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RESEARCH ARTICLE

Common Loons respond adaptively to a black fly that reduces nesting success

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ABSTRACT

Nesting birds must often cope with harassment from biting insects, but it is difficult to ascertain what effect such pests might have on breeding success and population dynamics. We tested the hypothesis that a black fly (*Simulium annulus*) that feeds on the blood of nesting Common Loons (*Gavia immer*) causes nest abandonment in this charismatic diving bird. In addition, we measured effects of fly-induced abandonment on a loon population, and examined potential predictors of fly abundance and nest abandonment. We also tested a second hypothesis, which holds that loon pairs that abandon a nest owing to flies should often remain at the site for their subsequent nesting attempt, since fly outbreaks last only 1–2 weeks. All predictions of the fly-induced abandonment hypothesis were supported, including strong correlations between fly counts and rate of abandonment, reduced incubation during severe fly years, and increased abandonment during cool springs, which promote longevity of the flies. The correlation between nest abandonment and population breeding success suggests that *S. annulus* reduced the chick fledging rate by as much as 23% in a year of severe infestation. Fly numbers on loons and their nests were highest when temperatures were high and winds were light. Surprisingly, however, exposure to the prevailing wind increased, not decreased, nest abandonment, perhaps because of wave action. Lake size was inversely and female age directly correlated with abandonment rate, possibly due to food limitation in small lakes and senescence of females, respectively. Finally, pairs that abandoned a first nest re-nested at the same site with much greater frequency than did pairs that lost eggs to a predator, indicating that loons are capable of responding adaptively to a cause of nest failure that is time- but not space-dependent.

Keywords: abandonment, black fly, *Gavia immer*, loon, nest, senescence, Simuliidae, *Simulium annulus*, win-stay lose-switch

Los individuos de *Gavia immer* responden de manera adaptativa a una mosca negra que reduce el éxito reproductivo

RESUMEN

Las aves que se encuentran anidando deben frecuentemente hacer frente al acoso de los insectos picadores, pero es difícil determinar qué efectos podrían tener estas plagas en el éxito reproductivo y las dinámicas poblacionales. Evaluamos la hipótesis de que una mosca negra (*Simulium annulus*) que se alimenta de la sangre de los individuos anidando de *Gavia immer* causa el abandono del nido de esta ave buceadora carismática. Adicionalmente, medimos los efectos del abandono inducido por la mosca en una población de *G. immer* y examinamos los potenciales factores que predicen la abundancia de la mosca y el abandono del nido. También evaluamos una segunda hipótesis, que establece que las parejas de *G. immer* que abandonan un nido debido a las moscas deberían usualmente permanecer en el sitio para un intento de anidación subsecuente, ya que las epidemias de moscas duran solo una a dos semanas. Todas las predicciones de la hipótesis de abandono inducido por las moscas fueron apoyadas, incluyendo fuertes correlaciones entre conteos de moscas y tasa de abandono, reducción de la incubación durante años de gran cantidad de moscas y aumento del abandono durante primaveras frías, lo que promueve la longevidad de las moscas. La correlación entre el abandono del nido y el éxito reproductivo poblacional sugiere que *S. annulus* reduce la tasa de emplumamiento del polluelo hasta un 23% en un año de infestación severa. El número de moscas sobre individuos de *G. immer* y sus nidos fueron más altos cuando las temperaturas fueron altas y los vientos fueron suaves. Sorprendentemente, sin embargo, la exposición al viento predominante aumentó, en lugar de disminuir, el abandono del nido, debido quizás a la acción de las olas. El tamaño del lago estuvo inversamente correlacionado y la edad de la hembra estuvo directamente correlacionada con la tasa de abandono, posiblemente debido a la limitación de alimentos en los lagos pequeños y a la senescencia de las hembras, respectivamente. Finalmente, las parejas que

abandonaron un primer nido volvieron a anidar en el mismo sitio con una frecuencia mucho mayor que la de las parejas que perdieron huevos por depredación, indicando que los individuos de *G. immer* son capaces de responder de modo adaptativo a una causa de fracaso del nido que es dependiente del tiempo, pero no del espacio.

Palabras clave: abandono, ganar-quedarse, *Gavia immer*, mosca negra, nido, perder-cambiar, senescencia, Simuliidae, *Simulium annulus*

INTRODUCTION

Black flies (Diptera: Simuliidae) are hematophagous (blood-ingesting) insects that comprise over 2,000 species worldwide (Adler and Crosskey 2015). Many species depend upon the blood of birds for reproduction (Adler et al. 2004). Simuliids transmit a variety of nematodes, viruses, and especially protozoans, including *Leucocytozoon simondi* and *L. smithi*, which cause a malaria-like disease in waterfowl and turkeys (Adler et al. 2004). Owing to their occasional massive outbreaks and tendency to feed on humans and domestic animals, black flies have caused negative economic impacts on forestry, tourism, and agriculture (Adler and McCreddie 1997). Attacks of black flies have been shown to compromise the breeding efforts of avian breeding pairs through their attacks on adults (Urbanek et al. 2010, Solheim et al. 2013) and young (Hunter et al. 1997, Smith et al. 1998, Franke et al. 2016). However, no study has yet demonstrated an impact of black flies on a natural avian population (Adler et al. 2004).

