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HABITAT TYPE IS RELATED TO NEST MASS AND FLEDGING SUCCESS OF ARCTIC WARBLERS

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ABSTRACT.—Relatively little is known about Arctic Warblers (*Phylloscopus borealis*) that breed in central Alaska. We monitored Arctic Warbler populations in two adjacent but distinct habitat types in central Alaska (high elevation, ‘open shrub’ and lower elevation, ‘dense shrub’). We collected 95 nests over three breeding seasons to learn more about nest-building behavior, nest mass, composition, fledging success, and nest parasites. Females were the sole builders of ground nests, which were primarily comprised of moss, grass, and a lining of moose (*Alces alces*) hair. Dry weight of nests was ~20 g, but differed up to ~3-fold within each habitat type each season. Nests from open shrub habitats were more massive and contained less moose hair lining than nests in dense shrub. Open shrub nests fledged more young during the most productive breeding season. We report the first record of the parasitic blowfly *Protocalliphora tundrae* in Arctic Warbler nests and for Alaska. Blowfly parasitism (55% of nests with hatchlings) was similar in both habitat types and did not correlate with fledging success, or nest mass. Nests with greater amounts of moss tended to have lower levels of blowfly infestation. Received 26 September 2009. Accepted 10 June 2010.

The Arctic Warbler (*Phylloscopus borealis*) is an understudied old-world warbler that winters in southeast Asia and has an expansive subarctic breeding range that extends from Norway through Siberia into central Alaska (Tucker 1949, Price and Beck 1989, Lowther and Sharbaugh 2008). Little is known about its cryptic ground-nesting habits throughout its range. Alaska is the only location in North America where Arctic Warblers (Fig. 1A) breed and these populations are considered a separate subspecies (*P. b. kennicotti*) (Lowther and Sharbaugh 2008, Reeves et al. 2008).

Documentation of Arctic Warbler nests in Alaska prior to our observations included a report on 11 nests near Nome (Price and Beck 1989) and two nests in Denali National Park by Murie (1956). Our objectives are to present detailed information about: (1) nest construction, (2) orientation, (3) composition, (4) fledging success, and (5) nest parasites in two adjacent, but distinct habitat types (high elevation, ‘open shrub’ and low elevation, ‘dense shrub’) in a central Alaskan population of *P. b. kennicotti*.

METHODS

Study Site.—We studied a breeding population of Arctic Warblers between 2004 and 2006 in the Tangle Lakes region of the Denali Highway in interior Alaska (63° N, 146° W). All data were collected from four 10-ha plots, each 150 m from the Denali Highway at mileposts 23, 26, 30, and 33, respectively. Pairs of plots represented two distinct habitat types of the region. ‘Open shrub’ plots were at higher elevation (1,121–1,154 m) and included north and east-facing slopes. This habitat type contained meadow-like clearings surrounded by 1–2 m tall willow shrubs (*Salix* spp.) and dominated by graminoids (*Deschampsia caespitosa* and *Carex* spp.), lupines (*Lupinus arcticus*), and burnet (*Sanguisorba* spp.). Nests were collected from open shrub plots in all 3 years. ‘Dense shrub’ plots were at lower elevations (910–1,012 m) with flat ground or a gradual, east-facing slope. This habitat type was dominated by dwarf birch (*Betula nana*) and willow. Nests were collected in dense shrub habitats only in 2004 and 2005, as birds typically nested in these locations at much lower densities.

Nest Monitoring, Collection, and Composition.—We located most nests by systematically searching the ground in areas where we observed singing males. Each nest was monitored at least once every 4 days through laying, hatching, and rearing of young. Daily nest checks began 2 days prior to the expected fledging date to ascertain the number of young successfully fledged.

Observations of nest building were made each season and we collected each nest once fledging

