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Effects of predator exclosures on nest survival of Red-necked Phalaropes

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English, W.B., E. Kwon, B.K. Sandercock & D.B. Lank. 2017. Effects of predator exclosures on nest survival of Red-necked Phalaropes. *Wader Study* 124(1): 00–00.

We placed wire mesh predator exclosures around the nests of Red-necked Phalaropes *Phalaropus lobatus* nesting at a tundra site outside of Nome, Alaska, in 2011 and 2012. Exclosures were made of 2.5 cm x 5.1 cm wire mesh and were approximately 0.8 m high, 0.8 m in diameter, with a flat top, and were secured to the ground with three metal stakes. We compared rates of nest success for these enclosed nests to those of unexclosed phalarope nests in 1994, 2010 and 2013. Both daily nest survival and apparent nest success of phalarope nests was higher in years with exclosures (daily nest survival of 0.990 ± 0.003 vs. 0.940 ± 0.007). We also compared the hatching success of enclosed phalarope nests to that of sympatrically nesting (unexclosed) Western Sandpipers *Calidris mauri* and Semipalmated Sandpipers *C. pusilla* in 2011 and 2012. Daily nest survival of enclosed phalarope nests was higher than for unexclosed sandpiper nests in the same years. The rate of nest abandonment was slightly higher for enclosed versus unexclosed phalarope nests (13 vs 2%), but we found no evidence that this was a result of adult mortality. At our site, predator exclosures were effective at substantially increasing hatching success. The effectiveness of similar exclosures elsewhere is likely to vary with the local predator community.

Keywords

abandonment
Arctic
hatching success
daily nest survival
Red-necked Phalarope
Phalaropus lobatus
predation
predator management

INTRODUCTION

Predators are the main cause of nest failure in ground-nesting birds, including shorebirds (Angelstam 1986). Increasing nest success by reducing predation can be desirable for conservation reasons, or for pursuing research questions that require successful nests (Schamel *et al.* 2004, Smith *et al.* 2011). Predation control must consider effectiveness, cost, ethics, and risks to the species of concern. Predator removal can be effective at increasing nesting success, but is costly and can be ethically contentious (Smith *et al.* 2011). Alternatively, predator exclosures placed around nests can be a cost effective way to increase nesting success. However exclosures can also have negative consequences, such as making nests more visible to predators and increasing nest abandonment or adult mortality (Isaksson *et al.* 2007, Hardy & Colwell 2008). Exclosures have been used successfully with several species of shorebirds, for example Snowy Plovers *Charadrius nivosus* (Hardy & Colwell 2008), Pectoral Sandpipers *Calidris melanotos* (Estelle *et al.* 1996), and Northern Lapwings *Vanellus vanellus* (Isaksson *et al.* 2007). However, even exclosures that increase nest success can have net negative effects on a population. For example, the mortality of

incubating adults can be increased if exclosures make incubating adults more visible or delay them from flushing from the nest when threatened (Barber *et al.* 2010). Finally, exclosures might increase predation on newly-hatched chicks by making predators aware of the location of a nest.

The effectiveness of predator exclosures has varied with factors such as a species' flight response, exclosure design and the community of predators in an area (Estelle *et al.* 1996, Mabee & Estelle 2000, Isaksson *et al.* 2007, Barber *et al.* 2010). For example, if exclosures impede birds from quickly leaving the nest, shorebird species that flush only when predators are close may suffer from higher adult mortality than species that flush when predators are distant. Predator exclosures used for shorebirds have varied greatly in size, shape, weight and cost, ranging from a circumference of 3 m for Western Sandpipers *C. pusilla* (Niehaus *et al.* 2004) to 30.5 m for Piping Plovers *Charadrius melanotos* (Rimmer & Deblinger 1990). While larger exclosures may be feasible when nest numbers are low and nests are easily accessible, smaller designs may be more suitable for remote areas, accessed on foot, or where large numbers of exclosures are needed. Exclosures

used to deter mammalian predators that are adept at digging, such as foxes, may benefit from being more firmly anchored to the substrate, and having elements of the enclosure that go below the ground surface (e.g. Estelle *et al.* 1996).

