J. Raptor Res. 57(2):238–250
DOI: 10.3356/JRR-22-12

AMERICAN KESTREL NESTING BIOLOGY AND LONG-TERM TRENDS IN THE ALASKAN ARCTIC: 2002–2021

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ABSTRACT.—We monitored a population of American Kestrels (*Falco sparverius*) nesting in boxes at the northern extent of the kestrel range (between 66° and 68°N) in the Alaskan Arctic, 2002–2021. There was no significant trend in occupancy during the study period but yearly variation in occupancy was high (range = 17–70%). Occupancy rate was positively related to the lowest temperature recorded in May (7–20°C). The mean estimated clutch initiation date was 16 May ± 6 d; we observed a slight but significant trend for later clutch initiation (4 d) during the study period. Kestrel clutch size averaged 4.7 ± 1.0 (range = 1–7), brood size averaged 4.6 ± 0.8, and the mean minimum number of young fledged/successful pair was 4.9 ± 0.4. Clutch and brood sizes remained stable from 2002–2021, with no significant trend. Nest failure was low (16%). We report a late nesting and possible double brooding attempt in 2018, suggesting a possible response to the warming trend (2002–2021) in average temperatures at the end of the normal nesting season.

KEY WORDS: *American Kestrel*; Falco sparverius; *Alaska*; *Arctic*; *nest box*; *peripheral populations*; *reproductive rate.*

BIOLOGÍA REPRODUCTIVA DE *FALCO SPARVERIUS* Y TENDENCIAS A LARGO PLAZO EN EL ÁRTICO DE ALASKA: 2002–2021

RESUMEN.—Entre el 2002 y 2021 se llevó a cabo el seguimiento de una población de *Falco sparverius* anidando en cajas nido en la parte norte del área de distribución de la especie (entre 66° y 68°N) en el Ártico de Alaska. No hubo una tendencia significativa en la ocupación de las cajas nido durante el período de estudio, pero la variación anual en la ocupación fue alta (rango = 17–70%). La tasa de ocupación se relacionó positivamente con la temperatura más baja registrada en mayo (7–20°C). La fecha media estimada de inicio de la puesta fue el 16 de mayo ± 6 d; observamos una tendencia leve pero significativa para el inicio tardío de la puesta (4 días) durante el período de estudio. El tamaño de la puesta promedió 4.7 ± 1.0 (rango = 1–7), el tamaño de nidada promedió 4.6 ± 0.8, y el número mínimo medio de volantones por pareja exitosa fue 4.9 ± 0.4. Los tamaños de la puesta y de la nidada se mantuvieron estables entre 2002 y 2021, sin una tendencia significativa. El fracaso del nido fue bajo (16%). Reportamos una nidificación tardía y un posible intento de doble nidada en 2018, lo que sugiere una posible respuesta a la tendencia al calentamiento (2002–2021) en las temperaturas promedio al final de la temporada normal de nidificación.

[Traducción del equipo editorial]

INTRODUCTION

Peripheral populations can play an important role in understanding the causes of population declines elsewhere within a species' range (Lesica and Allendorf 1995). In fact, populations remote from the center of their geographic distribution often persist when those at the center do not, perhaps because they may not be exposed to the same environmental conditions causing the declines (Lesica and Allendorf 1995, Channell and Lomolino 2000a, 2000b, Channell 2004). Identifying the differences between stable and declining popula-

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tions is vital for understanding the root causes of the decline in the greater population (McClure et al. 2021). This requires gathering information on the basic ecological characteristics of disparate geographic populations.

The American Kestrel (*Falco sparverius*) is the most widespread and abundant raptor in North America (Smallwood and Bird 2020). Kestrel population status was once thought to be stable over much of the species' range (Smallwood and Bird 2020) and the International Union for Conservation of Nature (IUCN) listed it as a species of least concern on the Global IUCN Red List in 2022 (www.iucnredlist.org/). However, range-wide analyses of trends since the 1960s indicate that kestrels are experiencing declines across much of North America (Farmer and Smith 2009, Smallwood et al. 2009, Downes et al. 2011, Sauer et al. 2013, McClure et al. 2017b). Various hypotheses have been proposed for this decline. Some research indicates that climate change may be an underlying factor in many of the changes, as well as human-related modifications of habitat (Steenhof and Peterson 2009, Strasser and Heath 2013, Paprocki et al. 2014, 2017, Smith et al. 2017, Bossu et al. 2022, Callery et al. 2022a, 2022b). Many studies of American Kestrels have been conducted in the temperate regions of the continent (see Smallwood and Bird 2020 for an overview), but the causes of the declines are still largely unknown.

The Birds of the World account (Smallwood and Bird 2020) describes the northern limit of American Kestrel distribution to be the southern edge of the Brooks Mountain Range (hereafter Brooks Range) in Alaska. However, others have found that kestrels sometimes occur farther north, if only incidentally (Irving 1960, J. Reakoff pers. comm., E. Craig unpubl. data). Our study area lies farther north than the current described kestrel distribution (Smallwood and Bird 2020), and we have documented regular nesting of American Kestrels in the Arctic. These kestrels are remote from nesting populations at lower latitudes and their ecology has not previously been described. Nest boxes can be an effective tool to monitor and study the ecology of cavity-nesting raptors (Katzner et al. 2005, McClure et al. 2017a, 2017b). We here report the results of a nest box study of American Kestrels north of the Arctic Circle in the Brooks Range of Alaska (2002–2021). We document long-term trends in occupancy and nesting phenology, and present previously undescribed baseline information on kestrel nesting biology in the Arctic. Finally, we examine the potential influence of local weather on kestrel nesting.

