ORIGINAL ARTICLE

How robust are risk-taking associations in incubating birds? A test and a review

Kylee F. Graham[1] · Dave Shutler[1] (ORCID)

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Abstract
Flushing distance (FD, the horizontal distance between a parent bird when it leaves its nest and an approaching predator) is one measure of nest defense and of risk-taking; parents that stay too long risk being killed, whereas those that flush too early risk at the very least impairing development of their young, and at the very worst leaving them unprotected against predators. Thus, FD should be under strong natural selection. A general prediction is that incubating birds will remain on a nest being approached by a predator until risks of staying reach a threshold that outweighs costs of fleeing. This threshold is predicted to vary depending on a brood's value, parental characteristics, environmental conditions, and learning that repeated visits pose a limited or no threat. We evaluated FD in a nest box population of tree swallows (*Tachycineta bicolor*) relative to each of these. We obtained 246 FDs from 66 different nests over 2 years. We found some evidence that FD increased with clutch size (tendency), female age, and air temperature, and decreased with greater overhead vegetation density; six additional associations were not significant. Given the lackluster support for the predictions we tested, we did a review of the literature and similarly found limited support for most of the associations we tested despite the entrenched view that these relationships are commonplace. We submit that further insights are needed into understanding predictors of FD in incubating birds.

Significance statement
Parent birds sitting on eggs are proverbial sitting ducks, although they do have the option of fleeing predators. However, parents may be willing to sacrifice themselves to protect their eggs if the latter become sufficiently valuable. One assumption is that eggs increase in value closer to hatch, and one prediction is that parents will be more reluctant to fly from their nests later in incubation. We tested this and other predictions in a population of nest-box-using tree swallows in eastern North America. The relatively weak support we obtained for our predictions suggests that we need to reevaluate our assumptions in this area of research.

Introduction

Organisms are assumed to allocate resources to broods in a way that maximizes lifetime reproductive success (Williams 1966; Charnov and Krebs 1974; Perrins and Moss 1975). As one element of lifetime reproductive success, parental investment is of theoretical interest because it is defined as a tradeoff between investment in current versus future offspring (Trivers 1972; Clutton-Brock 1991). Parental investment is predicted to increase as brood value increases, or as residual reproductive value of a parent decreases (Dale et al. 1996). Brood value is assumed to increase as embryos and young age, as their survival probability increases, with the number in a brood, and if broods are produced earlier in the season, because recruitment (when animals first join a breeding population) improves with each of these metrics (Montgomerie and Weatherhead 1988; Shutler et al. 2006). Parental reproductive value is predicted to decrease with senescence or other negative influences on health (Pressley 1981; Clutton-Brock 1984; Dale et al. 1996). Although benefits of parental investment are predicted to outweigh costs incurred by parents (Pressley 1981; Pavel and Bureš 2008), greater parental investment should be favored where net benefits are highest (Stearns 1976).

In birds, nest defense may be particularly sensitive to natural selection (Rytkönen 2002). Predators can potentially injure or kill both broods and parents at nests, often leading to a tradeoff between risks to parents and risks to potentially helpless broods (Trivers 1972; Caro 2005; Ellis-Felege et al. 2013). Risks are assumed to influence net benefits of investment, and therefore strong selective pressures are expected (Montgomerie and Weatherhead 1988). For these reasons, nest defense is considered an excellent behavior for studying parental investment (Trivers 1972; Montgomerie and Weatherhead 1988).

Flushing distance (FD, the horizontal distance at which a bird leaves its nest when a predator approaches) is one form of nest defense that can incur serious risks (e.g., Regelmann and Curio 1983; Keeley and Bechard 2011; Møller 2015). (Flush initiation distance usually has a vertical component (Møller 2015) that was not part of this study.) Nest defense during incubation can expose parents to high risks of predation while they are simultaneously constrained by the need to remain on a nest to speed growth and other aspects of brood fitness (Durant et al. 2013). A general prediction is that nesting birds will remain on nests when being approached by a predator until risks of staying reach a threshold that outweighs costs of fleeing (Montgomerie and Weatherhead 1988).