We conducted a longitudinal investigation of black fly impacts on a breeding population of Common Loons (*Gavia immer*) that has been under continuous study since 1993. Loons are monogamous territorial breeders (Piper et al. 1997) that maintain strong fidelity to their freshwater breeding lakes until evicted from them by conspecifics (Piper et al. 2000, 2015). The species is well-loved by residents and vacationers across northern North America owing to its haunting nocturnal vocalizations and curious diving habits (McIntyre 1988). Because they rely upon a broad range of fish and invertebrates as food, loons are also indicators of the health of aquatic ecosystems (Evers 2006, Evers et al. 2010).

Several studies have reported on the relationship between a single species of black fly, *Simulium annulus* (previously *S. euryadmiculum*), and the Common Loon. This work has shown that, while *S. annulus* is strongly drawn to loons (Fallis and Smith 1964, Lowther and Wood 1964, Weinandt et al. 2012), it also uses other hosts, notably cranes (Hellgren et al. 2008, Weinandt et al. 2012, King et al. 2013). Still, the observation that hundreds of *S. annulus* females often attack incubating loons at once (McIntyre 1988, Adler et al. 2004, King et al. 2013) suggests that this species might reduce breeding success of loon pairs and even negatively influence loon populations (Weinandt et al. 2012).

A fundamental goal of our study was to use a longitudinal approach to determine if nest abandonment by loons is associated with harassment by *S. annulus* (McIntyre 1988, Adler et al. 2004). We tested 4 predictions of the “fly-induced abandonment” hypothesis. First and most obviously, the hypothesis predicted that the rate of nest abandonment should be high in years and at times when black flies were abundant. Second, loons with active nests should spend less time incubating their eggs, because of the biting flies (Adler et al. 2004). Third, years of high abandonment should co-occur with singleton chicks, because fly-related disruption of incubation should often result in the hatching of only one of two eggs. Finally, unseasonably cool spring weather, which prolongs lives of female black flies (Davies 1953), should lead to a high rate of nest abandonment by loons.

Use of longitudinal data permitted us to assess further the impact and possible causes of nest abandonment. Indeed, a second major goal of the study was to measure influences that black flies might have on loon population dynamics. In addition, study of nest abandonment across 24 years within a marked study population of loons made it possible to examine a variety of biotic (e.g., age, duration of pair bond) and abiotic (e.g., wind exposure) factors as potential predictors of nest abandonment.

A final goal of the study was to test loons’ behavioral response to nest abandonment. Like many animals, loons use the “win–stay, lose–switch” rule (Greenwood and Harvey 1982, Switzer 1993) in nest site selection. That is, male loons, which select the nest site (Piper et al. 2008), tend to move the nest to a new location following predation but reuse the precise nest site if successful hatch occurred there. In contrast, if nest abandonment is caused by black flies, then an adaptive response from loons should not entail movement of the nest for 2 reasons. First, a nest site predated once is likely to be predated again, because of the continued presence of the predator and/or possible vulnerability of the site owing to unfavorable microhabitat (Switzer 1993, Hoover 2003). But a nest site plagued by black flies is unlikely to suffer the same fate during the subsequent nesting attempt, because female black flies of *S. annulus* only occur in large numbers for 2–3 weeks each spring (Adler et al. 2004), and renesting occurs 3 weeks after the initial failure (mean \pm SD = 20.6 days \pm 6.5; n = 202 nests). Second, abandonment of a nest does not imply poor nesting microhabitat; simuliids disperse widely and, unlike raccoons (*Procyon lotor*), can

reach any nest in flight. In summary, we tested the hypothesis that loon pairs should often reuse nest sites where eggs had been abandoned owing to fly outbreaks.

METHODS

Study Animals and Study Area

Common Loons are diving birds with males (mean \pm SD = 4,500 \pm 320 g) 25% larger than females (3,600 \pm 360 g). Loons winter along Atlantic and Pacific coasts of North America and breed from Alaska and British Columbia to Newfoundland. Territorial adults return to their breeding lakes once they are ice-free, usually in April or May. Following courtship and nest-building on a shoreline, island, or emergent vegetation near shore, females lay 2 eggs that are incubated equally by the pair until hatching at 28 days (McIntyre 1988). Pairs whose nests fail commonly attempt a second, or even a third nest (Evers et al. 2010).