METHODS

Study Area and Nest Box Placement. Our study area is located along the Dalton Highway between 66.6° and 68.0°N. The highway is one of only two all-weather roads in North America that cross the Arctic Circle and ultimately reach the Arctic Ocean. Most of the land proximal to the Dalton Highway in the study area is in the public domain and managed by the Central Yukon Field Office of the Bureau of Land Management (BLM), Fairbanks, Alaska, USA. We placed nest boxes on either side of the highway where it passes through the upper Koyukuk and Dietrich River drainages (Fig. 1). The number of nest boxes available varied from 14 to 26 (2002–2021; Fig. 1, 2). The average distance between neighboring boxes was 3.8 ± 1.7 (SD) km (range = 1.0–7.5 km) in the part of the study area north of the village of Coldfoot, Alaska, and 6.6 ± 2.1 km (range = 1.2–9.8 km) in the part of the study area south of Coldfoot. Boxes south of Coldfoot were relocated to north of Coldfoot after 3 yr of non-use. Consequently, all results we report are for kestrel nesting in nest boxes located in the mountain valleys of the Brooks Range north of Coldfoot (67.3°N). There are few human-made structures along the Dalton Highway, so we placed boxes on spruce (*Picea* spp.), birch (*Betula* spp.), or poplar (*Populus* spp.) trees. The precise locations of nest boxes varied with extant habitat characteristics and the presence of appropriately sized trees. Box height (±3 m) and orientation on the tree was based on the configuration of the limbs and the orientation of the tree relative to the highway and appropriate habitat. We attempted to place boxes so they were not visible from the highway (average distance from the highway: 55 ± 37 m; elevation range: 314–782 m, mean: 480 ± 141 m). The northernmost of these nest boxes was positioned near a tree identified by BLM as the "last tree" along the Dalton Highway and was on one of the northernmost trees on the entire continent. Minor yearly variations in the total number of boxes available resulted when a nest box tree fell down, or a box was destroyed during the nesting season by wildfire, humans, or animals. We attempted to locate replacement boxes as near as possible to the original location so that they were available for the next nesting season. Four of the boxes kestrels used were moved from their original locations; three of these boxes were relocated ≤10 m

