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An Ongoing Shift in Mammalian Nest Predators of Yellow-billed Loons in Arctic Alaska

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ABSTRACT. The Coastal Plain of northern Alaska is an important nesting area for a variety of avian species, where the productivity of ground-nesting species can be strongly influenced by nest predators. Recently, the density of red foxes (*Vulpes vulpes*) has increased in many areas of the Arctic, likely because of climate warming as well as the availability of anthropogenic food sources during winter. In areas where they occur sympatrically, red foxes can outcompete and kill the smaller Arctic fox (*Vulpes lagopus*). There is considerable dietary overlap between the fox species, but if the red fox is a more successful nest predator, this ongoing shift in canid species could have important implications for ground-nesting species like the Yellow-billed Loon (*Gavia adamsii*). We examined time-lapse photographs from 186 nests of Yellow-billed Loons in northern Alaska during the years 2008–15 and 2019 for the presence of foxes and other nest predators and quantified nest predation by species. Although both Arctic and red foxes were photographed near nests, we found that all successful predation of Yellow-billed Loon nests by foxes was attributable to red foxes, which were the second most frequent predator of Yellow-billed Loon nests after Glaucous Gulls (*Larus hyperboreus*). Arctic foxes photographed at Yellow-billed Loon nests were unsuccessful at displacing incubating loons. Several data sources suggest that the prevalence of red foxes has increased in Arctic Alaska over the last three decades, a change that is likely to have negative impacts on the nesting success of Yellow-billed Loons and possibly other large waterbirds.

Key words: Alaska; anthropogenic food; Arctic fox; climate change; *Gavia adamsii*; nest predation; time-lapse cameras; red fox; *Vulpes lagopus*; *Vulpes vulpes*; Yellow-billed Loon

RÉSUMÉ. La plaine côtière du nord de l'Alaska est une aire de nidification importante pour une variété d'espèces aviaires, où la productivité des espèces nichant au sol peut être grandement influencée par les prédateurs de nids. Récemment, la densité de renards roux (*Vulpes vulpes*) a augmenté en maint endroit de l'Arctique, vraisemblablement en raison du réchauffement climatique et de la disponibilité de sources alimentaires anthropiques en hiver. Là où ils se retrouvent de manière sympatrique, les renards roux peuvent l'emporter sur les renards arctiques (*Vulpes lagopus*) plus petits et réussir à les tuer. Il existe un chevauchement alimentaire considérable entre les espèces de renards, mais si le renard roux est un prédateur de nids plus prolifique, le virage caractérisant les espèces de canidés pourrait avoir d'importantes incidences sur les espèces nichant au sol, comme le plongeon à bec blanc (*Gavia adamsii*). Nous avons examiné les photographies accélérées de 186 nids de plongeons à bec blanc du nord de l'Alaska prises entre les années 2008 et 2015 ainsi qu'en 2019 afin de repérer la présence de renards et d'autres prédateurs de nids, en plus de quantifier la prédation des nids en fonction des espèces. Même s'il y a des photographies de renards roux et de renards arctiques à proximité de nids, nous avons pu constater que toutes les prédations réussies de nids de plongeons à bec blanc étaient attribuables au renard roux, le deuxième plus grand prédateur de nids de plongeons à bec blanc après le goéland bourgmestre (*Larus hyperboreus*). Les renards arctiques photographiés aux nids de plongeons à bec blanc n'ont pas réussi à déplacer les plongeons en période d'incubation. Plusieurs sources de données suggèrent que la prédominance des renards roux a augmenté dans l'Arctique alaskien au cours des trois dernières décennies, un changement qui est susceptible d'avoir des incidences négatives sur le succès de la nidification des plongeons à bec blanc, voire d'autres oiseaux aquatiques plus volumineux.

Mots clés : Alaska; aliment anthropique; renard arctique; changement climatique; *Gavia adamsii;* prédation de nids; appareils pour prises de vues en accéléré; renard roux; *Vulpes lagopus; Vulpes vulpes;* plongeon à bec blanc

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INTRODUCTION

The Arctic is warming approximately three times faster than the rate for the planet as a whole (ACIA, 2004; Walsh et al., 2011; AMAP, 2021), resulting in direct and indirect effects on Arctic ecosystems and wildlife species. At the same time, the anthropogenic footprint is expanding in the Arctic with increasing oil and gas, mining, and other human development (Tolvanen et al., 2019; BLM, 2020a). These changes will result in multiple direct and indirect impacts and changes in populations and species assemblages that could change predator-prey dynamics in ways that complicate predictions of wildlife population status and the health of Arctic ecosystems.

