнездовой популяции очковой гаги в дельте рр. Юкон-Кускоквим, предположительно обусловленное низкой выживаемостью взрослых самок из-за сильного пресса хищников и отравления птиц свинцом в районах гнездования. Мы сравнивали показатели ежегодной выживаемости взрослых самок очковой гаги на о. Кигигак, дельта рр. Юкон-Кускоквим, Аляска, США и на о. Айопечан, дельта рр. Чаун-Пучевеем, Чукотка, Россия. Идентичные полевые протоколы были разработаны и применены в обоих районах исследования. Метод максимального правдоподобия Кормака-Джоли-Себера использовался для оценки ежегодной выживаемости (ф) и вероятности обнаружения (р) птиц по данным повторных отловов. Мы проверяли: а) существование статистически значимых различий в выживаемости самок очковой гаги чукотской и аляскинской популяций в период с 2002 по 2015 гг.; б) межгодовые колебания ежегодной выживаемости; в) наличие тенденций повышения или понижения выживаемости с течением времени в каждой из популяций. Мы не выявили статистически достоверных различий в выживаемости самок из двух районов гнездования, а так же не обнаружили тренда выживаемости со временем ни в одной из популяций. Данные, которыми мы располагаем, позволили оценить ежегодную выживаемость самок на о. Кигигак и, по причине недостатка данных, среднюю межгодовую выживаемость самок на о. Айопечан. Наши выводы о том, что выживаемость самок одинакова в обеих популяциях, позволяют предположить, что на выживаемость очковых гаг в меньшей степени влияют условия гнездовых территорий, чем комплексные условия акватории зимовки.

Ключевые слова: очковая гага; Somateria fischeri; о. Кигигак; о. Айопечан; ежегодная выживаемость; вероятность обнаружения

INTRODUCTION

Among the four species of eiders, the Spectacled Eider (Somateria fischeri, Brandt 1847) has the smallest geographical range, which includes the environs of the Bering Strait to Beringia. Most, if not all, Spectacled Eiders overwinter in pack ice leads (polynyas) in a small area (about 50×75 km) centered between St. Lawrence and St. Matthew Islands in the Bering Sea (62° N, 173° W, Petersen et al., 1995, 1999). Winter surveys indicate a worldwide population of more than 370 000 Spectacled Eiders (Larned and Tiplady, 1999). There are three distinct breeding populations of Spectacled Eiders worldwide: (1) western Alaska, on the Yukon-Kuskokwim Delta (hereafter Y-K Delta); (2) the Arctic Coastal Plain in northern Alaska; and (3) Russia, along the Arctic coast of eastern Siberia. The Russian population occupies a coastal strip 1740 km long from the Yana Delta $(136^{\circ} E)$ in the west to the Ekvyvatap Delta (179° E) in the east (Dau and Kistchinski, 1977; Hodges and Eldridge, 2001; Solovyeva, 2015). Historically, the number of Spectacled Eider breeding pairs on both sides of the Bering Strait was thought to be almost equal (Dau and Kistchinski, 1977; Petersen et al., 2000). But in recent years, the vast majority of Spectacled Eider breeding pairs have been observed in Russia (Hodges and Eldridge, 2001). The Y-K Delta population of Spectacled Eiders has increased from a low of 1066 breeding birds in 1992 to 5838 birds in 2014, with a growth rate of 1.064 (90%) CI = 1.056 - 1.075; Platte and Stehn, 2015). The Russian population has not been monitored as extensively, but populations on Ayopechan Island on the Chaun Delta were assessed as stable between 2002 and 2007, but decreased between 2007 and 2015 (Kokhanova and Solovyeva, 2015). The Spectacled Eider is listed as threatened throughout its range in North America (U.S. Federal Register, 1993)

and is proposed for listing under the Red Data Book of the Russian Federation.