The most extensive use of predator exclosures for North American shorebirds has been to protect the nests of Piping and Snowy Plovers. The Piping Plover is listed as endangered in Canada, and populations of both species are federally listed as endangered in the United States (Barber *et al.* 2010). For these species, the effectiveness of nest exclosures has been mixed. In Colorado, Mabee & Estelle (2000) found that exclosures had no significant effect on daily nest survival for nests of Snowy Plovers, Piping Plovers, or Killdeer *C. vociferous*. Exclosures increased nest success, but also adult mortality, for a population of Piping Plovers on Prince Edward Island (Barber *et al.* 2010). Rimmer & Deblinger (1990) found that large exclosures (perimeter length of 30.5 m) increased nest success with no known negative effects for Piping Plovers in Massachusetts. These mixed results underscore the variability in the effectiveness of exclosures across species, sites and predator communities.

We used exclosures to protect the nests of Red-necked Phalaropes *Phalaropus lobatus*, to maximize nest survival for another study (English 2014, English *et al.* 2014). Here, we report on the effectiveness of these exclosures at increasing nesting success, and evaluate their potential effects on the mortality of incubating males. We compare daily nest survival in two years when exclosures were used (2011 and 2012) with daily nest survival in years when no exclosures were used (1994, 2010, and 2013). As nest success can be highly variable among years for Arctic-breeding shorebirds (Smith *et al.* 2007), we also tested whether phalarope nest survival was higher in years with exclosures relative to nest survival of two sympatrically nesting sandpiper species whose nests were unexclosed in all years. Although species differ in nest survival and the magnitude of its year-to-year variation (Underhill *et al.* 1993, Smith *et al.* 2012), we nonetheless believe that this comparison provides some information on the general effectiveness of predator exclosures in the tundra environment.

Predator exclosures may increase nest survival, but if they also increase predation of adults, there can be a net negative effect on population growth rate (Barber *et al.* 2010); without evidence of mortality (i.e., feathers or remains; Murphy *et al.* 2003) or subsequent sightings of living, banded adults, this adult mortality can be difficult to distinguish from nest abandonment. We tested whether males who apparently abandoned an exclosed nest were less likely to be resighted in a subsequent year than other breeding males. If a lower proportion of birds who abandon are resighted, this suggests that some of the abandoned nests may have been the result of adult mortality. Ours is the first study of nest exclosures for any species of phalarope, a group of small-bodied shorebirds in which only males incubate. Red-necked Phalaropes

nest on wet tundra throughout the circumpolar Arctic, and their nesting habitat and parental care strategy differs from the few species on which exclosures have been used in the Arctic (e.g., Estelle *et al.* 1996, Niehaus *et al.* 2004). In light of variable effectiveness observed in previous studies, our results add to knowledge of the effectiveness of exclosures in Arctic environments.

METHODS

We searched for Red-necked Phalarope, Semipalmated Sandpiper and Western Sandpiper nests over ~4 km² area of coastal tundra 21 km east of Nome, Alaska (64°20'N, 164°56'W; see also Sandercock 1997, 1998a,b, English *et al.* 2014) during five breeding seasons in 1994 and 2010–2013. The majority of nests were found by flushing incubating adults, however a smaller number were found by following birds as they returned to their nests. Incubating males were banded with unique colour band combinations and a metal band. As phalaropes spend most of their time in the water where colour bands are difficult to resight, most returning birds were recaptured or resighted at the nest.