Simulium annulus is a widespread black fly whose range overlaps the Common Loon's extensively. This fly is found across Canada (except the west coast), upper midwestern United States, New England, Fennoscandia, and western Russia (Adler et al. 2004). Immature stages develop in flowing water, including rivers more than 10 m wide and streams as narrow as 2 m (Adler et al. 2004). *S. annulus* is often found downstream of lake outlets, perhaps because this places them in proximity to lake-dwelling loons (Malmqvist and Hoffsten 2000). Females, which require a blood meal to reproduce, generally emerge in May and live about 2–3 weeks (Adler et al. 2004). They typically disperse less than 2.5 km, but occasionally as far as 8 km (Bennett and Fallis 1971).

We investigated impacts of simuliids on common loons in a 2,000 km² study area in northern Wisconsin, USA. Centered at 45.7077°N, –89.5930°W, the study area contains about 200 glacial lakes, each surrounded by northern hardwood and coniferous forest. Territories used by breeding loons include entire small to medium-sized lakes (mean size \pm SD = 55 \pm 36 ha; accounting for 96 pairs in 2017; Figure 1), as well as protected coves in large lakes (358 \pm 347 ha; 29 pairs; Figure 1).

Capture and Observation of Loons

Beginning in 1993, we spotlighted adult Common Loons and their chicks from a small motorboat during July and August and captured them in a large fishing net (Evers 1993). All adults and chicks with legs large enough to hold bands were fitted with a single U.S. Geological Survey metal band and 3 colored plastic leg bands (2 bands per leg) in unique combinations.

We observed marked loon breeding pairs from canoes using 10 \times 50 binoculars at least once each week per territory from late April through early August, starting in

1994. Most observations took place between 0500 and 1300 hours. Observations were simplified by the tameness of our study animals, most of which make no attempt to flee from humans within 20 m in boats. On each 60-min visit, observers recorded identities of both pair members and all breeding activity, including courtship, copulation, nest-searching, nest-building, incubation, and chick-rearing. Observers also plotted nest locations on lake maps (1993–2000) or recorded them using a handheld GPS device (2001–2017; Garmin eTrex Legend, DeLorme PN-40 or PN-60; Garmin, Olathe, Kansas, USA). Beginning in 1998, observers estimated numbers of black flies on or around heads of loons when above water (fewer than 10 flies or 10 or more flies) and around nests (fewer than 50 flies or 50 or more flies), either with or without a loon on them. Finally, beginning in 2001 observers conducted scan samples (Altmann 1974) at 5-min intervals, recording proximity to mate (either within or farther apart than 20 m) and behavioral state (foraging, resting, preening, swimming on lake's surface, incubating, or socializing with intruders) at the moment of each scan. Observers visited all nests that had been active at the time of the last visit to confirm continued incubation or, if incubation had ceased, to describe contents of the nest and all shoreline area within 5 m of the nest site. Descriptions included presence of eggshell fragments or intact eggs and, beginning in 1998, an estimate of number of black flies on eggs, nests, or surrounding vegetation.

Determination of Nesting Outcome

We recognized 5 possible outcomes from nesting attempts by loons. Successful hatch of eggs (47.8% of all outcomes, n = 2,053 nests) was indicated by more than 10 angular eggshell fragments mostly ranging in diameter from 0.2 to 3 cm in or adjacent to the nest; one mostly intact shell membrane on or near the nest for each hatched egg; and, of course, a chick or chicks found with the adult pair. Predation (usually by raccoons; see McIntyre 1988, McCann et al. 2005) resulted from 33.9% of all recorded attempts and was implied when nests were either wholly empty or contained fewer than 5 eggshell fragments (see also Piper et al. 2008). In addition, large eggshell fragments, held together by the shell membrane, were often found in adjacent vegetation within 5 m of predated nests. Abandoned nests (15.2%) contained 1 or 2 intact eggs that were neither being incubated nor defended by the pair by close approach to the observer, loud-diving, or penguin dancing (holding body vertically on top of water by splashing feet loudly on water's surface; McIntyre 1988, Jukkala and Piper 2015). Nests that failed owing to embryo death prior to hatching or infertility (2.0%) were identified when the period of incubation had exceeded 35 days (a week longer than the incubation period) and eggs were