Populations of Spectacled Eiders appear to respond strongly to variation in adult female survival (Flint et al., 2016), which is thought to be a function of predation rates, lead exposure on the breeding grounds (Grand et al., 1998; Flint et al., 2000), and weather conditions on the wintering grounds in the Bering Sea. There is evidence that adult survival on the Y-K Delta was influenced by the presence of lead shot (Grand et al., 1998), which may have contributed to declines in the 1980s and 1990s (Stehn et al., 1993). From 1995 to 1998, 14.2% of females sampled at Kigigak Island, Y-K Delta, had been exposed to lead prior to being captured (Grand et al., 1998). A ban on the use of lead shot for waterfowl hunting in 1991 likely reduced deposition of lead into wetlands in Alaska (Flint and Schamber, 2010); therefore, birds nesting on the Y-K Delta in recent years are expected to have relatively low lead exposure rates. In comparison, between 2003 and 2008, 10.7% of adult females captured on Ayopechan Island, Chaun Delta, were known to have lead levels over the exposure threshold (Solovyeva, 2009; Solovyeva and Solovyev, 2010). In addition to temporal differences in lead shot exposure, differences between the two sites in habitat quality, predator abundance, and hunting pressure may have resulted in different survival rates.

Conditions on the wintering grounds may be an important factor influencing adult survival (Flint et al., 2016). Typical conditions on the wintering area in the northern Bering Sea include short days, cold temperatures, variable ice cover, frequent storms with strong winds, and severe ice conditions. Under conditions of nearly continuous sea ice, Spectacled Eiders have been observed in very dense flocks concentrated in small patches of open water. Variation in benthic food availability mediated by

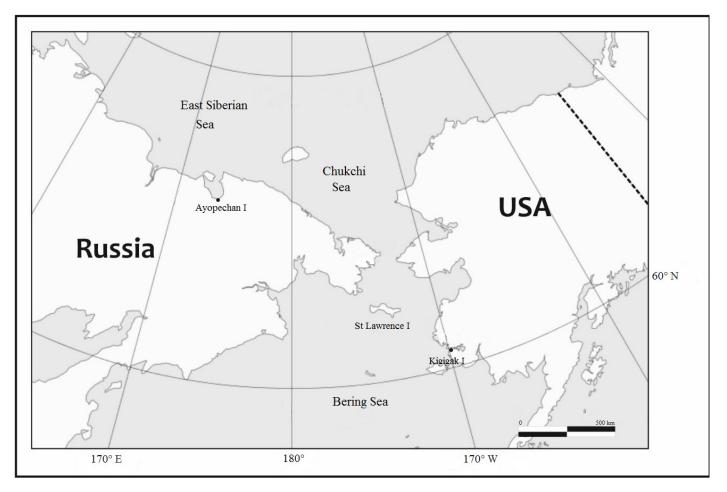


FIG. 1. General map of Beringia region showing Kigigak Island and Ayopechan Island, where Spectacled Eiders were studied from 2002 to 2015.

sea ice dynamics, as well as extreme weather events in the Bering Sea, are thought to influence eider survival in the winter (Bump and Lovvorn, 2004; Peterson and Douglas, 2004). Flint et al. (2016) found reductions in annual survival of Spectacled Eiders marked on the Y-K Delta in years with longer periods of very dense sea ice. If survival is primarily a function of conditions on the wintering grounds, we would expect concurrent fluctuations in annual survival across geographically disparate breeding populations.

Management of the worldwide Spectacled Eider population should account for the meta-population structure and consider variation in vital rates within and between sub-populations (Flint et al., 2016). The survival rates of adult females and ducklings have been published for the western Alaskan Spectacled Eider sub-population (Flint and Grand, 1997; Moran, 2000; Petersen et al., 2000; Flint et al., 2016). However, survival rates of Russian subpopulations have not yet been published or compared to those of other sub-populations. This paper compares the survival of Spectacled Eiders from breeding populations in western Alaska and the Chaun Delta, Russia, using capturemark-recapture data from 2002 to 2015. As far as we know, this is the first time a quantitative analysis comparing adult survival of Russian and Alaskan populations of Spectacled Eiders has been conducted. Our primary objective was to

test whether Russian and Alaskan populations differed in their survival rates over the study period. We also tested alternative hypotheses that survival varied across years or followed a linear trend over time.