In northern Alaska, Yellow-billed Loons (*Gavia adamsii*) number under 1000 breeding pairs and have low reproductive and recruitment rates (Earnst, 2004). They have a limited and patchy breeding range, are territorial, and typically nest on large, deep, fish-bearing lakes (Earnst et al., 2006). The Yellow-billed Loon is currently listed as a sensitive species by the Bureau of Land Management (BLM, 2019), which is responsible for managing the National Petroleum Reserve-Alaska (NPR-A), where 75% of the Alaska population of the species breeds (Schmutz et al., 2014). It was previously a candidate species for listing under the Endangered Species Act but was not listed because specific management requirements by federal and state agencies were deemed adequate to conserve the species (U.S. Fish and Wildlife Service, 2014). Because of its low annual reproductive potential, the species has a limited ability to recover quickly from population declines (Earnst, 2004). During the nesting season, egg predation is common. Avian predators of Yellow-billed Loon nests include Parasitic Jaegers (*Stercorarius parasiticus*), Glaucous Gulls (*Larus hyperboreus*), Golden Eagles (*Aquila chrysaetos*), Bald Eagles (*Haliaeetus leucocephalus*), and Common Ravens (*Corvus corax*). Mammalian nest predators include grizzly bears (*Ursus arctos*), wolverines (*Gulo gulo*), and red foxes (*Vulpes vulpes*) (Johnson et al., 2015, 2019). Other potential nest predators of Yellow-billed Loons include gray wolves (*Canis lupus*), Arctic foxes (*Vulpes lagopus*), Snowy Owls (*Nyctea scandiaca*), and Pomarine Jaegers (*Stercorarius pomarinus*) (Earnst, 2004).

Red foxes have occurred on the central Arctic Coastal Plain of northern Alaska at low densities for at least many decades (Bee and Hall, 1956; MacPherson, 1964; Smits et al., 1989) but have expanded their range in Arctic ecosystems, likely as a result of climate warming and an increase in anthropogenic food sources (Hersteinsson and Macdonald, 1992; Stickney et al., 2014; Elmhagen et al., 2017; Ims et al., 2017; Gallant et al., 2020). This northward expansion of the red fox results in more overlap with the range of the smaller Arctic fox (Elmhagen et al., 2017). The Arctic fox is endemic to tundra regions of the Arctic and has physiological and behavioral adaptations to withstand long winters and extreme temperatures with limited food sources. Arctic foxes often follow larger predators during winter, especially polar bears, allowing them to scavenge on carcasses of marine mammals (Pamperin et al., 2008). The northern distribution of red foxes has been hypothesized to be constrained by food limitations and climate, whereas the southern distribution of Arctic foxes may, in turn, be determined by the distribution of red foxes (Hersteinsson and MacDonald, 1992; Elmhagen et al., 2017).

Red foxes are approximately 60% heavier than Arctic foxes (Hersteinsson and Macdonald, 1992). Once they become established, red foxes can outcompete and largely displace Arctic foxes (Hersteinsson and Macdonald, 1992). Red foxes appropriate Arctic fox dens and kill Arctic fox adults and pups (Frafjord et al., 1989; Tannerfeldt et al., 2002; Pamperin et al., 2006; Rodnikova et al., 2011). Relatively small numbers of red foxes can have a strong negative impact on Arctic fox population size and distribution (Shirley et al., 2009). Hence, in parts of the Arctic, the most abundant canid species is being partially replaced by a larger and more aggressive red fox.

Red foxes have extensive dietary overlap with Arctic foxes (Elmhagen et al., 2002). Both Arctic and red foxes in the Prudhoe Bay oilfield of northern Alaska consume anthropogenic foods, which make up higher proportions of their diets in winter (39% and 49%, respectively) than in summer (11% and 14%, respectively), when both species relied on lemmings, voles, and bird eggs (Savory et al., 2014).

Although the Arctic fox is an effective summer predator of small birds and eggs, it may be less effective with some of the largest waterbird species nesting in the Arctic. Arctic foxes are successful nest predators of Lesser Snow Geese (*Anser caerulescens*; Bantle and Alisauskas, 1998), Black Brant (*Branta bernicla*; Anthony et al., 1991), Canada Geese (*Branta canadensis*; Reiter and Andersen, 2011), Common Eiders (*Somateria mollissima*; Quinlan and Lehnhausen, 1982), Spectacled Eiders (*Somateria fischeri*; Johnson et al., 2008), and Pacific and Red-throated loons (*Gavia pacifica* and *G. stellata*; Bergman and Derksen, 1977; Haynes et al., 2014b; Rizzolo et al., 2014). Other large waterbirds such as Yellow-billed Loons, Tundra Swans (*Cygnus columbianus*), and Greater White-fronted Geese (*Anser albifrons*) may defend their nests from Arctic foxes (Hawkins, 1986; Murphy and Anderson, 1993; Burgess, 2000; Johnson et al., 2003), but these species may be less successful at deterring the larger red fox.