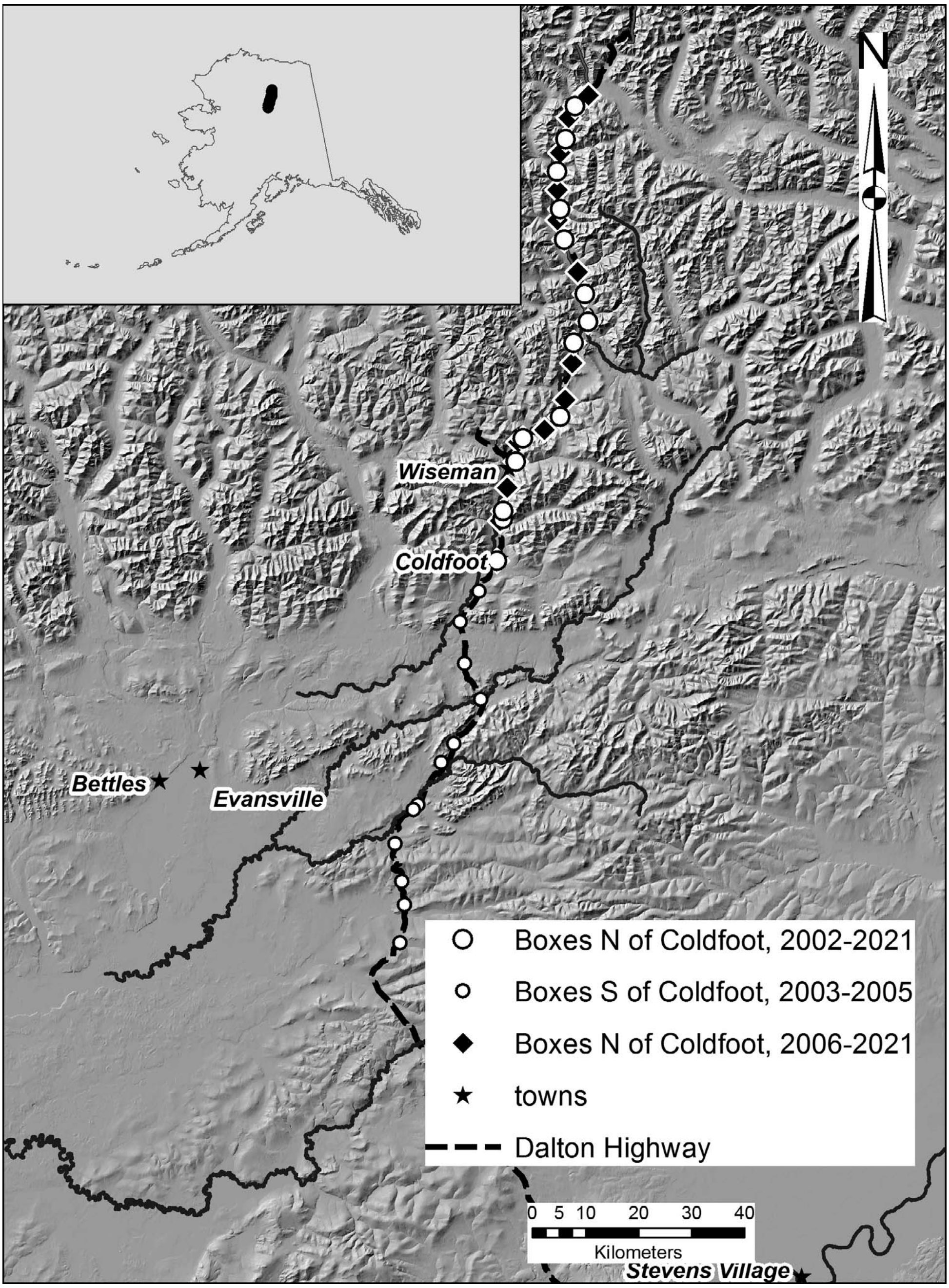

Figure 1. Study area and locations of nest boxes used for monitoring American Kestrels along the Dalton Highway in the Alaskan Arctic, 2002–2021. The dates monitored are listed for each group of boxes; all boxes were located north of Coldfoot, Alaska, from 2006–2021. Boxes south of Coldfoot extended approximately 75 km southward. Boxes north of Coldfoot extended northward about 100 km.

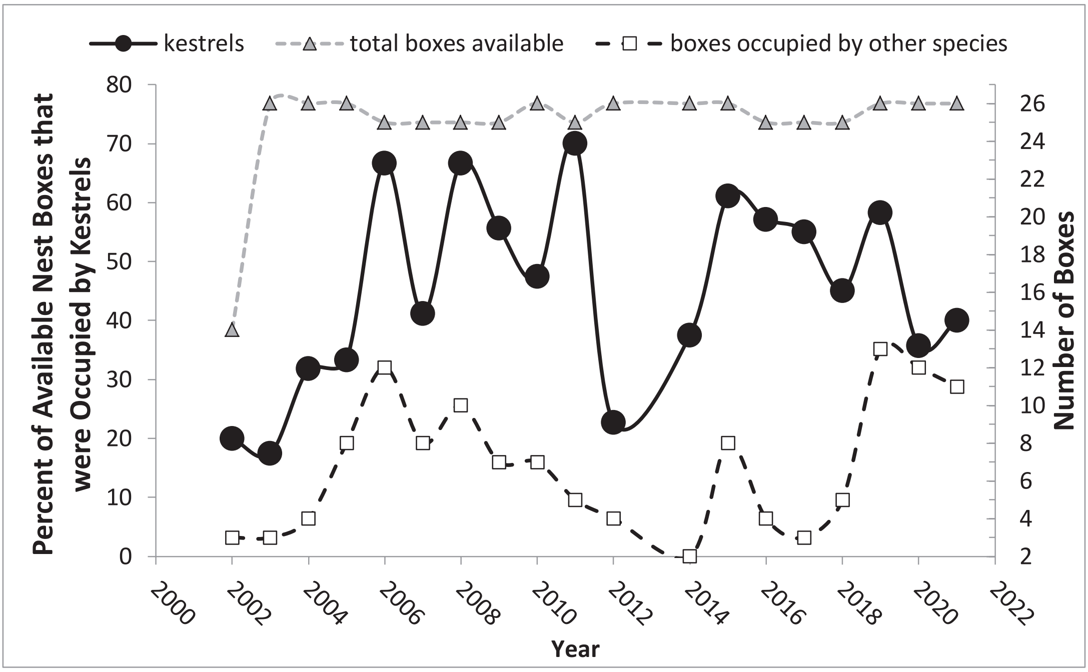

Figure 2. Left y-axis: Percent of available nest boxes in the Alaskan Arctic that were occupied by American Kestrels, 2002–2021. Right y-axis: The yearly total number of nest boxes in the study area is shown, as well as the number of boxes each year that were unavailable for nesting by kestrels because they were occupied by an earlier nesting species.

from their original location (mean = 15.5 ± 18.5 m, range: 4–43 m).

Nest boxes are not the only potential nest sites for kestrels in the study area. There are also a few snags containing natural cavities. However, cavities are uncommon in spruce trees in Alaskan boreal forests (Paragi 2010). This is particularly true in our Arctic study area, which is dominated by white and black spruce trees (*Picea alba* and *P. mariana*), many of which are not of sufficient size to accommodate larger cavity-nesting birds (Fyles and Kopra 2005) like kestrels. It follows that nest sites could be a limiting factor for secondary cavity nesters. However, "witches-brooms" (a type of dwarf mistletoe; e.g., *Razoumofskya pusilla*) also occur in the study area. Some of these are hollowed out by red squirrels (*Tamiasciurus hudsonicus*; Tinnin and Forbes 1999) and kestrels sometimes use them as nest sites in Alaska (E. Craig and T. Craig, unpubl. data).

The vegetation communities and terrain in the area are diverse. In the northern part of the study area, the highway passes through river valleys that are bordered by rugged mountains (some up to 2000 m). Alpine, shrub, and boreal forest habitats vegetate these mountain valleys (Gallant et al. 1995). The southern part of the study area is more open and rolling; the patches of open habitat are dominated by alders (*Alnus* spp.), willows (*Salix* spp.), and dwarf birch (*Betula glandulosa*). White spruce and black spruce are the most prevalent tree species across the entire study area. Balsam poplar (*Populus balsamifera*), paper birch (*Betula papyrifera*), and quaking aspens (*Populus tremulodies*) occur mostly on south-facing slopes (Gallant et al. 1995). The river valley constricts north of Coldfoot and elevations of the nest boxes increase with increasing latitude ($r^2 = 0.91$, $n = 26$, $P = 0.00$, slope = 524). This results in a progressive narrowing of adjacent forested patches, and more open habitats on the upper hillsides because the increasing elevation and latitude result in a local environment where trees cannot grow.