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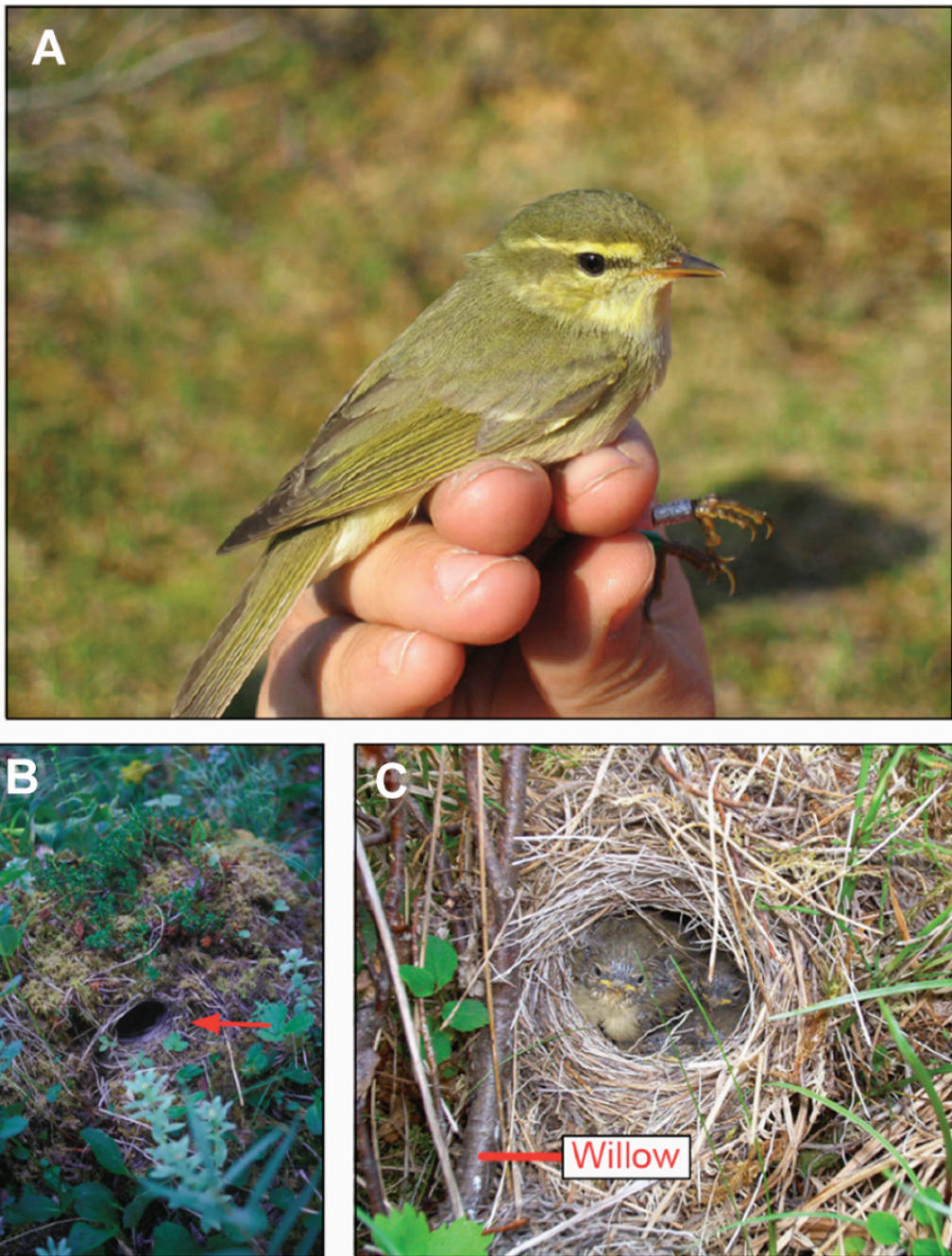


FIG. 1. (A) Color-banded adult Arctic Warbler (*Phylloscopus borealis kennecotti*). Males and females are monomorphic. (Photograph by Ron Teel). (B) Opening of Arctic Warbler nest in the side of a tussock in open shrub habitat. (Photograph by Sue Guers). (C) Nest with fledglings associated with willows in dense shrub habitat. (Photograph courtesy of Alaska Bird Observatory).

was complete (between 20 Jul and 1 Aug). We first recorded nest orientation (in 2005 and 2006 only) by obtaining a compass bearing from a stick inserted straight into the nest opening prior to removing the nest from the ground. Nests are a domed mass of material that can be removed by lifting up the sides and the bottom, once the edge of the nest is located within the surrounding tundra. We carefully removed non-nest material that clung to the outside of the nest during extraction and retrieved any bits of nest material left in the depression. Each nest was placed in a separate plastic collection container for transport to the laboratory, then transferred to a paper sack and dried overnight in an oven at 135° C.