Although there was some evidence of Red and Arctic Fox (*Vulpes vulpes*, *V. lagopus*) at our study site, the main egg-predators appeared to be avian. Quantitative estimates of the relative importance of each predator are lacking for this site. Common Ravens *Corvus corax*, Parasitic Jaegers *Stercorarius parasiticus*, Mew Gulls *Larus canus* and Glaucous Gulls *Larus hyperboreus* were observed daily at the site. Long-tailed Jaegers *Stercorarius longicaudus* and Sandhill Cranes *Grus canadensis* were occasionally present.

We estimated hatching date using the average incubation length for nests found during laying (Rubega *et al.* 2000), and by floating eggs of complete clutches (Liebezeit *et al.* 2007). We visited nests approximately every five days until four days prior to the estimated hatch date, when nests were visited every other day. Once signs of hatching were observed (e.g., star cracks), we visited nests daily until hatch. Nests were classified as successful if at least one chick was seen, or a nest survived until its predicted hatch date and shell fragments and a flattened nest cup were observed (Mabee *et al.* 2006). Nests were considered depredated if contents disappeared unexpectedly and no signs of hatching were present. Sandpiper nests were considered abandoned if the nest was visited three times with no parents seen and eggs cold. Data from two years when phalarope nests were protected with exclosures and instrumented with temperature monitors showed that multiple visits were required to correctly identify abandonment for phalaropes. Subsequent to this finding, phalarope nests were classified as abandoned based on the absence of an incubating male attending the nest during multiple visits. As few nests were classified as abandoned in years prior to the use of exclosures, we do not believe this change in classification has influenced our results. Nests where the fate was unknown and nests that were destroyed by flooding were excluded from our

analyses. We also excluded the nests of Semipalmated Sandpipers that were equipped with geolocators in 2013, as tags had a negative effect on nesting success (Weiser *et al.* 2016).

Data from 1994 were obtained from a previous study at the same site and using similar methods for nest searching, monitoring, and fate designation (see Sandercock 1997). No exclosures were deployed in that year. We used these data to describe nest success for Red-necked Phalaropes, Western, and Semipalmated Sandpipers.

For 2010–2014, we monitored unexclosed Western and Semipalmated Sandpiper nests in all four years. We monitored unexclosed Red-necked Phalarope nests in 2010 and 2013, and deployed predator exclosures on phalarope nests in 2011 and 2012. For nests found with four eggs, we installed exclosures 1–2 d after nest discovery, but we delayed deployment of the exclosure until the start of incubation for nests found during egg-laying, as birds are thought to be more likely to abandon due to disturbance during this time. Exclosures were left in place until after the chicks had left the nest (generally <24 h after hatch) or until the nest was classified as abandoned or depredated. Exclosures were cylindrical (ca. 0.8 m high and 0.8 m in diameter, with a closed top), and constructed of 2.5 cm x 5.1 cm (1" x 2") wire fencing. Exclosures were spray-painted a dark matte green, and once dry, were submerged in a pond for several days to decrease the scent of the paint. Exclosures were placed over the nests and secured by three 15 cm pieces of wire bent over the base of the cylinder, and pushed into the ground. Phalaropes often build their nests on loose substrates such as sedges and floating vegetation; therefore despite the wire used to secure the exclosure, some could be dislodged easily.

Analyses

We report apparent hatch success (successful/total nests) for each species in each year. To determine whether fate (hatched, depredated, or abandoned) differed between exclosed and unexclosed phalarope nests, we compared the distributions of fates across years with (2011, 2012) and without (2010, 2013) exclosures using a contingency chi-square test.

We used the RMark package in program R to estimate daily nest survival rate (DSR) for all species (Laake 2013). Because exclosures were deployed for another study, we lack nests of phalaropes with and without exclosures in

the same year for direct comparison. We therefore developed separate sets of candidate models for estimating the effect of exclosures on phalarope DSR among years, and for determining whether phalaropes and sandpipers showed a similar relationship between DSR and year. This allowed us to indirectly test for exclosure effects for Red-necked Phalarope nests while controlling for annual variation; higher phalarope DSR in the two exclosure years (2011, 2012), and higher DSR relative to sandpipers, is taken as evidence of a positive effect of exclosures on nest survival. We used Akaike's information criterion (AIC) to determine the most parsimonious model. Four phalarope nests from 2011 and 11 nests from 2012 were depredated prior to installing exclosures. We excluded these nests from our analysis as they would have introduced bias: the lack of the exclosure treatment was a direct consequence of depredation. We also excluded 31 exclosed phalarope nests for which clutch size was manipulated as part of another study, since the manipulation itself could have affected abandonment rates.