The climate in the study area is characterized by long, cold winters with snow depths usually exceeding 60 cm, and daily temperatures that can dip below –45°C (December–February). Summers are brief and warm with daily temperatures in June and July that can exceed 30°C. There was no significant change in average temperatures during the nesting season in the study area (2002–2021; March–May: $r^2 = 0.00$, $n = 20$ yr, $P = 0.80$; June–August: $r^2 = 0.17$, $n = 20$ yr, $P = 0.07$). Similarly, there was no significant trend in the minimum temperature during May, although it was highly variable from year to year ($r^2 = 0.01$, $n = 20$ yr, $P = 0.70$). However, average temperatures following the nesting season increased significantly (2.6°C) from 2002 to 2021 (September–November; $r^2 = 0.30$; $n = 20$ yr; $P = 0.01$; slope = 0.13; weather data were derived from the Coldfoot, Alaska, Snotel Site records at the southern end of the study area (67.250°N, 150.180°W; https://xmacis.rcc-acis.org/). Most migratory birds, including American Kestrels, arrive in the study area by early to mid-May and leave by mid-September (Jack Reakoff pers. comm., E. Craig and T. Craig unpubl. data).

Field Procedures. Logistical constraints related to the remoteness of the study area (approximately 500 km from our headquarters) allowed us only two annual visits during the nesting season most years. We made the first visit around mid-June and checked for occupancy; this visit was often at, or just a few days after hatching. We revisited any occupied boxes about 20–25 d later when nestlings were near fledging to determine nesting success and reproductive rate. We acknowledge that the limited number of nest visits could have caused us to miss some early nests that failed or were predated. However, unoccupied nest boxes were easy to identify because the substrate (e.g., wood shavings) in the boxes was undisturbed or contained no eggs or broken eggshells to indicate a nesting attempt by kestrels. Each occupied nest box was visited a third time sometime after the nesting season to clean and refurbish it. During the third visit, we collected the substrate from the bottom of each occupied nest box for future prey analysis. Samples collected from 2002 to 2009 were sent to The Owl Research Institute (https://www.owlresearchinstitute.org/), where the bony material, feathers, and insect parts found in the nest box detritus were recovered and identified. We also recorded prey items observed during nest visits. We acknowledge the limitations of prey analysis based on nest box materials (Marti et al. 2007). Nonetheless, we present our results as the first record of kestrel food habits at the northern extent of their range.

We considered a nest box occupied by a nesting pair, and a nesting attempt to have occurred if it contained a female kestrel, at least one kestrel egg, or other evidence that eggs had been laid (e.g., broken kestrel eggshells; Steenhof and Newton 2007). We estimated the age of nestlings using a photographic key (Griggs and Steenhof 1993), or by direct observation when we found both eggs and newly hatched nestlings during our first visit. Because the number of nest site visits was limited, our derived values for clutch initiation are estimates based on published accounts for timing during nesting (Steenhof and Newton 2007, Steenhof and Peterson 2009, Smallwood and Bird 2020). We estimated the date of the onset of incubation by subtracting 30 d from the estimated hatching date (after Steenhof and Peterson 2009). American Kestrels generally do not begin incubation until the clutch is complete (Smallwood and Bird 2020) so we estimated clutch initiation dates by multiplying 1.5 d (estimated egg-laying interval; Smallwood and Bird 2020) times the clutch size and subtracting it from the onset of incubation. The length of the nesting season was estimated by calculating the span between the mean dates for clutch initiation and fledging. We derived clutch and brood size (Smallwood and Bird 2020) from direct observation. We determined brood size during our second nest visit; brood size for successful nests was based on the number of nestlings estimated to be ≥22 d. We excluded broods from this calculation that were younger, or for which we observed an incomplete count because some of the young had already fledged. We considered a pair to be successful if at least one nestling reached approximately 22 d of age (Steenhof and Peterson 2009, McClure et al. 2017b), or we were able to document, by direct observation, that at least one young had fledged. We report only the minimum number of young fledged because timing of the second nest visit did not always coincide with fledging. As a result, this sample size is small and may be an underestimate. We did not calculate the percent of nesting pairs that were successful in our measures of reproductive rate, for two reasons: not all nests contained nestlings that were at least 22 d old during the second visit, and some nests had already fledged. We were unable to document how many of those nests succeeded. We did not collect any data in 2013.