Dry nest mass was measured using an analytical balance. Two key components of nests were measured each year: nest mass and mass of moose (*Alces alces*) hair, which comprised the lining of many nests. Our relatively large sample of nests from open shrub habitat ($n = 80$) allowed us to examine differences across years. Twenty-six nests from open shrub habitat were dissected further in 2006 to quantify the mass of moss and grass, two key components of nest structure. We calculated the percent composition of hair, moss, or grass as a proportion of nest mass.

A snowstorm on 21 June 2006 caused birds to abandon the eight nests (and clutches) that we had located at that point in the season. However, Arctic Warblers began re-nesting after snow began to melt (on 23 Jun 2006) and we subsequently located 22 new nests. We collected all 30 nests, including the eight that had been abandoned. This sample enabled us to examine any differences between nests built before and after the storm (e.g., With and Webb 1993).

Nest Parasites, Incidental Arthropods, and Fledging Success.—We removed, identified, and counted all puparia of an abundant nest parasite (a blowfly) after nests were dried but before they were weighed. We also identified incidental arthropods. Puparia are the rigid outer shells of developing blowfly larvae. The larval stage obligately feed on the blood of nestlings (Sabrosky et al. 1989). Counting puparia is a conservative measure of parasitism, because it avoids double-counting flies that have successfully pupated into adults. All nests that failed prior to hatching were excluded from analyses ($n = 8$ that failed during the Jun 2006 storm, $n = 3$ depredated or abandoned during other years), as puparia only occur after blowfly larvae have fed

on nestlings. All arthropod specimens were deposited in the University of Alaska Museum Insect Collection.

Statistical Analyses.—The mass of nest components and parasite counts exhibited strongly non-normal distributions, which made parametric statistics inappropriate. All data are reported as medians and 25–75% interquartile ranges [IQR]. We used Wilcoxon rank sum tests to examine differences in nest construction and fledging success between habitat types. We used Rayleigh tests to ascertain whether orientation of nest openings deviated from a random distribution (Wilkie 1983). We examined differences between years within each habitat type using Kruskal-Wallis ANOVA. We used Spearman's rho (ρ) tests to assess non-parametric correlation(s), including relationship(s) between nest mass, different nest components, fledging success, fledge date, and number of puparia per nest.

RESULTS

Nesting Behavior.—Our observations are based on 95 nests ($n = 80$ from open shrub habitat, $n = 15$ from dense shrub habitat) collected over 3 years ($n = 24$ in 2004, $n = 41$ in 2005, $n = 30$ in 2006). All nests were built on the ground with domed roofs and circular side entrances (Fig. 1B), and at times incorporated willow stems (Fig. 1C). Each nest consisted of an outer layer of moss and coarse grass with an inner layer of finer materials including grasses and moose guard hairs, which formed a tightly-compressed, disc-shaped mat upon which eggs were laid.

We witnessed construction of three nests in early June 2005. We observed two color-marked pairs at two nests for ~3 hrs. Males did not carry nesting material or enter the nest during construction. However, males flew to and from nests in close proximity to the female that was gathering nest material. The male perched above the nest while the female entered and built the structure itself. Females typically gathered materials within 100 m of the nest; we did not observe travel between study plots. Chasing and physical interactions between the resident male and other males occurred frequently in the air directly above the nest during construction.

The storm on 21 June 2006 blanketed the study area with 30 cm of snow which persisted for 5 days; eight nests identified at that stage of the season failed. Only one individual at each of six nests was color-marked. Two marked birds

(1 male and 1 unknown, each with an unmarked mate) re-nested in the study area after snowmelt. One nest was depredated, but the other fledged young. We only included the initial nests from the two marked birds in our data set, as re-nests lacked statistical independence.

Nest Construction.—Nests differed noticeably between habitats. Those in open shrub plots were ~30% more massive ($n = 68$, median [IQR] = 20.7 g [17.3–24.0]) than those in dense shrub ($n = 13$, median [IQR] = 15.2 g [13.4–20.0]; $df = 1$, $\chi^2 = 6.96$, $P = 0.0083$). Nests in dense shrub contained nearly four times the amount of moose hair ($n = 13$, median [IQR] = 1.1 g [0.4–1.3]) than nests in open shrub ($n = 68$, median [IQR] = 0.3 g [0.0–0.8]; $df = 1$, $\chi^2 = 6.18$, $P = 0.013$).