Yellow-billed Loons are larger than other species of loons in the study area (Earnst et al., 2006), exclude other loons from their territories (Haynes et al., 2014a; Uher-Koch et al., 2018), and may be able to defend their nests from predators more effectively than smaller species. Yellow-billed Loons select nesting sites that provide a good view of approaching terrestrial predators, preferentially using islands or peninsulas that have a single access point to defend (Haynes et al., 2014b) and are more likely to choose shoreline sites than are Pacific Loons, possibly because they are better able to defend their nests from terrestrial predators (Uher-Koch et al., 2018). If the red fox is a more effective predator on nests of large waterbirds than the smaller Arctic fox,

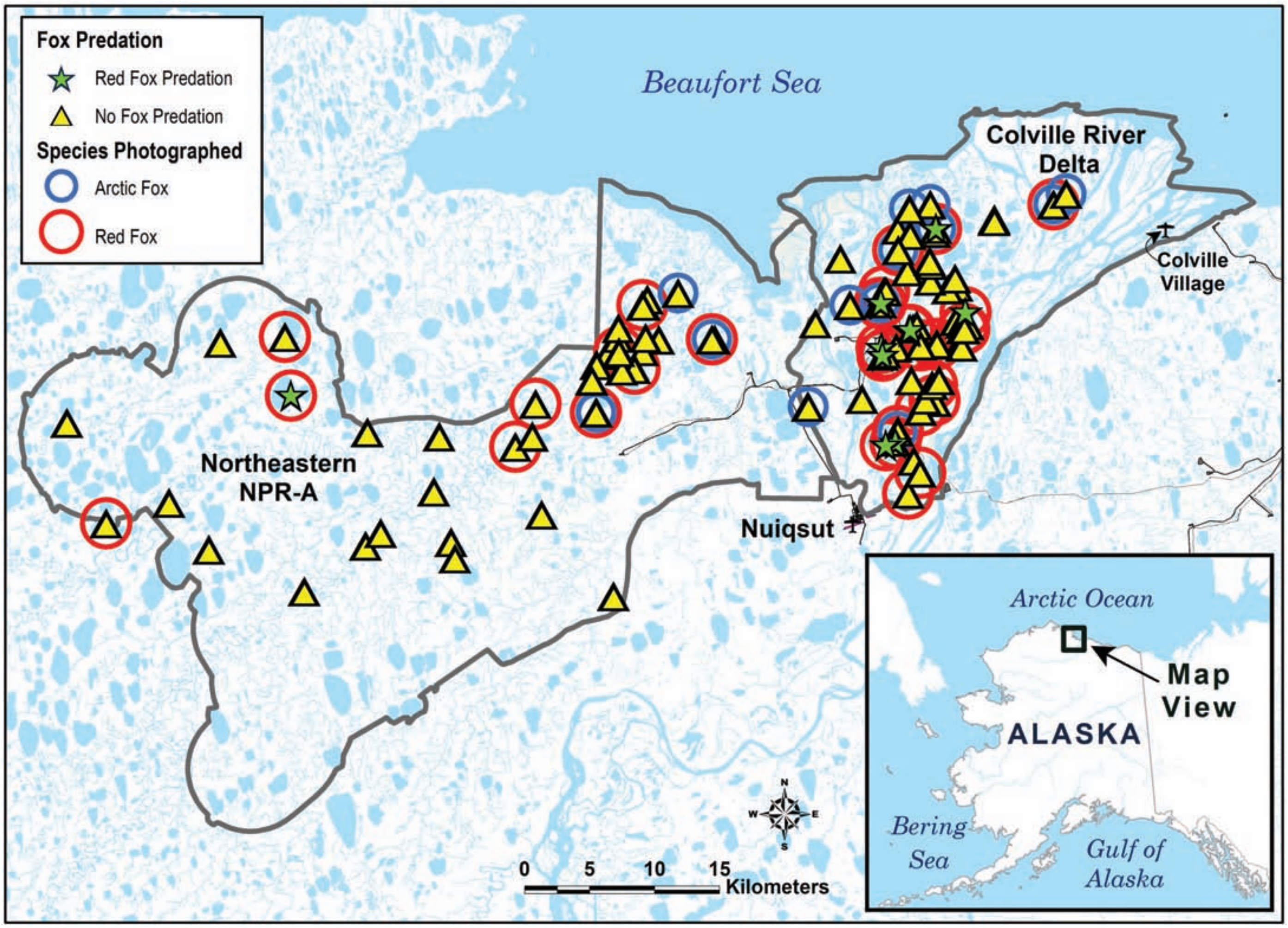

FIG. 1. Locations of 186 Yellow-billed Loon nests monitored with time-lapse cameras during 2008 – 15 and 2019 and the occurrence of Arctic and red foxes and nest predation by red foxes in the Colville Delta and NPR-A study areas, northern Alaska.

the increased presence and abundance of the red fox could depress the nesting success of Yellow-billed Loons.