Analysis. We used R (R Core Team 2013) and Excel 10.0 (Microsoft Corporation, Redmond, WA, USA) for linear regression analyses and to calculate descriptive statistics. We report means ±SD and results of statistical analyses at a significance level of $\alpha \leq 0.05$. We used ArcMap 10.1 (Esri 2011) and a

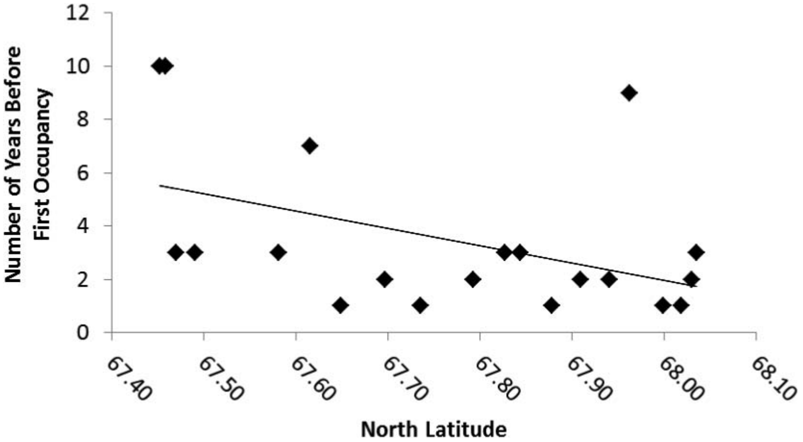

Figure 3. The number of years after a nest box was erected in the Arctic study area before it was first occupied by an American Kestrel, relative to latitude of the nest box, 2002–2021.

digital vegetation layer (Dewitz 2020) to describe generalized habitat characteristics surrounding the nest boxes. We compared vegetation around nest boxes that had never been occupied vs. boxes that were occupied by kestrels at least once during the study period. There are no published data on home range size of nesting American Kestrels at northern latitudes. We used a 500-m radius circle (78.5 ha) centered on each nest box because that value is within the home range size of kestrels reported for lower latitudes (Enderson 1960, Smith et al. 1972, Johnsgard 1990). We used chi-square tests for analysis of vegetation data surrounding nest boxes and orientation of occupied boxes in R (R Core Team 2013).

RESULTS

Occupancy and Reproduction. There was no significant trend in kestrel nest box occupancy rates during the study period, whether we report results from 2002 to 2021 (Fig. 2; $r^2 = 0.09$, $n = 19$, $P = 0.21$) or 5 yr after the onset of monitoring (2006–2021: $r^2 = 0.09$, $n = 15$, $P = 0.27$), as suggested by McClure et al. (2017b). Yearly occupancy varied (range = 17–70%; mean = 45 ± 16% of the nest boxes that were available from 2002–2021). Number of nesting pairs averaged 9 ± 3 pairs/year. There was a significant positive relationship between the lowest temperature recorded each year in May and occupancy rate ($r^2 = 0.24$, $n = 19$, $P = 0.04$; slope = 2.63). There was also a significant relationship between the number of years before kestrels first nested in a box after it was installed, and latitude (Fig. 3; $r^2 = 0.20$, $n = 20$ nest boxes, $P = 0.05$, slope = –6.51); there was not a similar relationship for elevation ($r^2 = 0.14$, $n = 20$, $P = 0.10$. Northernmost boxes were more likely to be occupied within 1–3 yr after the boxes were erected, were subsequently used more frequently, and had fewer nest failures than boxes at lower latitudes (Fig. 3, Supplemental Material Fig. S1, S2). Kestrels nested successfully in boxes oriented in all four compass directions. However, 65% of occupied boxes and 71% of successful nests were in boxes oriented to the south and west; kestrels occupied boxes exposed to the south more often than expected based on availability (Table 1).

The breeding season in the Arctic study area extended from May (Table 2) through July and averaged 66 d from clutch initiation through fledging. We found a slight, but significant, trend for later clutch initiation (4 d later from 2004 to 2021; Fig. 4, $r^2 = 0.04$, $n = 101$, $P = 0.05$, slope = 0.22). Clutch size, brood size, and minimum number of nestlings fledged/successful pair were all similar (mode = 5) and remained stable throughout the study period with no discernable trend, 2004–2021 (Table 2). We found evidence of a late nesting and likely double-brooding (re-nesting) attempt in 2018. It was unsuccessful and occurred in a nest box where nestlings had already fledged in late July (see Supplemental Material: Evidence of a likely second nesting attempt).

Competition with Other Species for Nest Box Occupancy. Other species in the study area, primarily red squirrels and Boreal Owls (*Aegolius funereus*), were competitors for nest boxes (mean annual

Table 1. Chi-square analysis of nest box orientation of boxes used by American Kestrels in the Alaskan Arctic, 2002–2021. Orientation of occupied and successful nest boxes differed significantly from the expected distribution.

		NUMBER OF NEST BOXES BY ORIENTATION				
NEST CATEGORY	TEST SPECIFICS	NORTH (315–360°, 0–44°)	EAST (225–314°)	SOUTH (135–224°)	WEST (45–134°)	TEST STATISTICS
Occupied nests	No. of observed boxes	28	23	38	55	$\chi^2 = 14.293$, df $= 3$, $P = 0.003$
	No. of expected boxes	27.7	27.7	22.2	66.5	
	Residuals	0.058	–0.892	3.367	–1.406	
Successful nests	No. of observed boxes	13	10	24	32	$\chi^2 = 14.182$, df $= 3$, $P = 0.003$
	No. of expected boxes	15.2	15.2	12.2	36.5	
	Residuals	–0.563	–1.332	3.398	–0.739	

occupancy of both species: 30 ± 14%; Fig. 2). We found evidence of a kestrel nesting atop a squirrel nest on only one occasion during the study and that nest failed. In contrast, we found squirrel nests built on top of the remains of kestrel nests on two occasions, indicating usurpation of the nest boxes and possible predation by squirrels on kestrel eggs. Boreal Owls nested about 2 wk earlier than kestrels but we did not find evidence that kestrels supplanted them at nest boxes. Owls were more likely than kestrels to nest in the southernmost, and more heavily forested, portions of the study area. No kestrels, squirrels, or owls ever nested in the boxes south of Coldfoot (2003–2006).