STUDY AREA

The study was conducted at Kigigak Island (KI) on the Yukon-Kuskokwim Delta, Alaska, USA, and at Ayopechan Island (AI) on the Chaun Delta, Chukotka, Russia (Fig. 1). Kigigak Island (32.5 km²; 60°50' N, 165°50' W; maximal elevation 1-3 m asl) is located off the western coast of Alaska, approximately 140 km west of Bethel, Alaska. Bordered by the Ninglick River and the Bering Sea, KI contains many shallow ponds, lakes, and a network of tidal sloughs. The habitat consists of low coastal and upland moss-lichen tundra and sedge meadows. Spring and autumn tides regularly inundate the island except for upland areas, which are flooded only during severe storm tides. KI has a subarctic climate, which includes moderate summer temperatures (daily mean temperature of 12.5°C in June and July, 2002-14) that are influenced by the Bering Sea (NOAA, 2017). Winter temperatures are mostly continental because of the presence of sea ice (November-March).

Overall waterfowl density on KI is 6–18 individuals per km² (Harwood and Moran, 1993). Breeding numbers of Common Eiders (*Somateria mollissima*) are similar to those of Spectacled Eiders, whereas King (*S. spectabilis*) and Steller's Eiders (*Polysticta stelleri*) are rare.

Ayopechan Island (91 km²; 68°50' N, 170°30' E; maximal elevation 5-6 m asl) is the largest island within the Chaun Delta and was formed by the joining of the Chaun, Pucheveem, and Palyavaam Rivers, where they enter Chaun Bay on the East Siberian Sea. The habitat of the island consists of well-developed peat bogs, thermokarst lakes, and alas depressions, which are typical on the higher parts of the island. AI contains many lakes and ponds of different form, size (up to 2 km²), and depth, and it is regularly flooded by wind-induced autumn tides. The water on AI is mostly brackish except for upland lakes and ponds, which tend to have fresh water. A well-developed network of tidal sloughs is located on the northern side of AI. The climate is typical for Arctic Siberia: mean daily July temperature in 2002-14 was 10.5°C, and snowfall and frost are possible in any season. Overall waterfowl densities on AI are approximately 9-11 individuals per km² (D. Solovyeva, unpubl. data.).

METHODS

Field Methods

Similar field protocols were developed and implemented at both study sites (Grand, 1993). During 2002-15, teams of two to four individuals searched 33 to 47 0.17 km² plots on KI and 15 to 52 1 km² plots on AI. Spectacled Eiders were captured in 2002-15 at KI and in 2002-05, 2007-13, and 2015 at AI. Bow nets and mist nets were used at both sites to trap nesting Spectacled Eider females between the 20th and 24th days of incubation (Salyer, 1962). At KI, adult females were marked with U.S. Geological Survey metal tarsal bands and alphanumeric yellow plastic tarsal bands and nasal discs (Lokemoen and Sharp, 1985). At AI, adult females were marked with Moscow metal tarsal bands and alphanumeric red plastic tarsal bands or individual combinations of colored tarsal bands. No nasal discs were applied to females at AI. At both sites, birds were re-sighted from live recaptures, visual observations, and photographs of nasal discs and coded plastic tarsal bands.

Data Analysis

We used a Cormack-Jolly-Seber maximum likelihood approach to estimate annual apparent survival (φ) and recapture probabilities (*p*) from the mark-resight data (Lebreton et al., 1992). We used program MARK (White and Burnham, 1999) with logit-link function for the analysis and estimated variance using the second partial derivative (Flint and Grand, 1997; Grand et al., 1998; White and Burnham, 1999). We considered only adult females in the survival analysis. Nesting females, brood-rearing females, and non-breeding females were combined for analysis to increase our sample size, assuming that survival was equal for breeding and non-breeding females (failed breeders). Adult females originally marked as ducklings first entered the capture history upon their first year of documented return (first encounter). A total of 594 encounter histories were obtained (459 on KI, and 135 on AI) for the years 2002–15 (Table 1).