We measured differences in nest mass up to ~3-fold every season (range: 2.0–3.5 fold) within each habitat. There was no correlation between nest mass and hair mass in either habitat type (open shrub: $n = 68$, Spearman's $\rho = -0.15$, $P = 0.22$; dense shrub: $n = 13$, Spearman's $\rho = -0.02$, $P = 0.95$). Orientation of nest entrances did not differ from a random distribution (open shrub plots: $n = 62$, mean vector (μ) = 48°, vector length (r) = 0.13, Rayleigh test $Z = 0.82$, $P = 0.82$; dense shrub plots: $n = 7$, $\mu = 228^\circ$, $r = 0.40$, $Z = 2.02$, $P = 0.13$). Entrances of nests built after the 2006 snowstorm were also randomly oriented ($n = 20$, $\mu = 42^\circ$, $r = 0.26$, $Z = 1.0$, $P = 0.37$). Mass of nests and moose hair did not differ between pairs of plots within each habitat type ($df = 1$, $0.055 \leq \chi^2 \leq 1.85$, $0.17 \leq P \leq 0.82$).

Dissection of 26 nests from open shrub habitat in 2006 indicated moss and grass accounted for most of the nest mass (83.4%), and that each was present in similar proportions (median [IQR] = 45.5% [31.0–54.4] and 37.9% [35.9–55.1], respectively). Moose hair, which was primarily incorporated into the nest cup, comprised 2.0% [0.7–4.2] of nest mass. Any remaining mass (~15%, or ~3.0 g) resulted from small pieces of leaves, twigs, and feather dander. Nest mass also correlated positively with moss and grass contained in the nest structure (moss: $n = 24$, Spearman's $\rho = 0.62$, $P = 0.0013$; grass: $n = 24$, Spearman's $\rho = 0.38$, $P = 0.065$).

Nests from open shrub habitat in 2006 were significantly lighter (by 3.2 g or 14.5%) than those from the previous two seasons (median [IQR] 2006: $n = 28$, 18.9 g [13.9–21.9], 2005: $n = 33$, 22.1 g [17.4–28.2], 2004: $n = 7$, 22.1 g [20.8–25.7]; $df = 2$, $\chi^2 = 8.13$, $P = 0.017$). The

analysis pooled pre-storm ($n = 8$) and post-storm ($n = 20$) nests from 2006, as all comparisons (of nest mass, mass of moose hair, moss, grass) failed to reach statistical significance ($df = 1$, $0.16 \leq \chi^2 \leq 0.44$, $0.51 \leq P \leq 0.68$). Moose hair in nests from open shrub did not differ over 3 years ($df = 2$, $\chi^2 = 2.23$, $P = 0.33$). Nest mass and moose hair in dense shrub did not differ over 2 years (2004, 2005; both analyses: $df = 1$, $\chi^2 = 0.18$, $P = 0.67$).

Fledging Success, Fledge Date, and Nest Construction.—The median number of young fledged in open shrub habitat differed each year ($df = 2$, $\chi^2 = 24.33$, $P < 0.0001$). Birds were most successful in 2005 ($n = 29$, median [IQR] = 6 young [5–6]), followed by 2004 ($n = 15$, median [IQR] = 4 young [4–5]), and the 2006 storm ($n = 20$, median [IQR] = 4 young [3–5]; pairwise comparisons: $df = 1$, $4.39 \leq \chi^2 \leq 22.74$, $0.0001 \leq P \leq 0.036$). Open shrub habitat had significantly greater fledging success in 2005 than dense shrub habitat ($n = 7$, median [IQR] = 3 young [0–6], $df = 1$, $\chi^2 = 5.46$, $P = 0.019$). The two habitats did not differ in 2004 (dense shrub: $n = 8$, median [IQR] = 4 young [3–5], $df = 1$, $\chi^2 = 0.018$, $P = 0.89$). We detected no yearly differences in fledging success in dense shrub habitat ($df = 1$, $\chi^2 = 0.22$, $P = 0.64$). The two plots within each habitat type also did not differ ($df = 1$, open shrub: $\chi^2 = 0.23$, $P = 0.62$; dense shrub: $\chi^2 = 0.032$, $P = 0.86$).

Median fledge date in open habitat differed significantly between years ($n = 14$, 2004: 20 July; $n = 32$, 2005: 22 July; $n = 20$, 2006: 27 July; $df = 2$, $\chi^2 = 34.49$, $P < 0.001$). The storm disrupted breeding in 2006 and resulted in a median fledge date that was 5–7 days later than in previous years ($df = 1$, $\chi^2 = 13.48$, $P < 0.001$). Median fledge dates in dense shrub habitat were identical to those reported for 2004 and 2005.