Nest Failures. We documented nest failure for 16% ($n = 13$) of the nesting attempts for which we were able to determine nest fate ($n = 81$). Most (69%) were in the southern part of the study area, just north of Coldfoot (67.3°–67.7°N; Fig. S1). Failures occurred for unknown reasons nine times and four times due to possible predation. When we examined nests that failed due to predation, we found evidence that implicated red squirrels ($n = 3$) and American marten (*Martes americana*; $n = 1$) as the primary culprits.

Prey. The kestrels in our study area preyed most heavily on small mammals (frequency of occurrence and biomass), particularly those in the subfamily Arvicolinae (*Clethrionomys rutilus, Microtus* spp., *Lemmus* spp.). More than half (55%, $n = 134$) of the nest boxes contained these small mammal remains. Birds (26%), insects (18%), and amphibians (<1%; wood frog [*Lithobates sylvaticus*]) were found in fewer nest boxes. We observed numerous dragonfly (Odonata) wings in several boxes, but because of their fragility, insect remains may be under-represented in the analysis of the nest box detritus.

Habitat Relationships and Latitude. The difference in vegetation surrounding occupied vs. unoccupied nest boxes was highly significant ($\chi^2 = 23406$, df $= 5$, $P < 0.001$; Fig. S3). There was more low shrub/scrub (47%) and low vegetation/barren land habitat (17%) surrounding occupied nest boxes than any other vegetation classes. Unoccupied nests were surrounded by a greater percentage of spruce forest (42% vs. 15%) within a 500-m radius of the nest boxes. Land around the unoccupied nest boxes north of Coldfoot shared some physiographic characteristics with the land surrounding the 12 boxes that were never used south of Coldfoot (i.e., more rolling terrain, remote from mountains, more forested habitat; Fig. S2, S4).

Table 2. Summary of reproductive parameters for a population of American Kestrels nesting in boxes in the Alaskan Arctic, 2002–2021. An asterisk indicates a significant trend during the study period.

REPRODUCTIVE PARAMETERS	MEAN	SD	RANGE	n	r^2	P	SLOPE
Estimated clutch initiation date	16 May	6 d	2 May–2 June	101	0.04	0.05*	0.22
Clutch size	4.7	1.0	1–7	132	0.00	0.99	—
Brood size	4.6	0.8	1–6	79	0.04	0.10	—
Nestlings fledged/successful nest (minimum)	4.9	0.4	1–6	37	0.01	0.56	—

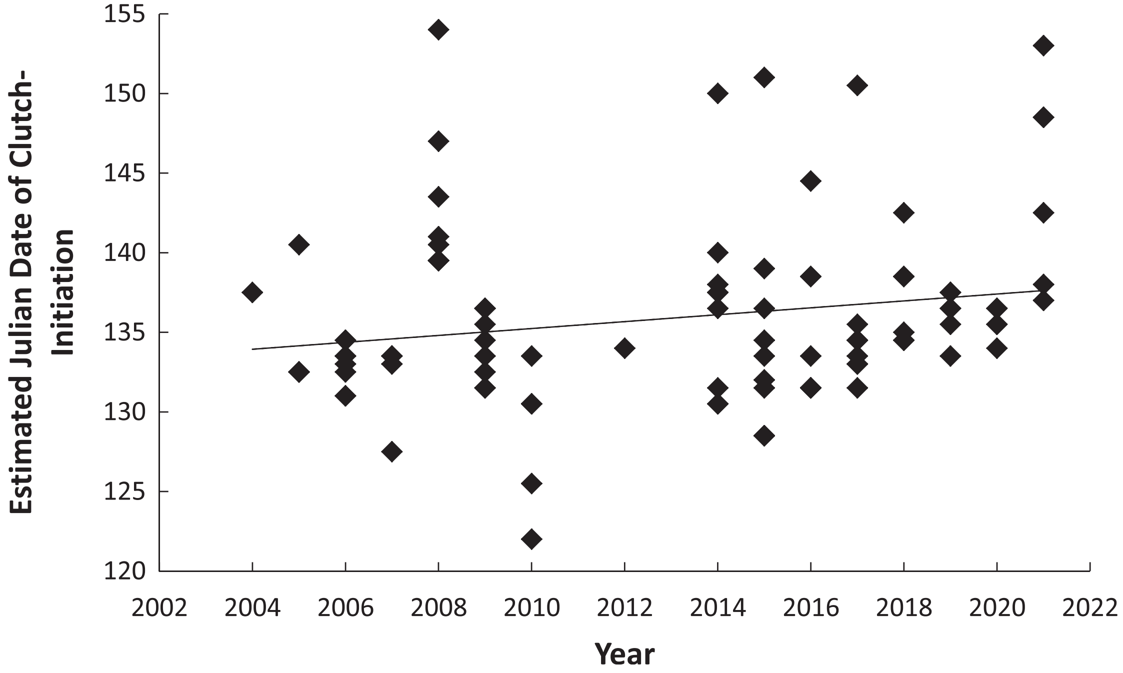

Figure 4. Estimated Julian dates of clutch initiation for American Kestrels in nest boxes in the Alaskan Arctic, 2004–2021.