We used an information-theoretic approach to evaluate models of p that varied between sites and over time (Burnham and Anderson, 2002). We considered p as a function of year (categorical), site, year + site, and year*site. For year*site models, we were unable to model annual p at AI because of sample size constraints; therefore, p was modeled as constant at AI, but annual at KI. Once the most parsimonious model of p was selected, models of φ were constructed. We modeled φ as a function of site, year, year as a continuous variable to reflect a trend over time (Time), year + site, site*Time, and site*year (KI only). For this model, sample size constraints precluded the estimation of annual survival at AI; therefore, survival was modeled as a constant at AI, but time-varying at KI. We also tested models assuming p and φ were constant. In addition to these models, we fit four models with year as a random effect. We fit the following random effects models: φ (intercept only, sites combined), φ (linear trend, sites combined), $\varphi($ intercept only, sites separate), $\varphi($ intercept only for KI, constant at AI). For random effects models, we interpret "shrinkage estimates," which reflect process variation in survival, equivalent to the maximum likelihood estimate with sampling variation removed (Burnham and White, 2002). Goodness-of fit was evaluated using the median ĉ test (Lebreton et al., 1998).

RESULTS

Because the number of females resighted at AI was low (31 birds), we could fully parameterize the time-dependent models of p and φ only at KI. We fixed p to zero at AI in 2006 and 2014 because no data were collected in those years, and also in 2004 because of the small sample size. Goodness-of-fit tests indicated that the global model fit the data reasonably well ($\hat{c} = 1.25$). We corrected for this slight overdispersion by incorporating ĉ (the variance inflation factor) into calculations of the quasi Akaike information criterion (QAIC). QAIC values were used in the subsequent model selection process. The best-fitting approximation model for *p* indicated that detection of adult female eiders varied over time at KI, with a constant *p* at AI (Table 2). Estimates of p ranged from 0.19 ± 0.04 (SE) to 0.62 ± 0.05 at KI, with a mean of 0.49 ± 0.02 across all years. Recapture probability at AI (all years combined) was 0.18 ± 0.04 (Table 3). The highest-ranked model of apparent survival was the intercept-only random effects model for KI, with survival modeled as a constant fixed effect at AI (QAICc

Year	Kigigak Island			Ayopechan Island			
	Adult females	Duckling females	Duckling males	Adult females	Adult males	Ducklings (sex unclear)	
2002	62	83	64	7	_	_	
2003	44	36	24	22	-	3	
2004	51	66	61	20	_	19	
2005	32	51	54	8	_	-	
2006	33	49	42	_	_	_	
2007	36	52	59	7	-	_	
2008	17	46	33	6	_	_	
2009	24	-	_	12	-	_	
2010	25	-	_	12	5	_	
2011	26	-	_	10	-	_	
2012	40	34	46	10	-	_	
2013	21	28	16	9	_	_	
2014	31	21	34	_	1	-	
2015	17	19	16	12	_	-	
Total	459	485	449	135	6	22	

TABLE 1. Number of Spectacled Eiders banded at two study sites, Kigigak Island, Alaska, and Ayopechan Island, Russia, from 2002 to 2015.

TABLE 2. Model selection results for recapture probability (p) and survival probability (φ) of Spectacled Eiders captured on Kigigak Island, Alaska (KI) and Ayopechan Island, Russia (AI) from 2002 to 2015. For models specifying "year at KI," survival was modeled as a function of year at KI but as a constant at AI because of sample size constraints at AI. For all survival models, p was modeled as a function of year at Kigigak Island.

	Model	Delta QAICc	AICc weights	Model likelihood	Num. Par	QDeviance
Survival probability	phi(.), Random Effects (intercept only for KI, constant at AI)	0.00	0.46	1.00	26	829.99
	phi(.), Random Effects (linear trend, sites combined)	1.79	0.19	0.41	26	831.78
	phi(.), Random Effects (intercept only, sites combined)	1.82	0.19	0.40	26	831.81
	phi(year)	3.61	0.08	0.16	27	831.52
	phi(year at KI)	3.77	0.07	0.15	28	829.59
	phi(year + site)	7.43	0.01	0.02	29	831.16
	phi(.), Random Effects (intercept only, sites separate)	25.85	0.00	0.00	37	832.75
	phi(linear trend*site)	39.29	0.00	0.00	18	885.84
	phi(linear trend)	40.73	0.00	0.00	16	891.39
	phi(site)	43.04	0.00	0.00	16	893.69
	phi(.)	42.06	0.00	0.00	15	894.76
Recapture probability	p(year at KI)phi(.)	42.06	0.00	0.00	15	894.76
1 1 5	p(year + site)phi(.)	59.04	0.00	0.00	16	909.69
	p(site)phi(.)	119.57	0.00	0.00	3	996.61
	p(year)phi(.)	140.44	0.00	0.00	14	995.19
	p(.)phi(.)	190.50	0.00	0.00	2	1069.55