We used Fisher's exact test (two-tailed) to compare the resighting rate in subsequent years for males that apparently abandoned nests with exclosures, versus all other nesting male phalaropes. To maximize sample size we used all exclosed nests in this analysis, including those subject to experimental clutch manipulation, as exclosure-related mortality was possible regardless of the experimental treatment.

RESULTS

Exclosures were in place from 1 to 36 days, with a mean of 14.3 ± 6.6 days. Apparent hatching success rates varied among years and species (Table 1). Rates ranged 25–87% for Red-necked Phalaropes, 41–81% for Western Sandpipers, and 25–77% for Semipalmated Sandpipers (Table 1).

For phalaropes, no exclosed nests were depredated whereas 58% of unexclosed nests were lost to predators. However, rates of nest abandonment were higher for exclosed nests (13 of 89 nests or 15%, 2011–2012) than unexclosed nests (2 of 91 nests or 2%, 2010, 2013; Table 2). The odds of nest abandonment by a male phalarope increased seven-fold if an exclosure was deployed at the nest (odds ratio = 7.54, 95% CI = 1.63–71.1, Fisher's exact test: $P < 0.003$). Within exclosure treatment, there was no difference in patterns of nest fate among years (Table 2; $\chi^2 = 0.74$, df = 1, $P = 0.39$ and $\chi^2 = 1.18$, df = 2, $P = 0.55$ for exclosed

Table 1. Apparent hatch success (% of nest found that were observed to hatch) for the species and years included in the study. Sample sizes (total number of nests found) are in parentheses. Red-necked Phalarope nests with exclosures are marked with *.

Species	1994	2010	2011	2012	2013
Red-necked Phalarope	25 (24)	39 (19)	86 (22*)	87 (67*)	40 (73)
Semipalmated Sandpiper	25 (59)	75 (24)	57 (56)	77 (56)	45 (38)
Western Sandpiper	48 (52)	81 (37)	60 (68)	65 (69)	41 (46)

and unexclosed nests, respectively). There was no significant difference between the likelihood of resighting a male that previously abandoned an exclosed nest, versus the likelihood of resighting any other male (Table 3; Fisher's exact test: $P = 0.76$, $n = 110$).

Daily survival rates for Red-necked Phalarope nests were substantially higher in the two years when exclosures were used as compared to the years without exclosures (0.990 ± 0.003 vs. 0.940 ± 0.007). A model including exclosure presence as a variable was an improvement of 46 AIC units over the null model, and was therefore strongly supported (Akaike weight ~ 1).

Phalarope nests also had higher survival rates than did the nests of sandpipers in years when exclosures were used (Fig. 1). For the three-species model of daily nest survivorship, the full model containing the effects of year, species, year*species was the most parsimonious (Table 4). Relative to phalarope DSR, both sandpipers had lower DSR in years when phalarope nests were protected by exclosures, and higher DSR when phalarope nests were not exclosed (Table 5).

DISCUSSION

Predator exclosures at our site east of Nome substantially increased nesting success of Red-necked Phalaropes. Exclosed nests had a DSR of 0.990, whereas unexclosed nests had a DSR of 0.940. Assuming constant DSR and a 21-day incubation period, these rates would result in a newly laid nest having a 76% chance of hatching if exclosed, and a 27% chance of hatching if unexclosed. The predicted difference in hatching success from the DSR estimate is consistent with the observed difference in apparent hatching success: hatching success was 54% higher in years when exclosures were used.