Aside from brood value and a parent's residual reproductive value, a number of other variables have been proposed to affect FD. First, nest concealment may affect FD because a parent may either determine that they are sufficiently concealed from predators that there is no risk to remaining on a nest, or a parent may believe they are hindered in their ability to detect approaching predators and determine that they need to flush more readily; they may also determine that they need extra time to escape through dense cover. On the other hand, if cover is limited, flushing early also risks tipping off a predator about a nest's location (Götmark et al. 1995; Wiebe and Martin 1998; Burhans and Thompson 2001; Miller et al. 2013). Second, time of day may be important to FD if it is associated with, for example, activity of predators. Third, air temperature often covaries with time of day, and in general may affect FD because cooler temperatures are associated with greater risks to embryos if they are temporarily abandoned. Fourth, learning has been proposed to make parents bolder if they determine that their risks are low from humans that repeatedly approach nests (Knight and Temple 1986).

Each of these relationships has been repeatedly tested, and one could easily get the impression from reading this literature that many predictions have overwhelming support. However, it is worth re-evaluating this perception because exceptions have been observed and their explanation has attracted less attention than have results offering support (see below).

Tree swallows (*Tachycineta bicolor*) are one of the most studied birds in North America; they have an extensive geographic range, breed at relatively high densities, readily adapt to nest boxes, and are extremely tolerant to human activity (Jones 2003; Winkler et al. 2011). Only female tree swallows incubate eggs (Winkler et al. 2011), which offers advantages in studying FD because potential confounding effects of parent sex can be eliminated. As evidence that parents take risks in remaining at nests, every year, we observe two or more adult mortalities from predators in nest boxes during incubation. We tested if FD in incubating female tree swallows was affected by brood value, parent age, nest concealment, air temperature, and number of visits we made to nests when a female was on eggs.

Methods

We maintained 178 nest boxes in Port Williams, King's County, Nova Scotia (45° 5′ 52″ N, 64° 24′ 34″ W). Surrounding areas included a diversity of habitats dominated by fruit orchards, field crops, and marshes (Shutler et al. 2004, 2012; Hainstock et al. 2010; Holland and Shutler 2018). Each box was ≥ 25 m away from its nearest neighbor (Muldal et al. 1985) elevated ~ 1.5 m above the ground on metal poles. There was variation in volumes of nest boxes that were used by swallows, but all boxes had 3.8-cm openings.

At the beginning of breeding seasons in early May of 2017 and 2018, nest boxes were cleaned of debris including those from various nesting birds and small mammals (debris may sustain ectoparasites; e.g., Møller 1989; Rendell and Verbeek 1996), and repaired if needed. After this, if it was not raining, all boxes were checked every 2 days to record clutch initiation date (day of first egg), clutch size, hatching date (of at least one nestling), and number of fledglings (number hatching minus number found dead in nests following fledge). At ~ 12 days, nestlings were banded and then nest boxes were avoided until after fledging (22 days after hatching) so that premature fledging was not provoked. Subsequently, nests were once again visited to count how many offspring perished before fledging. Adult tree swallows were also captured opportunistically at any time by covering box entrances before opening their doors, or trapped (Saunders and Shutler 2019) inside boxes when nestlings were between 3 and 8 days of age, and banded if not already so. Using banding data, we were able to determine minimum female ages for most individuals. Observation of nest boxes continued until early July.