weight = 0.46, Table 2). The next-highest ranked model was the linear trend model, with sites combined (QAICc weight = 0.19). Estimates of survival at KI ranged from 0.54 ± 0.05 in 2009 to 1.00 ± 0.00 in 2007, 2008, and 2012 (Table 3, Fig. 2). When survival estimates were close to 1, confidence intervals were not properly estimated, making it impossible to interpret the precision of these estimates. From 2003 to 2015, survival across all years was 0.77 ± 0.04 at AI and 0.82 ± 0.01 at KI.

DISCUSSION

We present a comparative analysis of survival of Spectacled Eiders from western Alaska and Russia based on data collected at two breeding sites: Kigigak Island in the Yukon-Kuskokwim Delta, Alaska, and Ayopechan Island in the Chaun Delta, Russia. Our analysis did not provide evidence that mean adult female survival rates differed substantially between AI and KI sub-populations or that the two sub-populations followed different trends over time. This finding lends support to the idea that adult female survival, over the study period, may be a function of conditions on the wintering grounds in the Bering Sea rather than on the breeding grounds in western Alaska and Russia (Flint et al., 2016). Apparent survival at KI fluctuated annually, from a low of 0.54 to a high of 1.00. Differences between sites may have existed, but they were likely relatively small compared to annual variability in survival and may not have been detectable because of the small sample at AI. Nevertheless, our data did not support the hypothesis that survival differed substantially between sites because of variation in lead concentrations or any other environmental factors that differed between breeding areas.

Site	Year	р	SE	Lower 95% CI	Upper 95% CI	φ	SE	Lower 95% CI	Upper 95% CI
Kigigak Island	2003	0.39	0.05	0.29	0.49	0.83	0.06	0.71	0.94
	2004	0.53	0.05	0.43	0.62	0.92	0.06	0.79	1.04
	2005	0.54	0.05	0.45	0.63	0.87	0.06	0.74	0.99
	2006	0.62	0.05	0.53	0.71	0.67	0.05	0.57	0.77
	2007	0.54	0.04	0.46	0.62	1.00	0.00	1.00	1.00
	2008	0.50	0.04	0.43	0.57	1.00	0.00	1.00	1.00
	2009	0.44	0.05	0.34	0.54	0.54	0.05	0.43	0.65
	2010	0.42	0.05	0.32	0.51	0.87	0.09	0.69	1.06
	2011	0.51	0.06	0.40	0.62	0.68	0.07	0.54	0.83
	2012	0.50	0.05	0.41	0.59	1.00	0.00	1.00	1.00
	2013	0.19	0.04	0.13	0.28	0.70	0.10	0.50	0.90
	2014	0.43	0.06	0.32	0.54	0.75	0.12	0.50	0.99
	2015	0.21	0.05	0.13	0.31	0.82	0.19	0.46	1.00
Avopechan Island	2003-15	0.18	0.04	0.12	0.27	0.77	0.04	0.68	0.84

TABLE 3. Parameter estimates for recapture (p) and survival (φ) probabilities from the best-supported model of Spectacled Eiders captured on Kigigak Island, Alaska, and Ayopechan Island, Russia, from 2002 to 2015.

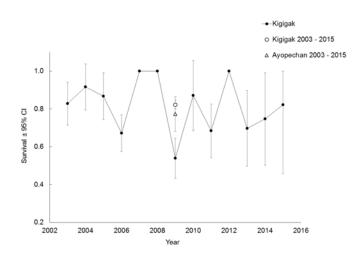


FIG. 2. Estimates of survival of adult female Spectacled Eiders at Kigigak Island, Alaska, and Ayopechan Island, Russia, from 2002 to 2015. Annual survival rates are shown for Kigigak Island, but only the mean survival rate is shown for Ayopechan Island, where the small sample size made it impossible to model annual rates. For comparison, we also show the mean survival rate from Kigigak Island.