The exclosures also increased nest abandonment, but the net effect on population growth rate is still assumed to be positive. If we assume that the small (and non-significant) difference in return rate between males who abandoned exclosed nests and those who did not was a result of mortality due to the exclosure, the maximum potential cost in terms of increased male mortality would be 1% (estimated from the % increase in abandonment multiplied

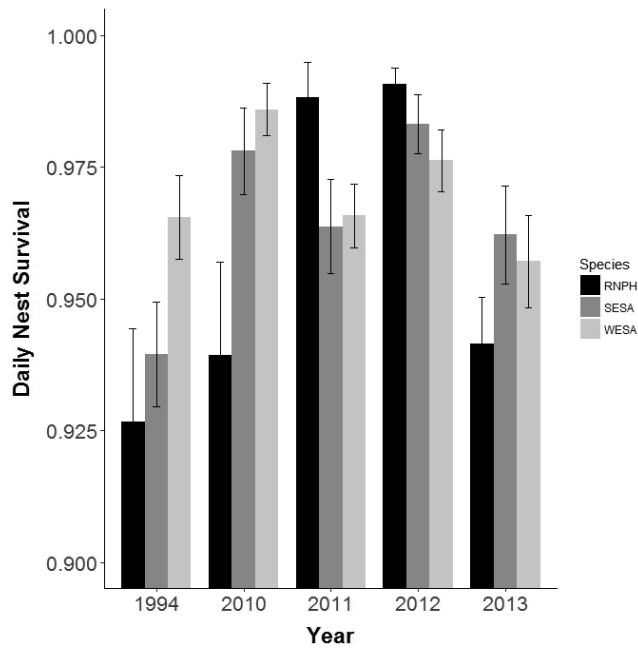


Fig. 1. Daily nest survival (\pm SE) in Red-necked Phalarope (RNPH), Western Sandpiper (WESA), and Semipalmated Sandpiper (SESA). Red-necked Phalarope nests were protected by predator exclosures in 2011 and 2012.

by the % decrease in return rate for exclosed nests). Although adult survival is often the most sensitive parameter in shorebird demographic models (Hitchcock & Gratto-Trevor 1997, Sandercock 2003), the large increase in reproductive success would in this case likely outweigh the small possible increase in male mortality.

Nest success

The main nest predators at our site are believed to be Parasitic Jaegers and Common Ravens, species that depredate the nests of both phalaropes and sandpipers. We therefore expected nest success to covary annually across species for unexclosed nests. This was observed in general, with sandpipers exhibiting higher nest-survival than phalaropes in all three years without exclosures (although the relative

Table 2. Apparent nest fate by year in Red-necked Phalaropes.

Year	2010		2011*		2012*		2013	
	Unexclosed		Exclosed		Exclosed		Unexclosed	
Nest fate	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>
Hatched	39	7	86	19	87	58	40	29
Depredated	56	10	0	0	0	0	59	43
Abandoned	6	1	14	4	13	9	1	1
Total		18		23		67		73

*Years with exclosures

survival of Western and Semipalmated Sandpipers varied). In both years with exclosures, this pattern was reversed; hatch success was highest overall for phalaropes. This result suggests that the high hatching success was the result of the exclosures preventing predators from depredating clutches, and not simply an effect of year.

Predators did not appear to learn to associate the exclosures with the presence of a nest. Nest exclosures at another location in western Alaska were detrimental due to Long-tailed Jaegers learning to use their presence to locate nests and preying on adults as they left the exclosures (Niehaus *et al.* 2004). At our site, a jaeger was seen sitting on a predator exclosure only once; and in that case the adult successfully escaped, although it later abandoned the nest. Although we regularly saw Parasitic and Long-tailed Jaegers, we found only one jaeger nest throughout the study (in 1994), and thus cannot say whether the individuals we saw were resident in the area or transients. Resident jaegers might be exposed to more cues that enable them to associate the nest exclosures with the presence of nests, and the risks of exclosures might thus be greater in areas with more resident predators.