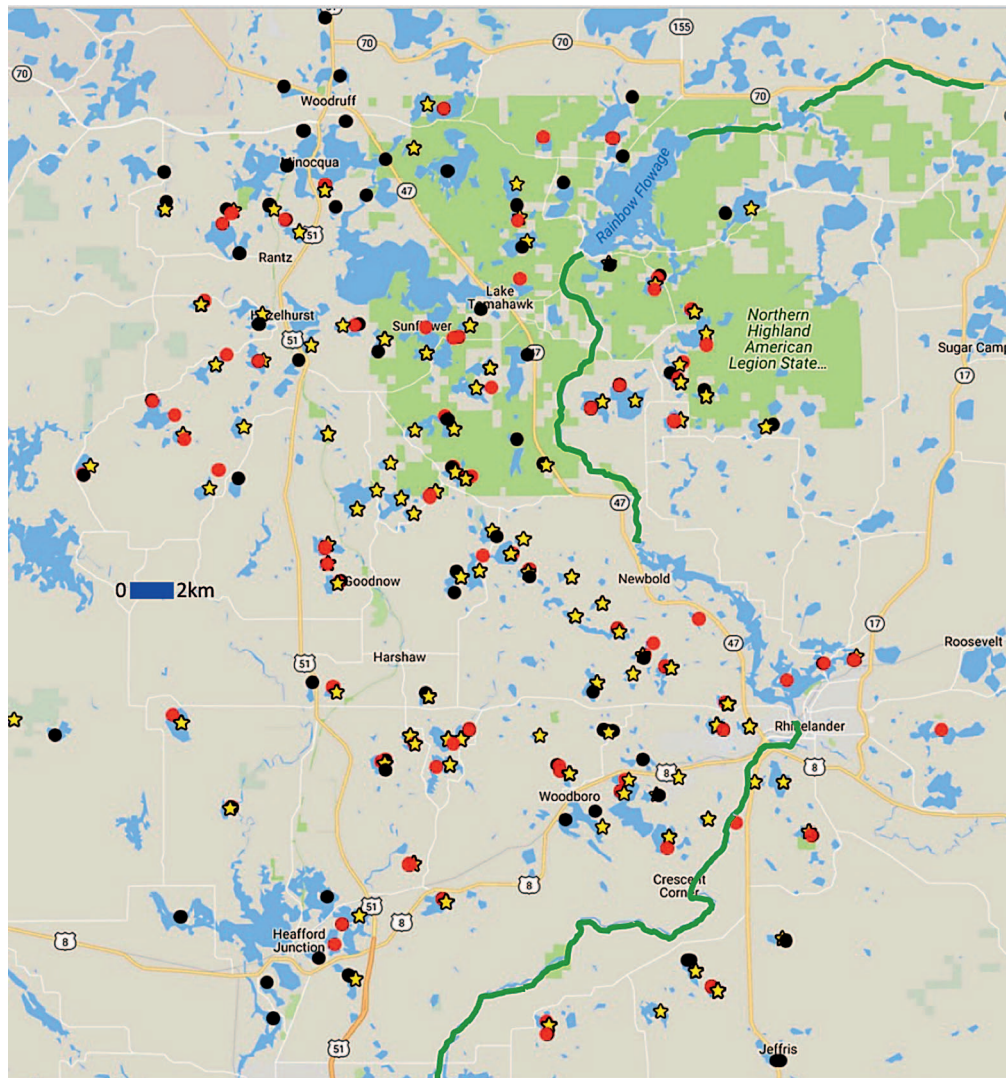


FIGURE 1. Sites with high numbers of black flies (yellow stars), and where nest abandonments (red dots) and successful hatches (black dots) occurred during 3 years with severe black fly outbreaks (2011, 2014, and 2017). Green line traces the path of the largest source of flowing water, the Wisconsin River, which is dammed at 4 points.

intact on the nest, either being incubated or not. Flooded nests (1.1%) were those in which intact eggs were at least half-submerged in lake water and were neither incubated nor defended.

We further narrowed the sample of abandoned nests used in estimating annual abandonment rate in 2 ways to focus attention on those possibly caused by black fly harassment. First, we excluded from the original sample of 312 abandonments 47 cases wherein one or both pair members had been evicted from the territory since nest initiation, as eviction typically leads to nest abandonment. Second we excluded abandonments that occurred among nests initiated after July 1 ($n = 5$), because adult female *S. annulus* are rarely found in July (Adler et al. 2004).

Measurements of Black Flies and Their Impacts

To measure annual rate of black fly abundance during the nesting period, we computed the total number of occasions from April 16 to June 10 of each year on which an observer had reported a large number of black flies (10 or more black flies on or around loons' heads and/or 50 or more flies around a nest) and divided by the total number of hours of observation for that year. In 1998 only, observers also counted the number of head shakes by incubating loons (rapid back-and-forth twisting of the head and neck, clockwise and counterclockwise, for 1–2 s; see McIntyre 1988) during the first minute of observation. We calculated proportion of time spent incubating, preening, or resting during the nesting period using 5-min scan samples beginning in 2001. Population breeding

success was measured as the number of chicks on all study lakes that reached at least 5 weeks of age divided by the total number of pairs present on territory during May of the year.