We used time-lapse photographs of Yellow-billed Loon nests to examine the occurrence and predation behavior of Arctic and red foxes during 2008 – 15 and 2019. We compiled the data to 1) identify the occurrence and behavior of avian and mammalian nest predators, 2) investigate whether nest predation rates and the behavioral responses of loons to predation attempts differed depending on which fox species was present, and 3) evaluate the frequency of occurrence of the two fox species near nests over this period. We hypothesized that, because of their larger body size and more aggressive behavior, red foxes might be able to effectively depredate Yellow-billed Loon nests, while adult loons generally would be able to defend their nests from smaller Arctic foxes.

STUDY AREA

The study areas included the Colville River delta (Colville Delta study area) and the adjacent northeastern portion of the NPR-A (NPR-A study area) on the Arctic Coastal Plain in northern Alaska (Fig. 1). Aquatic landforms, primarily freshwater lakes, marshes, and streams (not including polygon ponds), make up 32% of the Colville Delta and 19% of the adjacent NPR-A study areas (Johnson et al., 2004). Vegetation types in the area are predominately wet and moist tundra, with a mixture of low and prostrate shrubs. Taller shrubs occur along river channels and halophytic marshes occupy coastal areas. Well-developed polygonal surface forms arising from permafrost are characteristic of the area (Johnson et al., 2019). Snow typically melts in late May or early June, with lakes thawing from mid-June to early July and refreezing in September or October (Johnson et al., 2019).

Yellow-billed Loons arrive in the study area in late May or early June as water becomes available in river channels and meltwater begins to form narrow moats along lake margins (North, 1986). Nest-site fidelity is high, with 70% – 90% of breeders retraining their territories in successive years (Schmutz et al., 2014; Uher-koch et al., 2019); however, the percentage of territorial pairs that attempt to breed annually varies considerably (38% – 89%

of territory holders; Earnst, 2004). Yellow-billed Loons typically lay two eggs in mid-June (North and Ryan, 1988), but may lay as early as the first week of that month or as late as early July (ABR, Inc., unpubl. data). Both sexes share incubation duties, which last 27–28 days (North and Ryan, 1988). Chicks are reared on a brood-rearing lake until young are flight-capable in mid- to late September (ABR, Inc., unpubl. data). The density of nesting adults in the Colville Delta study area ranges from 0.09 to 0.22 loons/km² (Parrett et al., 2022).

Arctic foxes mate in March–April and give birth approximately 52 days later (Audet et al., 2002). They may be present at their den from March to August (Eberhardt et al., 1983). Arctic fox litter sizes in the Northwest Territories averaged 10.6 pups at birth and 6.7 pups at weaning but showed large interannual variation (MacPherson, 1969). The density of Arctic fox dens in the Colville River delta area during the 1990s was between 1/34 km² to 1/42 km² (Burgess, 2000). Red fox litter sizes range from one to 12 pups and vary with food availability and female age (Larivière and Pasitschniak-Arts, 1996).

Oil development began in the central Alaska Arctic Coastal Plain in the 1970s with construction of the Prudhoe Bay oilfield. That development expanded westward over subsequent decades with construction of the Kuparuk oilfield in the early 1980s, the Alpine oilfield on the Colville River delta beginning in 1998, and roads west into NPR-A beginning in 2014 (Johnson et al., 2019). Two human settlements are present on the Colville River delta: the Iñupiaq community of Nuiqsut (established in 1973 in an area long used by the Iñupiat) with a population of approximately 500 inhabitants (Decennial Census, 2020), and a small family home site known as Colville Village (established in the mid-1950s) in the northeastern Colville River delta. The distribution of Yellow-billed Loon nests relative to infrastructure was discussed by Johnson et al. (2019).

METHODS

Using digital time-lapse cameras, we monitored a subset (64%) of the 300 Yellow-billed Loon nests found during aerial surveys in the Colville Delta study area in 2008–15 and in the NPR-A study area in 2010–14 and 2019 (Fig. 1). Across all years we monitored 186 nests, including 129 nests in the Colville Delta study area and 57 nests in the NPR-A study area. Five cameras malfunctioned prior to nest failure and were excluded from analyses where noted. Some nest sites were monitored in multiple years; 46% were monitored only during 1 year, 28% during 2–3 years, 17% during 4 –5 years, and 8% during 6 –7 years. These nest sites were in 74 unique Yellow-billed Loon territories.