We saw no evidence of fox activity (digging, scat) around nest exclosures, as has occurred elsewhere (Estelle *et al.* 1996, Niehaus *et al.* 2004). While we found what appeared to be an active red fox denning site less than 500 m from the edge of our study plot, foxes were rarely seen, and we found few unprotected nests with evidence of fox predation (i.e. urine or scat in nest). Foxes in the area may have spent more time on the adjacent coastline, where marine mammal carcasses and abundant nesting geese, ducks and swans may have provided preferable food resources. The lack of fox activity at our site may be one of the main reasons that our exclosures successfully increased hatch success, as foxes have been implicated in mortality of adult birds at nests with exclosures (Barber *et al.* 2010),

and are more likely to dislodge exclosures than avian predators (Niehaus *et al.* 2004).

Abandonment and adult mortality

The overall increase in hatching success for nests with exclosures occurred despite an increase in rates of nest abandonment. When flushed by an approaching human, incubating males sometimes flew into the wire mesh before walking through it. This did not lead to any injuries, but this inability to flush quickly could have increased the likelihood of nest abandonment in two ways: birds may have viewed the exclosures as obstacles that prevented them from escaping effectively, or they may have incurred increased predation rates because their flushing was impeded by the exclosures. Although we documented no significant decrease in return rates for abandoning males, suggesting no increase in mortality, these effects are difficult to identify.

The use of exclosures has resulted in increased nest abandonment in several other shorebird species including Piping Plovers (Barber *et al.* 2010), Snowy Plovers (Hardy & Colwell 2008) and Northern Lapwings (Isaksson *et al.* 2007). Normal abandonment rates in shorebirds vary substantially among regions and species. Within the Canadian Arctic, Smith (2010) found low abandonment rates in a variety of species (3%), while Reynolds (1985) found rates of abandonment of 0–17% in Red-necked Phalaropes. Colwell & Oring (1988) found abandonment rates of 7–23% in Wilson's Phalaropes *Phalaropus tricolor* in Saskatchewan. We observed elevated rates of abandonment among phalaropes in years when exclosures were used, but these were still within the range of natural abandonment rates found in other studies of phalaropes. The year with the highest rate of abandonment (14% in 2011) also had two major storms during which many of the abandonments occurred. The additional energetic

Table 3. Resighting rates (n resighted in year $t+1$ / n banded in year t , and %) of male Red-necked Phalaropes that abandoned their enclosed nests, versus resighting rates for males with nests that were not abandoned.

Year	2011 n resighted / total	2011 n resighted / total	Pooled n resighted / total
Abandoned with enclosure	2/5 (40%)	1/7 (14%)	3/12 (25%)
All other fates	13/32 (41%)	25/66 (38%)	38/98 (39%)

Table 4. Models selection results for models of daily nest survival in Red-necked Phalaropes, Western and Semipalmated Sandpipers as a function of species, year, and species*year. K is the number of parameters, ΔAIC is the change in Akaike Information Criterion score relative to the top model and W_i is Akaike weight.

Model	K	ΔAIC	W_i
Species + year + species*year	15	0	0.997
Species + year	7	11.70	0.003
null	1	54.33	0.000

stress suffered by uniparental incubators during inclement weather is known to influence nest attendance and rates of abandonment (Tulp *et al.* 2009).

Increased adult mortality, which can resemble abandonment, has been found in other shorebird species when nest exclosures were used (e.g. Barber *et al.* 2010). In other shorebird species where adult predation was increased by exclosures, remains were found near the nests (Murphy *et al.* 2003, Isaksson *et al.* 2007, Barber *et al.* 2010). We found no direct evidence of predation on incubating male phalaropes at nests, or on the study plot, despite several carcasses of depredated sandpipers being found at the site, and scattered feathers at multiple sandpiper nests that were subsequently abandoned. We also did not find any significant difference in return rates between birds that abandoned and those that did not, which suggests that adult mortality was not the cause of the higher abandonment seen at nests with exclosures (although our sample size of males from abandoned nests was small). Moreover, return rates in shorebirds are often lower in unsuccessful breeders compared to successful breeders (Gratto *et al.* 1985, Colwell & Oring 1989, Flynn *et al.* 1999), thus we might expect the return rate of males who abandoned to be lower than those who did not regardless of survival effects.