Calculations Related to Physical Environment

All weather measurements were made using NOAA's historical records for Rhinelander Airport (southeastern portion of the study area; 45.6267°N, 89.4633°W). Cooling degree days were calculated as the difference between the daily high temperature and 0°C, summed across all days of a month. Wind fetch referred to exposure of a point to wind from a given direction and was computed using the fetchR software package (Blake Seers, University of Auckland, New Zealand) for each nest using its geographic coordinates and ArcGIS shapefiles depicting study lakes from Wisconsin Department of Natural Resources (WDNR 24K Hydro Geodatabase). Distance from each nest to the nearest lake inlet or outlet was also calculated using ArcGIS software and based on the locations of inlets and outlets in the WDNR geodatabase.

Statistics

We used simple correlation tests to examine all 4 predictions of the fly-induced abandonment hypothesis and the relationship between population breeding success and nest abandonment. All statistical tests were 2-tailed. Mixed-effects logistic regression (melogit in STATA 14.2; StataCorp, College Station, Texas, USA) was used to search for the best predictors of nest abandonment (i.e. abandoned or did not abandon a nest), including all nests in the analysis that either hatched chicks or were abandoned (excluding nests started after July 1 and those related to eviction). Since both breeder identity and lake were repeated within the sample, both variables were analyzed as random effects in this analysis. Potential predictors (fixed effects) examined for significance were lake size, fetch from the prevailing wind direction (240°), distance from nearest flowing water, use of floating nest platform for nesting, age of male, age of female, and duration of the pair bond. A second logistic analysis (xtlogit command in STATA) with lake as a random effect was used to examine factors that predicted high or low numbers of black flies on loons and nests at the time of specific lake visits. For this analysis, we used only measurements of fly numbers from the 3 years when field observations were most complete: 1998, 2011, and 2014. Potential predictors were temperature, wind speed, time of day (number of minutes before or after 1200 hours), barometric pressure, and change in barometric pressure from the previous hour. Model selection in both cases proceeded by including all potential predictors in a first model and computing Akaike's Information Criterion (AIC). Next, predictors were dropped from the full model one at a time, AIC

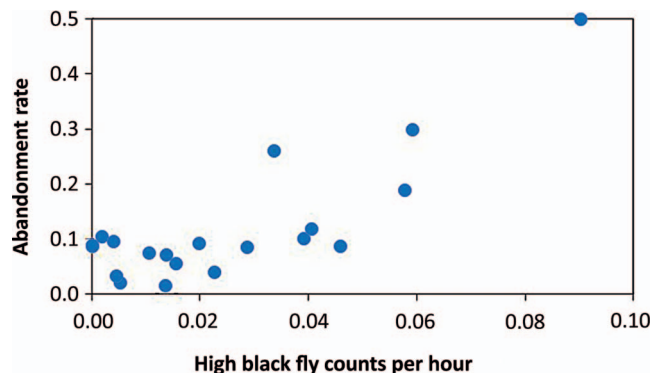


FIGURE 2. Correlation between rate of high counts of black flies (number of high counts per hour of observation time) between April 16 and June 10 and abandonment rate (proportion of all nests before July 1 that were abandoned) within years. Each point represents data from a single year, 1998–2017.

recomputed in each case, the predictor whose removal produced the lowest AIC left out of the working model, and the process repeated until removal of any predictor increased AIC.

We analyzed loons' behavioral responses to nest abandonment by comparing the distance that loons moved their nests between consecutive attempts following abandonment and egg predation, again using lake as a random effect (xtreg command in STATA).

RESULTS

Responses of Loons to Black Flies

Adults that had spent time incubating eggs during black fly outbreaks were easy to spot because they exhibited ruffled feathers in the nape region, perhaps caused by inflamed skin where numerous bites had occurred. Incubating loons harassed by flies engaged in constant head shakes, in apparent efforts to dislodge clinging flies. In 1998, head shakes ranged in frequency from 7.8 min⁻¹ in the first week of May to 3.2, 3.1, 0.4, and 0 in subsequent weeks. Frequency of head shakes was correlated with black fly numbers during this period ($r_{123} = 0.48$, $P < 0.001$).

Testing of the Fly-Induced Abandonment Hypothesis

All 4 predictions of the fly-induced abandonment hypothesis were supported. High counts of black flies on loons' heads and nests were strongly correlated with rate of nest abandonment across years ($r_{18} = 0.81$, $P < 0.001$; Figure 2). Severe fly years were characterized by reduced time spent incubating eggs ($r_{15} = -0.77$, $P < 0.001$; Figure 3). Singleton chicks were more frequent in years when the abandonment rate was high ($r_{18} = 0.52$, $P = 0.02$; Figure 4). Finally, years of frequent abandonment were characterized by cool springs, as measured by cooling degree days in April and May ($r_{22} = 0.50$, $P = 0.01$; Figure 5).