Cameras were installed at nests within one to six days of nest discovery in mid-to late-June. On average, nests were approximately one week old when cameras were deployed (mean = 8.2 ± 0.3 d [SE], n = 178 nests). We used three models of Silent Image™ Professional cameras mounted on tripods: PM35 cameras with a custom 8× telephoto lens taking 0.3-megapixel photographs, and PC85 and PC800 cameras with custom 2.5× and 2× telephoto lenses, respectively, taking 3.1-megapixel photographs (Reconyx, Lacrosse, WI). The PM35 cameras were programmed to take one photograph every 60 sec or 65 sec. The PC85 and PC800 cameras were programmed to take one photograph every 30 sec. We chose settings, memory cards, and batteries so that cameras could take the maximum number of photos possible for 23–28 days without requiring battery or memory card changes. Cameras were placed 20 to 170 m (mean = 57 m) from nests. Cameras were not installed at nests that lacked suitable views for camera monitoring (e.g., nests on small islands over 80 m from shore) or at nests close to a nesting Glaucous Gull, which posed a predation risk to loon eggs during camera setup. We removed cameras after hatching in mid-July to mid-August and checked nests for evidence of successful hatching. Based on the time-lapse photographs and inspection of the nest site, nests were defined as failed if no chicks hatched. Because most cameras were deployed after nests were initiated, we likely missed some nests that failed early in the nesting period; consequently, estimates of nesting success may be biased slightly high from camera monitoring alone.

We viewed all the photographs from the day of camera setup through the day of hatch or nest failure. We identified predators in the camera view to species, estimated their distances from nests, and described their behavior. Photographs during nest predation attempts were also used to provide information on the behavior of the nesting loons as well as the presence of predators. Following nest predation captured on photographs, loons swam next to the nest, climbed onshore to look into the nest, and often sat in the nest for several frames before ending incubation. We typically observed this behavior at nests for which we could not identify the cause of failure. We inferred that nest predation was likely the cause of failure at nests where predators were not seen and that predation likely occurred between photograph intervals. Although difficult to ascertain, we assumed that nests were abandoned when loons left nests, predators were not seen at the nest, and loons did not return to the nest to inspect contents or try to resume incubation, as described above. We quantified the number of predators observed by year, location, and species. We defined a nest-day as an individual nest photographed for one day. We used a Fisher's Exact Test to test whether or not the proportion of nests that were depredated (out of all the nests with foxes photographed) was different for Arctic and red foxes, and we used logistic regression to test whether or not the proportion of nests with foxes present in photographs changed over the years of the study for both Arctic and red foxes.

We present data summaries with means plus or minus standard errors (mean ± SE), unless otherwise noted and a threshold of significance of $\alpha = 0.05$.

RESULTS

Camera deployment took 41 ± 1.1 min (range 18–128 min) and all incubating birds that flushed from their nests returned to the nest. Yellow-billed Loons at 13 of 186 (7.0%) nests did not leave their nests during camera setup, loons at 26 nests (14.0%) returned to incubate before we departed, and loons at the remaining 147 nests (79%) returned 24 ± 3 min after we departed in the helicopter (range 1–208 min). In total, loons that left their nests were absent 23–246 min during camera installation (mean = 59 ± 3 min). No predation occurred during camera installation.

Of 181 camera-monitored nests (excluding five nests where cameras malfunctioned prior to nest failure), 85 nests (47%) failed. Predation was the primary cause of nest failure (Table 1). Avian predators accounted for 47% of predation events, mammalian predators accounted for 28% of predation attempts, and 18% of predation attempts were by unknown predators. Glaucous Gulls and Parasitic Jaegers were the most common avian nest predators. Ravens depredated only one nest. Red foxes were the most common mammalian nest predator and were responsible for 15.3% of the 85 nest failures, or 7.2% of the 181 monitored nests. In the Colville Delta study area, red foxes were the second-most frequent nest predator (20% of all nest failures) but rarely depredated nests in the NPR-A study area (4% of all nest failures; Table 1).

The cause of nest failure could not be determined at 18.3% of the nests in the Colville Delta and 16% of the nests in the NPR-A study areas (Table 1). In these cases, loon behavior was indicative of nest predation; therefore, we assumed that predation occurred between the 30 sec, 60 sec, or 65 sec photo intervals. In the Colville Delta, factors other than nest predation were responsible for 10% of all nest failures. Abandonment and wind-driven ice caused 8.3% and 1.7% of nest failures, respectively.

Red foxes, brown bears, eagles, and wolverines all flushed incubating Yellow-billed Loons to eat eggs. Foxes, bears, and wolverines were present at nests for 0.5–4 min, whereas eagles remained at nests for 15–20 min. Loons did not attempt to defend nests against eagles or mammalian predators. Glaucous Gulls, Parasitic Jaegers, and Common Ravens depredated nests when loons were not incubating eggs. These avian predators were not always successful because loons often chased them away from nests. On average, gulls, jaegers, and ravens that depredated nests were present in photographs for 10–15 min; however, gulls were sometimes observed carrying eggs from nests in under 1 min.