Table 5. Parameter estimates and SE for the best supported model describing daily nest survival for Red-necked Phalaropes, Western and Semipalmated Sandpipers. The intercept reflects the daily nest survival of Red-necked Phalaropes in 1994, with other parameters showing the relative effect of that parameter on nest survival.

Parameter	Parameter estimate	SE
Intercept	2.54	0.26
WESA	0.21	0.31
SESA	0.79	0.35
2010	0.20	0.41
2011	1.88	0.64
2012	2.14	0.42
2013	0.24	0.30
SESA*2010	0.85	0.59
WESA*2010	0.72	0.59
SESA*2011	-1.34	0.71
WESA*2011	-1.87	0.70
SESA*2012	-0.81	0.57
WESA*2012	-1.76	0.55
SESA*2013	0.25	0.43
WESA*2013	-0.47	0.44

The behavior of Red-necked Phalaropes may have played a role in the apparent lack of a survival effect arising from exclosures. Isaksson *et al.* (2007) found increased mortality in Common Redshanks *Tringa totanus*, but not Northern Lapwings, when both had exclosures in the same area. As redshank generally sit more tightly to their nests than lapwings, the proximity of the predator could have greater consequences if there is a delay in flushing caused by the exclosure versus lapwings, which flush when predators are further away (Isaksson *et al.* 2007). While we never directly observed phalaropes flushing in response to predators, incubating males did generally flush in response to humans at much greater distances than did Western or Semipalmated Sandpipers. Phalaropes would also often sneak off their nests and fly only when they were several metres away, unlike the sandpipers, which often flushed directly from the nest. Thus the phalaropes' normal predator response behaviour may have made potential delays in flushing off the nest due to the presence of the exclosure less likely to increase adult mortality.

Summary

Predator exclosures successfully increased the percentage of Red-necked Phalarope nests that hatched at our site, despite a potentially higher rate of nest abandonment. We found no evidence that increased nest abandonment was a function of increased mortality of adults at exclosed nests. Compared to studies where significant adult mortality at exclosures was observed, we had a minimal presence of mammalian predators and resident nesting jaegers; this may have contributed to the lack of such effects in our study. We suggest that, depending on the suite of predators in an area, exclosures can be a cost-effective method of increasing nest success for conservation or research reasons.

ACKNOWLEDGEMENTS

Acknowledgments relevant to collection of field data during 1993–1994 are listed in Sandercock (1997a,b, 1998) and Sandercock *et al.* (1999). Field work during 2010–2013 was supported by an NSERC Strategic Research Grant, the Alaska Department of Fish and Game (State Wildlife Grant T-16), the Office of Polar Programs of the National Science Foundation (OPP-1023396), and The Northern Studies Training Program. Access to the study plot and field camp on private land was granted by land use permits from the Sitnasuak Native Corporation. We thank the Bering Straits Native Corporation, National Park Service, and Alaska Department of Fish and Game for logistical support. We received tremendous help from Jim Menard, Peter Bente, Tony Parsons, Pearl Johnson, Dawyn Sawyer, Margaret Thomas, and Connor Thomas. Birgit Schwarz, Ian Jong, Nathan Hentze, Toby St. Clair, Erica Escajeda, Thomas Esson, Melanie Wilson, Michaela Haring, Thomas Riecke, Diane Borden, Samantha Franks, and David Hodgkinson were an integral part of field data collection. Reviews from Rick Lanctot and an anonymous reviewer substantially improved the manuscript.

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