FDs were measured at all active nest boxes where females were incubating. Observers were aware of the hypothesis being tested and were not blind to time of day or air temperature when FDs were collected. To some extent, the number of active boxes precluded observers remembering clutch size or days of incubation for particular boxes, although, again, it was not possible to ensure completely blind data recording. If females were present during laying, or if for various reasons, we had to visit boxes twice (e.g., to verify numbers of eggs), we

counted this as a visit. In all cases, an observer approached a nest at a walking pace (boxes were arranged in circuits so approach distances were always the same; maximum flush distance observed was 22.5 m; Table 1), with the distance between observer and box measured with a measuring tape to the nearest 0.1 m as soon as a female left her nest box. Boxes were oriented towards more open habitat and were on the periphery of fields and orchards, so that our approaches were almost always from the side. Elsewhere, we showed that tree swallows respond to humans with the same defense intensity as they do to natural predators (Hainstock et al. 2010). Nests were approached by different observers at various times of day (Table 1), with ~90% of observations before 12:00. Clutch size and time of day were recorded, but all data were not necessarily collected for each FD, so sample sizes vary among analyses. If FD was 0 m and a female tree swallow was captured, or if males were trapped (Saunders and Shutler 2019), the bird's age, sex, and band number were recorded (age and sex criteria described in Winkler et al. (2014)). Hourly temperatures were later obtained from Environment Canada (2018) for the Kentville Weather Station, 13 km west of the study area. Days of incubation was the number of days since the last egg was laid. Lateral and overhead vegetation density were obtained from Obomsawin (2017). Briefly, Obomsawin (2017) used the point quarter method to generate indices of lateral vegetation density (Mitchell 2010), and a standard densiometer procedure to generate indices of overhead vegetation density (Strickler 1959).

Statistical analysis

Data were analyzed in SAS 9.4 (Cary, NC, USA). We used correlations (PROC CORR) to test for relationships between FD and explanatory variables. Initial analyses treated each observation as independent; because we recorded multiple observations for most nests, this analysis included pseudoreplication. Subsequently, for explanatory variables that changed during the season (days of incubation, time of day, air temperature, and visit number), we coded nests as a random factor in general linear mixed models (PROC MIXED) to control for multiple observations at nests. For explanatory variables that were fixed throughout the season (initiation date, hatch date, clutch size, and vertical and lateral vegetation density), we randomly selected a single observation per nest and repeated statistical tests 1000 times (program syntax available from junior author): we report average results.

Data availability

Datasets analyzed in the current study are available from the corresponding author on reasonable request.

Results

Overall, we obtained 246 FDs for 66 different boxes (32 in 2017 and 34 in 2018). Descriptive statistics for variables are provided in Table 1; these results are partially pseudoreplicated. There was no difference in FDs between years ($F_{1,\ 244} = 0.6$, $P = 0.44$), so data were pooled. FDs were zero-inflated (i.e., largely zeros; Fig. 1), so transformations failed to improve normality. With the exception of mixed models, we therefore ran analyses non-parametrically.

FD was tendentially positively correlated with clutch size, positively correlated with female age, negatively correlated with overhead vegetation density, and positively correlated with air temperature; six other associations were not

Table 1 Descriptive statistics for variables measured for incubating tree swallows in Nova Scotia, Canada, and correlations between explanatory variables and flushing distance (FD). Because multiple observations were taken at most nests, these results are to some extent pseudoreplicated. SD is standard deviation. Significant results italicised