Arctic foxes were photographed at 18 different Yellow-billed Loon nests and red foxes were photographed at 44 different nests during our study (Table 2), but not all of the foxes photographed near nests involved nest predation attempts. These totals include six nests where both species of fox were observed. Arctic foxes were photographed on 34 different nest-days and red foxes were photographed on 59 different nest-days. Red foxes depredated 13 Yellow-billed Loon nests, whereas Arctic foxes were not observed depredating any. Arctic foxes sometimes approached Yellow-billed Loon nests but were unable to flush incubating loons from nests, whereas Yellow-billed Loons exhibited little defense against red foxes. Twelve of the nests depredated by red foxes were in the Colville Delta study area, and only one was in the NPR-A study area (Fig. 1). The ratio of nests depredated to nests with foxes in photos was significantly higher for red foxes (29.5%) than for Arctic foxes (0%; Fisher's Exact Test; $p = 0.013$).

The proportion of nests at which red foxes were photographed did not change significantly over the years of the study, but the trend was positive (logistic regression; $\beta = 0.058$; $p = 0.343$). The proportion of nests at which Arctic foxes were photographed also did not change significantly over the years, but the trend was negative (logistic regression; $\beta = -0.103$; $p = 0.198$).

DISCUSSION

Photographs from time-lapse cameras deployed at 181 Yellow-billed Loon nests (excluding five nests where cameras malfunctioned prior to nest failure) indicate that the red fox is a more effective nest predator than is the smaller Arctic fox. The red fox was the most frequent mammalian predator, whereas no Arctic foxes were recorded depredating nests. Multiple lines of evidence, including higher observed nest predation rates by red foxes in this study compared to previous studies, increased frequency of occurrence in photographs, and red foxes taking over Arctic fox dens in the area, suggest that, similar to the nearby Prudhoe Bay oilfield and other areas of the Arctic, the prevalence of red foxes has increased in the Colville River delta region over the last three decades. Hence, the increasing population of red foxes in the area is likely to have negative effects on the nesting success of Yellow-billed Loons and potentially other large waterbirds (i.e., swans and geese) that can successfully defend their nests from Arctic foxes.

We acknowledge that 17.6% of the predation events were not identifiable to species because the predator was not observed on photographs and some of these unknown predation events could have been caused by one or both fox species. In general, mammalian predators spent less time at nests than did avian predators; however, red foxes, wolverines, brown bears, and Glaucous Gulls were all observed depredating nests in under 1 min (one photograph). Bears, wolverines, Parasitic Jaegers, and eagles generally remained at nests to eat eggs. Glaucous Gulls either consumed eggs at the nest or removed them, leading to considerable variation in the length of time spent at nests during predation events. One gull predation event lasted 45 min but we also observed gulls flying from nests with whole loon eggs in 0.5 min. In contrast, jaegers were not observed removing eggs from nests and required several minutes to consume eggs, which generally resulted

TABLE 1. The causes of nest failure for 85 Yellow-billed Loon nests in the Colville Delta and NPR-A study areas, northern Alaska, 2008–15 and 2019.

			Colville Delta		NPR-A		Both areas combined	
Failure type	Description	Predation strategy[1]	Number failed	%	Number failed	%	Number failed	%
Avian predation	Glaucous Gull, Parasitic Jaeger, Common Raven	Unattended	23	38.3	13	52.0	36	42.4
	Bald and Golden Eagles	Flushed	1	1.7	3	12.0	4	4.7
Mammalian predation	Red fox	Flushed	12	20.0	1	4.0	13	15.2
	Brown Bear, Wolverine	Flushed	7	11.7	4	16.0	11	12.9
Other	Abandoned	–	5	8.3	0	0	5	5.9
	Ice	–	1	1.7	0	0	1	1.2
	Unknown	–	11	18.3	4	16.0	15	17.6
Total[2]			60	100.0	25	100.0	85	100.0

[1] Unattended = predator took eggs while loons were not incubating. Flushed = predator flushed incubating loons to take eggs.
[2] Total = number of nests that failed from 126 and 55 camera-monitored nests in the Colville Delta and NPR-A study areas, respectively. Cameras that malfunctioned prior to nest failure are excluded.

TABLE 2. Photographs taken and nest predation events for Arctic and red foxes at 186 Yellow-billed Loon nests monitored with time-lapse cameras by species and year, Colville Delta and NPR-A study areas, northern Alaska, 2008–15 and 2019.

			Nests with foxes in photographs			Nest-days present[1]		Nests depredated[2]	
Area	Year	Total nests	Arctic fox only	Red fox only	Both	Arctic fox	Red fox	Arctic fox	Red fox
Colville Delta	2008	12	0	1	0	0	2	0	0
	2009	16	0	3	0	0	3	0	2
	2010	19	2	4	3	15	8	0	3
	2011	20	1	5	0	1	12	0	3
	2012	18	3	5	1	5	6	0	2
	2013	13	1	3	0	1	3	0	1
	2014	19	2	5	0	2	6	0	1
	2015	12	1	4	0	2	5	0	0
	Total	129	10	30	4	26	45	0	12
NPR-A	2010	10	0	2	0	0	3	0	0
	2011	6	0	1	0	0	1	0	0
	2012	11	2	1	0	6	2	0	0
	2013	9	0	1	0	0	1	0	0
	2014	11	0	0	2	2	2	0	0
	2019	10	0	3	0	0	5	0	1
	Total	57	2	8	2	8	14	0	1
Total		186	12	38	6	34	59	0	13