Differences in recapture probability between the two sites may be explained by differences in tagging methods, survey effort, or rates of temporary emigration. Nearly all females tagged at KI during our study period had nasal discs, which may have influenced recapture probability. Females on KI were marked with nasal discs to increase recapture rates for incubating hens without disturbing them during incubation. In contrast, females on AI were marked only with leg bands, which could be difficult to read if the female was on the nest, moving through vegetation, or swimming. This fact may explain the higher overall recapture rate at KI ($p = 0.49 \pm 0.02$) compared to AI ($p = 0.18 \pm 0.04$).

Finally, breeding propensity, in which females forego breeding in some years, may also have influenced p. In Spectacled Eiders, female breeding propensity may be a function of body condition upon arrival at the breeding grounds, or it may be related to conditions on the nesting grounds such as snow cover, local food abundance (Federer et al., 2012), presence of protective species (Solovyeva and Zelenskaya, 2016), and predators (Flint et al., 2016).

Estimates of apparent survival will be biased low if permanent emigration is occurring. However, Spectacled Eiders are known to show strong site fidelity to breeding areas (Moran, 2000). Distances between nests of the same female Spectacled Eiders in consecutive years did not exceed 5 km on AI, with 40 km² of the 91 km² island searched annually (Kokhanova, 2014). On KI, distances between nests of Spectacled Eiders did not exceed 2.2 km in consecutive years, with 25 km² of 32.5 km² searched annually (Moran, 2000).

Spectacled eiders breeding on the Y-K Delta experienced a precipitous decline from 1957 to 1989, and then appeared to stabilize in subsequent years (Stehn et al., 1993; Ely et al., 1994; USFWS, 1996; Petersen and Douglas, 2004). This decline was attributed to decreased adult female survival, influenced at least in part by high predation rates and lead exposure on the Y-K Delta breeding grounds (Grand et al., 1998; Flint et al., 2000). Flint et al. (2016) developed demographic population models for Spectacled Eiders and demonstrated that the population growth rate would respond most strongly to variation in adult female survival. Thus, understanding geographic variation in survival is crucial to inferring variation in population dynamics. In our case, we found no evidence for variation in mean survival rates of females from two geographically distinct breeding populations. Flint et al. (2016) showed that with the annual survival and productivity observed at Kigigak Island, this sub-population should be increasing. We therefore suggest that the level of survival estimated for AI should be adequate to maintain the population at current levels, although further analyses will be required to assess geographic variation in productivity. Fluctuating annual survival may be a result of variable ice concentrations in the Bering Sea, which have been shown to correlate negatively with survival and population indices for this species (Petersen and Douglas, 2004; Flint et al., 2016). Our results, which show no difference in survival between Spectacled Eiders breeding in Alaska and in Russia from 2002 to 2015, support this idea. Accordingly, long-term patterns in population trends may be driven primarily by at-sea conditions during the non-breeding period (Flint, 2013).

ACKNOWLEDGEMENTS

We express our gratitude to the field crews that worked hard at both sites and made this paper possible. Logistics and transportation were provided to AI staff by Wrangel Island State Reserve in 2002-07, and transportation for personnel and cargo was provided by Chukotka Mining and Geological Company (a subsidiary of Kinross Gold) in 2010-15. Thank you to Andrey Semenov who completed many hours of technical work for the draft paper. We are extremely grateful to Paul Flint for his help with data analysis and interpretation, and we thank the anonymous reviewers for their helpful comments on the manuscript. We also thank two anonymous reviewers and David Safine for their help with earlier drafts. Fieldwork on AI was funded by the Fairbanks Fish and Wildlife Field Office of the U.S. Fish and Wildlife Service in 2003-05 and 2007-13 and by International Affairs of the U.S. Fish and Wildlife Service in 2015. Statistical analyses and draft writing were supported by the Russian Foundation for Basic Research (grant # 15-34-50267). Logistics and transportation were provided to KI staff by Yukon Delta National Wildlife Refuge pilots, Ptarmigan Air, Herman's Helicopters, and Hagelund Aviation Service. In addition, we thank the staff of the Yukon Delta National Wildlife Refuge, the Spectacled Eider Recovery Team, the Endangered Species Office in the Fairbanks Fish and Wildlife Field Office, the University of Alaska Fairbanks, the Alaska Sea Life Center, and others who have provided guidance and support for the KI project over the years.

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