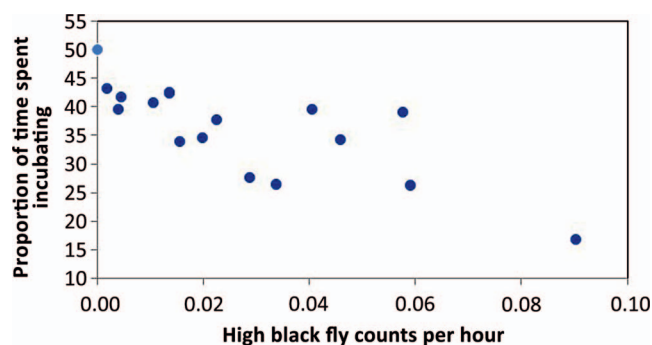


FIGURE 3. Correlation across years between rate of high black fly counts between April 16 and June 10 and proportion of time spent incubating eggs by nesting pairs during the same period. Each point represents data from a single year, 2002–2017.

Effect of Black Flies on Breeding Success and Population Dynamics

The proportion of early-season nests that were abandoned varied from year to year, which suggested that black fly outbreaks affected loons more strongly in some years than others (Figure 6). Although 116 of 262 abandoned nests (44%) on closely monitored territories were followed by renesting attempts, the rate of nest abandonment owing to black flies was negatively correlated with breeding success across the study population ($r_{16} = -0.50$, $P = 0.03$). The slope of the line, -0.46 , indicates that every 10% increase in abandonment rate results in a 4.6% decline in number of chicks fledged. Thus, the impact of *S. annulus* on fledgling production was negligible in years like 2006, with a 1.6% reduction in chicks fledged, but very strong in years like 2014, when an estimated 23% fewer juveniles fledged. Over the 24 years of the study, nest abandonments reduced number of fledglings by an estimated mean of 6.1% (unweighted mean of yearly rates).

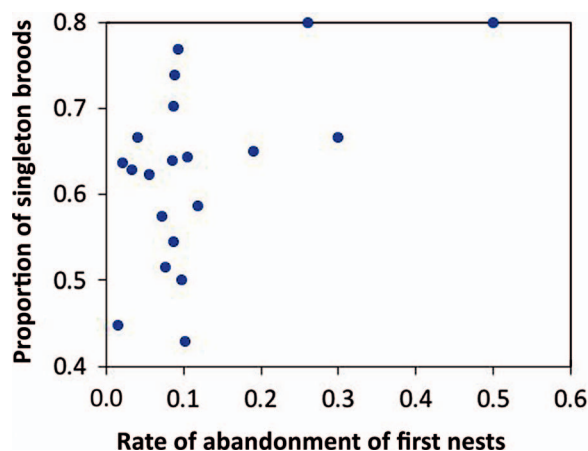


FIGURE 4. Correlation across years between abandonment rate and proportion of singleton broods. Each point represents data from a single year, 1998–2017.

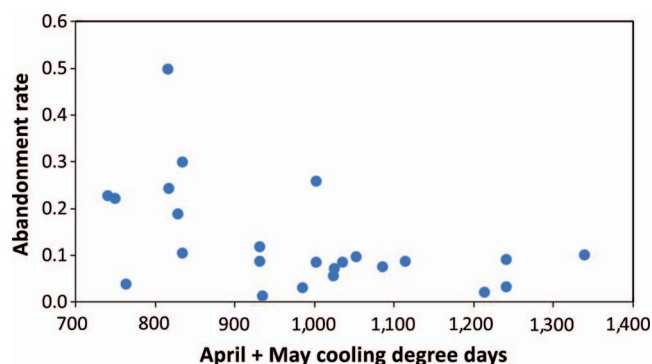


FIGURE 5. Correlation between April and May cooling degree days (cumulative difference between daily high temperature and 0°C), a measure of warmth, and abandonment rate across years. Each point represents data from a single year, 1994–2017.

Predictors of Black Fly Numbers and Nest Abandonment

The number of black flies on loons' heads or their nests varied according to time of year and weather conditions (Table 1). High black fly numbers tended to occur in the middle of the season, when the temperature was high, and when wind speed was low. Time of day, barometric pressure, and change in pressure from the previous hour had no impact on the number of flies on loons' heads or their nests.

Three very different factors emerged as significant predictors of nest abandonment. Abandonment was more likely (1) on small lakes, (2) as female age increased throughout life, and (3) if the nest location had a substantial fetch in the direction of the prevailing wind (Table 2). Distance to the nearest stream or lake outlet was not a significant predictor of nest abandonment. Indeed, nest abandonments occurred throughout the study area, and their distribution showed no obvious relationship to flowing water (Figure 1).