Nest mass in open shrub habitat correlated positively with three measures of reproductive success when all years were combined ($n = 60$, young fledged per nest: Spearman's $\rho = 0.28$, $P = 0.039$; young hatched: Spearman's $\rho = 0.33$, $P = 0.012$; clutch size: Spearman's $\rho = 0.30$, $P = 0.024$). Nest mass also correlated negatively with fledge date ($n = 60$, Spearman's $\rho = -0.26$, $P = 0.05$). The relationships were not detectable, however, when the disrupted 2006 season was excluded ($n = 44$, $0.03 \leq$ Spearman's $\rho \leq 0.09$, $0.60 \leq P \leq 0.86$), or when each year was analyzed separately ($7 \leq n \leq 33$, $-0.48 \leq$

Spearman's $\rho \leq 0.15$, $0.27 \leq P \leq 0.74$). Hair mass in open shrub nests did not correlate with any measure of reproductive success ($n = 60$, $-0.11 \leq \text{Spearman's } \rho \leq 0.12$, $0.35 \leq P \leq 0.49$). Nest mass, hair mass, reproductive success or fledge date of nests from dense shrub had no detectable relationships ($7 \leq n \leq 14$, $0.078 \leq \text{Spearman's } \rho \leq 0.20$, $0.52 \leq P \leq 0.80$).

Nest Parasites, Incidental Arthropods, and Fledging Success.—We extracted 1,241 parasitic blowfly puparia and 187 adults from Arctic Warbler nests. The blowfly was identified as *Protocalliphora tundrae*. Incidental arthropods included three families of beetles (Order: Coleoptera) (Leioididae: *Catops alpinus*, Carabidae: *Patrobus foveocollis*, Staphylinidae: *Quedius brunnipennis*).

Forty-six of 84 nests that successfully hatched young (55%) contained blowfly puparia, and the proportion of parasitized nests was similar in both habitats (open shrub habitat: 39 of 70 [56%], dense shrub: 7 of 14 [50%]). Most nests contained few puparia (median [IQR] = 1 [0–22]). The greatest number of puparia recorded in one nest was 157 (from open shrub habitat in 2006). Blowfly parasitism did not differ by habitat type (open shrub plots: $n = 69$, median [IQR] = 1 [0–23]; dense shrub plots: $n = 14$, median [IQR] = 1 [0–13]; $df = 1$, $\chi^2 = 0.29$, $P = 0.59$) or by study plot ($df = 3$, $\chi^2 = 3.76$, $P = 0.29$). There was no correlation between puparia count per nest and fledging success ($n = 81$, Spearman's $\rho = -0.056$, $P = 0.62$) or nest mass ($n = 73$, Spearman's $\rho = 0.12$, $P = 0.29$).

Parasite incidence per nest in open shrub habitat differed significantly between years with nests in 2004 containing few puparia ($n = 15$, median [IQR] = 0.0 [0.0–0.0]) compared to those in 2005 ($n = 33$, median [IQR] = 4 [0–28]) and 2006 ($n = 21$, median [IQR] = 12 [0–28]; $df = 2$, $\chi^2 = 15.74$, $P = 0.0004$). The mass of moss contained in open shrub nests tended to be negatively associated with puparia count ($n = 17$, Spearman's $\rho = -0.45$, $P = 0.07$). Nests from dense shrub plots had no correlations between nest characteristics (mass, hair), puparia count, or young fledged ($12 \leq n \leq 13$, $-0.07 \leq \text{Spearman's } \rho \leq 0.26$, $0.40 \leq P \leq 0.83$).

DISCUSSION

Nesting Behavior and Nest Composition.—The 95 nests we examined add new details to our understanding of Arctic Warblers that breed in

central Alaska. First, consistent with other studies of *Phylloscopus* warblers, including other populations of *P. borealis* (Barlein 2006, Clement 2006), females are the primary, if not sole, nest builder while males sing nearby and defend the site. Second, nests weigh ~20 g, and over 83% of nest mass is attributable to moss and grass. Our observations of nest location, shape, and lining of animal hair are consistent with other reports from Alaska (Murie 1956, Price and Beck 1989), and other *Phylloscopus* species (Bi 2004). Third, our data indicate nest openings were randomly oriented. Exposure can influence a nest's microclimate (With and Webb 1993), and several ground-nesting species exhibit clear patterns with regard to orientation, including birds that build domed nests or breed at high latitudes (e.g., Burton 2007, Long et al. 2009). The position of openings of Arctic Warbler nests may be based on other parameters that we did not measure, including shelter near the nest site. It is also possible orientation is opportunistic given the uneven topography of tundra hummocks.