DISCUSSION

Our results provide the first description of the nesting biology of American Kestrels north of the Arctic Circle in Alaska, and at the northern edge of the continent's tree line. Importantly, the nest box population showed no significant evidence of decline during the study period, 2002–2021. Our findings contrast with many other studies that report significant declines in populations at lower latitudes (Katzner et al. 2005, Farmer and Smith 2009, Smallwood et al. 2009, Sauer et al. 2013, McClure et al. 2017b), and increases in some areas (Steenhof and Peterson 2009, Heath et al. 2012). For example, a monitoring study of kestrels nesting in boxes in the Yukon Territory, Canada (60°N to approximately 66°N) detected a significant mean annual decline in percent occupancy (2.7%) from 1987 to 2007 (Smallwood et al. 2009). Similarly, seven other kestrel monitoring studies from the eastern United States and Saskatchewan, Canada, all experienced significant declines (range = 0.6–4.7% mean annual decline in nest box occupancy; Smallwood et al. 2009).

The length of the breeding season (clutch initiation–fledging) in the Brooks Range was slightly longer (66 d) than reported for temperate zone populations (about 60 d; Smallwood and Bird 2020). Interestingly, we observed a slight but significant trend for later clutch initiation by kestrels (2004–2021), which contrasts with results from many areas farther south. Weather, specifically temperature, has important effects on reproductive timing in raptors (Newton 1979, Heath et al. 2012, Tapia and Zuberogoitia 2018). In the western United States, the onset of kestrel nesting is advancing, not retreating, in correlation with warming temperatures associated with climate change (Smith et al. 2017). In southwestern Idaho, clutch initiation advanced 21 d from 1986 to 2006 and is almost a month earlier than clutch initiation in our Arctic study area (Steenhof and Peterson 2009, Heath et al. 2012). As expected, both the mean clutch initiation and fledging dates we observed are later than for many of the kestrel populations studied in the central and southern temperate zones (Steenhof and Peterson 2009, Smallwood and Bird 2020). Conversely, mean clutch initiation dates in our study area (16 May) are slightly earlier than in Saskatchewan (about 20 May, $n = 559$; G. R. Bortolotti unpubl. data reported in Smallwood and Bird 2020), a study area that is over 2500 km farther south (55°N) than ours. This seems contradictory, given that southern raptor populations generally lay eggs earlier than those located farther north (Tapia and Zuberogoitia 2018, Smallwood and Bird 2020). Perhaps the extremely abbreviated spring/summer in the Arctic simply does not allow kestrels to nest any later and still be successful. The Arctic is warming at an accelerated rate compared to the rest of the continent (Kasischke and Turetsky 2006, Lawrence et al. 2008, Liebezeit et al. 2012, Box et al. 2019). However, we did not observe a long-term warming trend during the nesting season in our study area. There is strong evidence that climate change may be influencing kestrel migration and distribution patterns (Heath et al. 2012, Paprocki et al. 2014, 2017, Powers et al. 2021). Perhaps a warming environment elsewhere resulted in earlier spring arrival dates for Arctic-dwelling kestrels and permitted a longer pre-egg laying period, though we have no data to test this. As a caveat, we note that clutch initiation dates in our study were estimated by back-calculating from the age of nestlings at our first visit; thus, there may be errors if individual kestrels adjusted their laying or incubation behavior. As a result, these data should be considered preliminary.

It is not uncommon for American Kestrels to attempt to nest a second time (double brooding) at lower latitudes where temperatures are moderate (Toland 1985, Steenhof and Peterson 1997, 2009, Smallwood and Bird 2020). However, the likelihood of double brooding decreases with increasing latitude; the previous northernmost published record is from Ontario, Canada, at 44°N (Tozer and Richards 1974, Smallwood and Bird 2020). Even in southwestern Idaho, successful double brooding is uncommon (Smith et al. 2017). Climate change is affecting the Arctic and the species that occur there (Beever et al. 2017, Box et al. 2019). The trend we observed for timing of clutch initiation, as well as evidence of a likely double-brooding attempt in our Arctic study area, may be related, at least in part, to the influence of a warming climate.

We observed considerable yearly variability in nest box occupancy rates, as did Steenhof and Peterson (2009; Idaho: 20–74% vs. Alaska: 17–70%). The minimum temperature in May was highly variable during our study period and was positively correlated to occupancy rate; thus occupancy was lower when the minimum temperature for the month was lower. If climate change ultimately moderates temperature extremes during the early nesting season, it could positively influence kestrel occupancy rates in the Arctic.

Previous research has identified a strong association between the spatial and temporal availability of vole populations and reproduction in raptors (Newton 1979, Korpimaki and Norrdahl 1991, Sundell et al. 2004, Korpimäki et al. 2009). This has been suggested to explain some of the annual variation in reproduction in the American Kestrel (Steenhof and Peterson 2009, Smith et al. 2017). Like kestrels elsewhere, those in the Brooks Range use nest sites in relatively open habitats, have a broad food-niche, and prey on similar life forms (Sherrod 1978, Smith et al. 2017, Smallwood and Bird 2020). Voles are common prey items of kestrels in the study area, and can be cyclically irruptive (3–5 yr cycle; Johnson and Johnson 1987). Our kestrel occupancy data also exhibit a somewhat cyclic pattern. Unfortunately, we have no data on prey abundance and distribution in the study area for comparison. The kestrels that nest in our study area are all migrants. Other research (1960–2009) relates a significant decrease in kestrel migration distances to climate change (Heath et al. 2012). Perhaps the annual variability in occupancy rates that we observed reflects not only a response to seasonal weather conditions during early nesting, but also to yearly variations in migrant population numbers, and/or cyclic prey abundance.