[1] Nest-day = an individual nest photographed for one day.
[2] Excludes 5 cameras that malfunctioned prior to nest failure.

in many photographs of each predation event. Red foxes removed eggs for consumption but could usually be seen approaching or leaving nests. It is possible that some of the unknown predation events were due to Arctic foxes, but because no successful depredation by Arctic foxes was photographed, it is unlikely that they accounted for a large number of the unknown predation events.

We observed a stark difference in loon behavior during predation attempts by the two fox species. Arctic foxes were unsuccessful in flushing Yellow-billed Loons from nests in this study. Although Arctic foxes approached within a few meters of incubating loons on multiple occasions, Yellow-billed Loons did not leave their nests. In one encounter, an Arctic fox spent at least 4 min trying to force a Yellow-billed Loon off a nest. Eventually, what was assumed to be the mate of the incubating loon rushed across the lake toward the fox and the fox left (Fig. 2). The next night, an Arctic fox again tried to depredate the nest; it appeared to be barking and posturing at the incubating loon for 8 min without flushing the loon from its nest. In contrast, the presence of red foxes within 30 m of nests typically caused Yellow-billed Loons to flush. Based on the photographs, Yellow-billed Loons exhibited little defensive behavior toward red foxes and typically swam near nests, occasionally in fencing posture, or left the camera view during nest predation events (Fig. 3).

The extent of predation on Yellow-billed Loon nests by red foxes appears to have increased over the last three decades. In 1983 and 1984, a Yellow-billed Loon study with repeated nest visits was conducted in a portion of our Colville Delta study area. During those two years, Yellow-billed Loons had very high nesting success (94%; n = 34 nests). Only two nests failed to hatch—one was crushed by shifting lake ice, and the other was depredated by Glaucous

FIG. 2. A Yellow-billed Loon mate arrived to help successfully defend a nest from an Arctic fox in the Colville Delta study area, northern Alaska, on 28 June 2010. The Arctic fox had been trying to displace the incubating loon for approximately 4 min before the mate arrived.

FIG. 3. A photograph of a red fox depredating a Yellow-billed Loon nest in the NPR-A study area, northern Alaska, on 25 June 2019.

Gulls (North and Ryan, 1988). At that time, Arctic foxes were frequently observed, but red foxes were uncommon on the Colville River delta (North, 1986). In contrast, during our later study in the 2008–15 time period, the nesting success of Yellow-billed Loons on the Colville River delta was much lower (51%, $n = 129$ camera-monitored nests) and the increasing prevalence of red fox predation is one factor that likely contributed to the decline.

Although most nest predation (42%) in our study areas was caused by Glaucous Gulls and Parasitic Jaegers, red foxes appear to be an effective and increasingly common Yellow-billed Loon nest predator. Unlike gulls and jaegers, red foxes easily flushed loons from nests and because loons did not defend against red foxes, these nest predation attempts were always successful in our study. Over the long term, this additional source of egg loss could reduce the nesting success of Yellow-billed Loons, a species that already has a low annual reproductive output and a limited ability to recover from population declines (Earnst, 2004).

Some movement of red foxes north into the range of the Arctic fox has been noted since the early 1900s (MacPherson, 1964; Smits et al., 1989). In the mid-1970s, the most northerly red fox den in the Sagavanirktok River drainage of northern Alaska was approximately 85 km inland from the coast, and red foxes were confined almost entirely to the northern foothills of the Brooks Range mountains (Eberhardt, 1977). Large riparian areas like the Sagavanirktok and Colville Rivers in northern Alaska provided a productive area for red foxes (Burgess, 2000), but anthropogenic food available at Trans-Alaska Pipeline System construction camps and elsewhere along the Dalton Highway might have aided the northward range expansion of red foxes (Eberhardt, 1977; Savory et al., 2014). Red fox dens were first reported in the Prudhoe Bay oilfield in 1988 (Savory et al., 2014), but by 2010 the majority of dens monitored in the area were occupied by red foxes (Streever and Bishop, 2013; Savory et al., 2014; Stickney et al., 2014).

A similar shift in den occupancy appears to be occurring in the Colville Delta and NPR-A study areas, suggesting a delayed increase in red foxes 60 miles west of Prudhoe. During a 13-year period (1992 –2004) before our loon nest-monitoring began, 11 of 79 dens (14%) in the Colville Delta and adjacent area to the east and two of 41 dens (5%) in the NPR-A study area had been used by red foxes (Johnson et al., 2004; ABR, Inc., unpubl. data). The prevalence of red fox dens increased during that decade, with at least five dens switching from Arctic fox to red fox occupancy on the Colville River delta between 1992 and 2004. After 2004, at least five more dens on the delta are known to have switched from Arctic fox to red fox occupancy, based on incidental observations (ABR, Inc., unpubl. data).