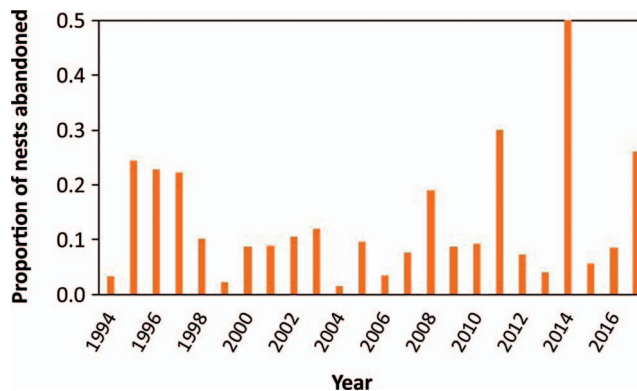


FIGURE 6. Proportion of all nests initiated before July 1 that were abandoned from 1994 to 2017.

TABLE 1. Predictors of black fly abundance from mixed-effects logistic regression on 1,324 daily observations across 169 lakes. Wald $\chi^2 = 54.9$; $P < 0.001$ for overall model.

Predictor	Coeff	SE	z	P
Temperature	0.0485	0.0122	3.99	<0.001
Wind speed	-0.032	0.014	-2.25	0.03
Days from peak of fly abundance	-0.146	0.0224	-6.49	<0.001

Shifting of Nest Site Location after Abandonment and Its Effect on Breeding Success

Loon pairs moved their nest sites greater distances after predation than after abandonment (Wald $\chi^2 = 12.7$; $P < 0.001$; $n = 625$ nests on 128 lakes). In fact, males moved nests no farther after abandonments than after successful hatch (Wald $\chi^2 = 2.2$; $P = 0.14$; $n = 793$ nests on 138 lakes). Loon pairs that re-nested precisely on the same nest site following abandonment produced chicks in 55% of all cases (47 of 85 different pairs), whereas a statistically indistinguishable 47% of pairs (45 of 95) that moved the nest more than 20 m after abandonment produced chicks in their subsequent effort ($P = 0.30$, Fisher's Exact Test).

DISCUSSION

Weinandt et al. (2012) worked on 26 different lakes within and adjacent to our study area in 2005 to investigate host preference in *S. annulus*. All 552 simuliids collected by Weinandt et al. from decoys that mimicked loon appearance and odor were *S. annulus*. We infer from this work (and 3 specimens of this species that we collected ourselves in 2007) that *S. annulus* was the predominant, if not the only, species of black fly feeding on our study animals (see also Fallis and Smith 1964, Lowther and Wood 1964). In support of this conclusion, the Adler et al. (2004) review of Simuliidae maintained that *S. annulus* is the only black fly that feeds on the Common Loon.

Effect of Black Flies on Loons

Others have suggested that black flies cause loons to abandon their nests (McIntyre 1988, King et al. 2013), but only anecdotal observations had been available previously to test this hypothesis. Our findings provide strong correlative evidence for loon nest abandonment in response to black flies.

The 6.1% estimated reduction in fledglings owing to black fly-induced abandonment suggests that black flies have a small impact on loon population dynamics through their effect on nest abandonment, partly because population growth is only weakly affected by chick production (Gear et al. 2009). However, adult loons are bitten by hundreds of black flies each year, and *Leucocytozoon* protozoa have been detected in loon blood (Weinandt et al.

TABLE 2. Predictors of nest abandonment from mixed effects logistic regression on 1,034 nests across 149 lakes and 277 different female loons. Wald $\chi^2 = 28.8$; $P < 0.001$ for overall model.

Predictor	Coeff	SE	z	P
Lake size	-0.00519	0.00187	-2.77	0.006
Age of female	0.0739	0.0176	4.20	<0.001
Fetch @ 240°	0.00133	0.00052	2.56	0.01

2012). So it is likely that *S. annulus*, a vector of *Leucocytozoon* protozoa in captive passerines under experimental laboratory conditions (Adler et al. 2004), reduces adult loon survival, which is a strong driver of population growth (Gear et al. 2009). The prevalence of *Leucocytozoon* protozoans in loons and their impact on loon longevity and reproductive success remains unexplored.

Effect of Weather and Timing on Black Fly Numbers

We estimated numbers of black flies as they harassed loons and buzzed around loon nests, while most other studies have collected flies in traps. Still, our findings with respect to fly abundance and weather patterns mostly echoed what others have found: simuliids are most abundant and feed most actively when temperatures are warm (Choe et al. 1984) and winds are light (McCreadie et al. 1986, Shipp et al. 1987, Roberts and Irving-Bell 1996, Martínez-de la Puente et al. 2009). We found no evidence that female black flies are more active at low atmospheric pressures or following a pressure drop, despite an early report to that effect (Underhill 1940).