In spite of the variability in occupancy among years, kestrel clutch size, brood size, and number of young fledged remained consistent for the duration of our study. In fact, all three of those parameters were equal to, or exceeded, those of populations at lower latitudes (Balgooyen 1976, Craig and Trost 1979, Toland and Elder 1987, Steenhof and Peterson 2009, Touihri et al. 2019, Smallwood and Bird 2020), though our annual samples sizes were fairly small for some of these parameters. Furthermore, we documented few nest failures (16%) in our study area and only four instances of failure due to apparent predation. In contrast, 36% of nesting attempts in a study in Idaho failed and the authors implicated human disturbance as an important factor (Strasser and Heath 2013), something we did not observe in our remote study area.

Weather conditions can play an important role in nest site selection by raptors (Balgooyen 1976, Wightman and Fuller 2006, Craig and Craig 2016). It seems counterintuitive then, that kestrels preferred the northernmost nest boxes in the study area, several of which were at the northern edge of the continent's tree line (68°N), while eschewing boxes farther to the south. Interestingly, not only did kestrels avoid the nest boxes south of Coldfoot, but Boreal Owls and red squirrels never used them either. Differences in habitat may partially explain these results for kestrels (i.e., open, low shrub and barren landscapes; Smallwood and Bird 2020). However, Balgooyen (1976) reported that kestrels nesting in the Sierra Nevada of California appeared to select nest sites that were protected from the direction of prevailing storms. It is possible that the narrow valleys north of Coldfoot may provide a buffer against spring storms, and a more benign environment than that in the more exposed low hills south of Coldfoot. Unfortunately, there are no data available on differing weather conditions at a fine scale within the study area to test this hypothesis. However, there is evidence that kestrels in the study area took advantage of favorable microclimates to enhance reproductive success. Kestrels nested most often in boxes that were oriented to take advantage of warmer daily temperatures (south and west) and showed a significant preference for the warmest, south-facing nest boxes. In contrast, kestrels nesting in Florida avoided nest boxes that were oriented to the west (Smallwood and Bird 2020) and kestrels in California that nested in boxes facing west had the highest failure rates (Bloom and Hawks 1983). Obviously, American Kestrels in the Arctic have developed strategies to sustain productivity in spite of the abbreviated nesting season, potential predators, and intermittent severe weather due to the extreme northern latitudes.

Management and Conservation Implications. Researchers have hypothesized a wide range of potential reasons for kestrel declines over much of their range, including contamination by agricultural pesticides, shifts in life history patterns, infection by West Nile virus, intensive agricultural lands that act as ecological traps, or an increase in intra-guild predation, specifically by Cooper's Hawks (*Accipiter cooperii;* Farmer and Smith 2009, Paprocki et al. 2014, 2015, McClure et al. 2017b, Smith et al. 2017, Touihri et al. 2019). Kestrels that nest in our remote Arctic study area are not subject to most of these forces because: (1) pesticides have not been widely used in the region, (2) West Nile Virus has not been a widespread disease in birds in Alaska (http://www.adfg.alaska.gov/index.cfm?adfg=disease.wnv), (3) there are no agricultural lands in the study area, and (4) Cooper's Hawks do not occur in Alaska. Although kestrels that nest in Arctic Alaska may be subjected to some of these threats during migration or wintering, at least during nesting, they are secure from them in our study area. However, Alaskan kestrels may be susceptible to shifts in prey availability or other life-history patterns due to climate change, which is occurring more rapidly in the Arctic than elsewhere (Lawrence et al. 2008, Liebezeit et al. 2012, Box et al. 2019). Therefore, this population of American Kestrels can provide a comparison over time with populations at lower latitudes that are more subject to some environmental perturbations.

SUPPLEMENTAL MATERIAL (available online). Evidence of a likely second nesting attempt. Figure S1: Number of times nest boxes along the Dalton Highway in the Alaskan Arctic were occupied by American Kestrels from 2002–2021 and the number of times nesting failure was documented at each nest box. Figure S2: Terrain surrounding the locations of nest boxes and frequency of occupancy by American Kestrels along the Dalton Highway in the Alaskan Arctic, 2002–2021. Figure S3: Percent of each of five vegetation categories within a 500-m radius of nest boxes occupied by American Kestrels vs. nest boxes that were never occupied along the Dalton Highway in the Alaskan Arctic, 2002–2021. Figure S4. Comparison of vegetation types within a 500-m radius of nest boxes north of Coldfoot and those south of Coldfoot along the Dalton Highway in the Alaskan Arctic.

ACKNOWLEDGMENTS

We acknowledge the BLM, Central Yukon Field Office of the Fairbanks District Office, and Aquila Environmental for their support. We thank the many BLM personnel, interns and volunteers who have assisted in the project through the years. Rick Thoman, Alaska Center for Climate Assessment and Policy, University of Alaska Fairbanks, provided invaluable assistance in obtaining the weather data for the study area. We especially thank Denver Holt and the Owl Research Institute (https://www.owlresearchinstitute.org/) for donating time and personnel to analyze prey remains. We also thank three anonymous reviewers for their helpful comments. This nest box monitoring study was in compliance with guidelines outlined by the Ornithological Council (Fair and Jones 1997, Gaunt et al. 2010) and Federal United States Geological Survey Bird Banding Permit 23727. The views presented in this paper are those of the authors and do not necessarily represent those of the BLM. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

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Received 27 January 2022; accepted 28 August 2022
Associate Editor: Jean-François Therrien