The spatial pattern in red fox abundance, with the highest levels near Prudhoe Bay, intermediate levels on the Colville Delta, and lower levels in NPR-A, could be due to differences in the amount and timing of anthropogenic food availability in the three different areas, movements of red foxes north along the Dalton Highway and Trans-Alaska Pipeline System to the Prudhoe Bay area (Savory et al., 2014), and a greater diversity of prey in large riparian areas (Burgess, 2000). Because the Prudhoe Bay area is near a riparian area and has anthropogenic food sources and infrastructure facilitating northward range expansion, the shift to red fox dominance occurred earliest and proceeded the most rapidly in this area.

Understanding the causes of changing fox distribution is important for predicting future changes in nest predation rates. In addition to a warming climate, the availability of anthropogenic food may allow red foxes to persist outside of their climate-mediated distribution (Savory et al., 2014; Elmhagen et al., 2017; Gallant et al., 2020), similar to how anthropogenic food supplements the winter diet of Arctic fox and appears to reduce their seasonal movements. Arctic foxes captured near Prudhoe Bay remained in the area during winter, where anthropogenic food made up more than half of their diet, whereas Arctic foxes captured in the NPR-A traveled long distances during winter to consume marine foods (Lehner, 2012). Food waste is strictly regulated within the oilfields, but anthropogenic food availability is likely higher in the unincorporated community of Deadhorse, Alaska (approximately 80 km east of our study area; Savory et al., 2014; Pedersen, 2019), which provides services to the oilfields, and from local communities on the North Slope of Alaska.

In addition to warming temperatures and anthropogenic changes that have occurred on or near the Colville River delta in recent decades, a number of ecosystem-level changes may be providing food resources to enable red fox expansion. The Teshekpuk caribou herd largely winters on the coastal plain west of the Colville River delta and has increased in size from approximately 5000 animals in the 1970s to a peak of 69,000 animals in 2008 (Prichard et al., 2020). Red foxes may be able to overwinter on the Coastal Plain when caribou carcasses or remains from harvested caribou are available (Elmhagen et al., 2017). Red foxes were reportedly temporarily common near Utqiaġvik, Alaska (formerly Barrow) when a reindeer herd was present in the 1920s (Savory et al., 2014). Climate-related expansion in the northern distribution of snowshoe hares (*Lepus americanus*; Tape et al., 2016), a recently established muskrat population in areas of the NPR-A (*Ondatra zibethicus*; BLM, 2020b), and the recent expansion of a Lesser Snow Goose colony on the Colville River delta from fewer than 1000 geese in 2005 to over 45,000 geese in 2019 (ABR, Inc., unpubl. data) are other recent changes that could be contributing to the ability of red foxes to expand their population in the area.

The impact on Yellow-billed Loons from the northern expansion of red fox populations into the Arctic may be modulated by several factors. Red foxes are territorial, which may limit population density, and the availability of alternative prey may influence how dependent red foxes are on nest predation. Climate change may increase the length of lemming population cycles and decrease the maximum population densities of lemmings (Gilg et al., 2009; Schmidt et al., 2012), which would be expected to have large impacts on the diet composition of red foxes (Summers, 1986; Summers and Underhill, 1987; Summers et al., 1998; Klein and Sowls, 2015).

The impacts of climate change and other human impacts may be complex and indirect, sometimes affecting predator-prey dynamics (Ims and Fuglei, 2005; Lensing and Wise, 2006; Wilmers et al., 2006; DeGregorio et al., 2015; Terraube et al., 2015), especially in the Arctic where cyclical population cycles have large ecosystem impacts (Ims and Fuglei, 2005). For example, climate change and declining sea ice have resulted in polar bears using terrestrial environments near Hudson Bay earlier in the summer, which resulted in higher nest predation in large and expanding Snow Goose colonies (Van Hemert et al., 2015).

Increasing red fox numbers in the Arctic and their greater success as nest predators of Yellow-billed Loon eggs relative to Arctic foxes adds one more example of an indirect effect of a warming climate and anthropogenic food on predator-prey relationships. Given the predation success at Yellow-billed Loon nests, the increasing population of red foxes in the area is likely to depress productivity of Yellow-billed Loons and potentially of other large waterbirds. Yellow-billed Loons are a long-lived species and show high fidelity to breeding sites (Shmutz et al., 2014); therefore, changes in productivity may not initially result in lower nesting density, especially in areas where loons are limited by suitable nesting lakes. Continued monitoring of red fox populations and Yellow-billed Loon nests in northern Alaska will be useful to quantify the impacts of red fox nest predation as they become more prevalent in the Arctic.

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