Effect of Female Age on Nest Abandonment

Recent work has shown that loons of both sexes senesce once they reach their mid-20s (Piper et al. 2017). Since old birds of many species show declines in reproductive performance with age (e.g., Reed et al. 2008, Sergio et al. 2011, Pardo et al. 2013), the strong tendency for pairs containing old females to abandon nests is perhaps not surprising. Old females are apparently unable or unwilling to tolerate the energetic cost, exposure to disease, or discomfort required to incubate eggs while being bitten by scores of black flies. Still, shared incubation of eggs by breeding pairs prevents us from inferring the precise mechanism of nest abandonment by old females. For example, mere reduction in an old female's willingness to endure fly harassment might explain the pattern, if males mated to old females are unable to make up for their mate's reluctance to remain on the eggs. But it is also possible that male loons are prone to abandoning nests plagued by black flies and that younger females, but not older ones, can compensate for such a shortfall. Clearly detailed observation of nesting pairs confronting large

outbreaks of black flies will be required to pinpoint the mechanism of nest abandonment.

The lack of an impact of male age on abandonment provides an interesting contrast to females and sheds more light on the sexual difference in breeding success with age among loons. Both sexes senesce, as annual survival rate falls steeply when loons reach their mid-20s, but fledgling production increases with age in males, while showing no clear change in females (Piper et al. 2017). The fact that old males resist nest abandonment better than old females is consistent with the conclusion that males, but not females, might make a terminal investment in incubation that accounts, at least in part, for their greater fledgling production (Piper et al. 2017).

Effect of Lake Size on Nest Abandonment

It is not immediately obvious why loon pairs inhabiting large lakes should be less prone to nest abandonment than pairs on small lakes. Large lakes cannot experience lower abandonment rates because of greater mean exposure of nests to wind, because wind fetch was tested and found to be related to a greater, not a lower, rate of abandonment.

The simplest explanation for reduced abandonment on large lakes seems an energetic one. Large lakes provide a more robust food supply for loons, as suggested by the direct relationship between lake size and body mass among males ($r^2 = 0.06$, d.f. = 300, $P < 0.001$) and reduced juvenile mortality and greater chick growth rates on large lakes (Piper et al. 2012). The greater food supply on large lakes probably permits loons breeding on them to maintain good body condition and better immune system function. If so, large-lake loons are well equipped to cope with blood loss and parasitism that might result from black fly bites and are thus more apt to persist with a nesting effort during a fly outbreak.

Impact of Wind Fetch and Distance from Flowing Water

In light of the strong negative impact of wind on activity patterns and biting of female black flies seen in this study and by others (e.g., Shipp et al. 1987, Roberts and Irving-Bell 1996), we might have expected wind exposure to protect a nest from abandonment. Not only did fetch affect nest abandonment weakly, wind exposure actually made loons more, not less, likely to abandon their nests. Thus, we have shown that, while high winds can reduce black fly activity in the short term, even substantial wind exposure does not deter black flies sufficiently to prevent nest abandonment, perhaps because wind speeds inevitably fluctuate, permitting flies to attack nesting loons at least intermittently on most days. The simplest explanation for the tendency of wind exposure to increase, rather than decrease, the rate of nest abandonment was that waves caused by a large fetch in the direction of the prevailing

wind (perhaps in combination with rising water levels caused by heavy rainfalls in some years) washed over some nests, causing abandonment.

We were surprised that distance from the nearest stream was unrelated to nest abandonment. *Simulium annulus*, like all black flies, is dependent on flowing water for development of adults; immatures of this species occur commonly in streams and rivers more than 10 m wide but down to 2 m wide (Adler et al. 2004). Despite this strict geographic constraint on its development, *S. annulus* caused nest abandonments up to many kilometers away from the only major body of flowing water in the study area (the Wisconsin River, see Figure 1). Furthermore, no statistical relationship occurred between abandonment and distance from the nearest stream. These patterns suggest either that (1) *S. annulus* females routinely disperse much farther than the typical distance of 2.5 km reported by Bennett and Fallis (1971), or (2) small streams, lake outlets, and other small flowing water bodies support sufficient fly development that no breeding lake used by loons was far from one or more sources of black flies.

Loons Do Not Treat Nest Abandonment like Nest Predation

While countless animals use the “win–stay, lose–switch” rule to govern breeding attempts following predation (Switzer 1993), nest abandonment resulting from fly harassment poses a very different challenge. As noted earlier, one case of black fly–induced abandonment is unlikely to be followed by another within a season, because of the short duration of fly abundance. This is especially true in Common Loons, which are attacked by only one species of short-lived black fly (Adler et al. 2004). The decision of many male loons to reuse nest sites where a recent nest attempt failed illustrates that birds can respond adaptively to nest failure that is time- but not space-dependent. We predict that other avian species that face short-term disturbances unrelated to nesting microhabitat, like early spring snowstorms (Krapu 1977, Hendricks and Norment 1992), will show a high rate of nest reuse as well.

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