Nest Construction.—Nests in open shrub habitat were more massive and contained less moose hair lining than those in dense shrub. Two non-exclusive explanations may account for this result. We hypothesize that local availability of nest materials differs between habitat types. For example, we often saw moose hair snagged on branches in dense shrub habitat, but moose were less common and had less opportunity (fewer shrubs of adequate height) to snag hair in open shrub habitat. The extensive breeding range and variety of nesting habitats of *Phylloscopus borealis* (Lowther and Sharbaugh 2008) are also consistent with an opportunistic focus upon local resources during nest building (Barlein 2006).

An inverse relationship between nest mass and moose hair is suggestive of a thermal trade-off between the two habitat types. Pilot studies conducted on nests *in situ*, but after fledging, failed to detect any positive correlation between nest mass or the mass of moose hair lining and the insulation quality of nests ($n = 41$ nests, unpubl. data). We believe this warrants additional research, preferably during incubation or brooding, as thermal properties likely result from a combination of factors, including amount and kind(s) of nest material, local topography of the breeding site, and parental behavior (Skowron and Kern 1980).

Fledging Success, Fledge Date, and Nest Construction.—Habitat type was associated with

a measurable difference in fledging success. Birds in open shrub plots during 2005 fledged twice the number of young as those in dense shrub. Open shrub plots at our study site also had a greater nest density (Sharbaugh et al. 2007), which supports the conclusion that open shrub habitat is generally more favorable to Arctic Warblers.

The snow storm on 21 June 2006 interrupted breeding, as the median fledge date in 2006 occurred 5–7 days later than previous years. Nests were significantly lighter only in 2006, suggesting birds built somewhat smaller nests due to the shortened season caused by the storm. We detected no difference, however, between nests built before and after the 2006 storm, possibly due to our small sample of pre-storm nests ($n = 8$).

It is unclear why Arctic Warblers exhibit such striking (~3-fold) differences in nest mass within each habitat type. Nest mass correlated positively with fledging success and negatively with fledge date in open shrub habitat when all years were combined. These patterns were no longer evident, however, when the disrupted 2006 season was removed, or in smaller (yearly) samples. Nest mass in other avian species can indicate quality of the female nest builder (e.g., Soler et al. 1998, Mainwaring et al. 2008), or enhanced parenting effort (e.g., Szentirmai et al. 2005, Broggi and Senar 2009).

Nest Parasites, Incidental Arthropods, and Fledging Success.—The puparia collected represent the first Alaska record of the avian blowfly *Protocalliphora tundrae*. Our observations increase the number of known avian hosts of *P. tundrae* from two (Snow Bunting [*Plectrophenax nivalis*] and Savannah Sparrow [*Passerculus sandwichensis*]) to three, all of which are ground-nesting birds (Sabrosky et al. 1989). *P. tundrae* is considered a rare tundra inhabitant of northern Canada and the Yukon (Sabrosky et al. 1989). Incidental arthropods included *Catops alpinus*, a dung and carrion scavenging beetle known to occur in alcid nests (Perreau 1998, Peck and Cook 2002), and two other beetles that are generalist predators (*Patrobus foveocollis* and *Quedius brunnipennis*). *Q. brunnipennis* in Alaskan tundra is unusual, as it has been reported to be a mature forest specialist from Alberta (Pohl et al. 2007).

Blowfly parasitism of young varied annually but did not correlate with fledging success. This result is consistent with both observational and experimental investigations of other *Protocalli-*

phora species and passerine hosts (Roby et al. 1992, Wittmann and Beason 1992). One recent investigation, however, suggests blowflies contribute to mortality and reduced movement soon after fledging (Strebly et al. 2009).

There are at least two different, non-exclusive explanations for the negative relationship between blowfly puparia and moss mass that warrant future study. First, moss may create a cool microhabitat. Cool environments can cause *Protocalliphora* to delay or fail during larval development (Bennett and Whitworth 1991). Second, moss may cause nests to retain moisture, and *Protocalliphora* larvae, unlike other blowflies, survive poorly when humidity is high (Bennett and Whitworth 1991).

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