| Variable	N	Minimum	Maximum	Median	$\bar{x}$	SD	r_S	P
FD (m)	246	0.0	22.5	3.0	4.8	5.6		
Initiation date (day of year)	246	134.0	154.0	140.0	140.7	3.9	−0.03	0.64
Clutch size	246	3.0	7.0	6.0	5.6	0.8	0.12	0.06
Days incubation when flush measured	246	1.0	18.0	8.0	7.8	4.3	−0.01	0.82
Hatch date (day of year)	235	153.0	172.0	160.0	160.1	3.6	−0.05	0.42
Female parent age (years)	159	1.0	8.0	2.0	2.2	1.8	*0.31*	*< 0.0001*
Overhead vegetation density (%)	243	0.0	98.3	0.5	12.4	23.3	*− 0.14*	*0.03*
Lateral veg. density (trees/100 m^2)	233	0.1	13.5	0.5	1.4	2.3	−0.05	0.42
Time (minute of day)	238	495.0	870.0	585.0	594.4	65.7	−0.04	0.50
Air temperature (°C)	238	6.3	25.7	13.2	12.7	4.3	*0.14*	*0.02*
Visit number	246	1.0	13.0	5.0	5.0	2.6	−0.07	0.25
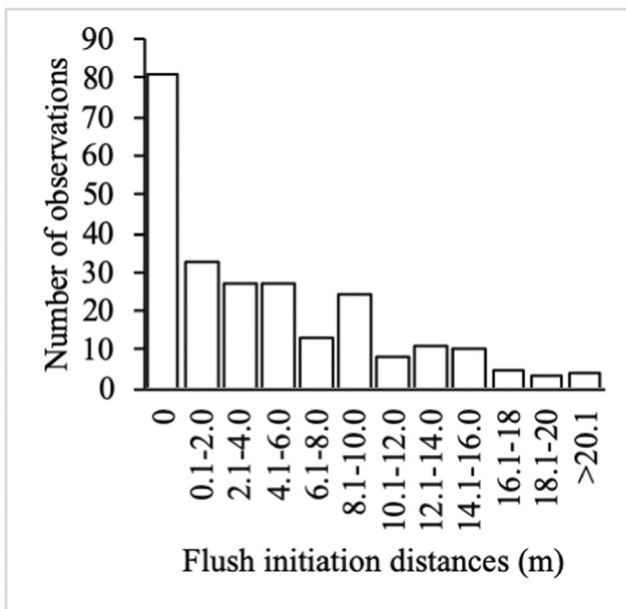
Fig. 1 Frequency distribution of 246 flushing distances recorded for tree swallows

significant (Table 1). For variables that changed with each recorded FD, within-nest regressions suggested roughly equal numbers of decreasing and increasing trends (Fig. 2a–d), echoing the preceding results with the exception of air temperature, which no longer was clearly associated with FD.

In mixed models, the only significant association was that FDs were greater with higher air temperatures (Table 2). For variables that did not change over the course of the year, there was a tendentially positive association between FD and female age but sample size was relatively small (Table 2).

The high proportion of 0-m flushes (Fig. 1) may suggest that risks to incubating birds are flat until predators get extremely close. We thus repeated analyses comparing data from 0-m to > 0-m FDs using Wilcoxon tests. FDs were tendentially higher for larger clutches, higher for older females, lower with greater overhead canopy cover, and tendentially higher at higher air temperatures (Table 3), echoing results above. However, once again, nests appeared multiple times in these analyses.

We were surprised at how few associations emerged from our analyses when there appears to be broad consensus for the apparently sound theory we tested. We therefore decided to evaluate how much support there is for this body of theory; we compiled data from other published studies, some of which provided multiple tests on variants of explanatory variables, and some of which provided data from multiple species; we treated each result as independent in counting results (Table 4; many authors of older studies that we contacted no longer had their data). These studies considered several different measures of risk-taking other than FD (e.g., mobbing); for simplicity, we pooled all forms of risk-taking to evaluate its

association with the explanatory variables we tested as well as a few others (note that positive relationships between a variable and FD are indicative of lower risk-taking). Perhaps, the most compelling result from this review was that the majority of tests failed to find support for theoretical predictions (Table 4). Also, for each explanatory variable, there were often studies finding results opposite to predictions. Of the variables considered and for which there were large numbers of studies providing data, there tended to be more studies finding less risk-taking for nests initiated and hatching earlier in the year (contrary to most predictions), more risk-taking for larger clutch sizes (consistent with predictions, but note that 84.0% of studies failed to support the hypothesis), many more studies with more risk-taking for nests later in incubation (consistent with predictions, with 60.7% failing to support the hypothesis), and more risk-taking with later visit numbers (consistent with predictions with 77.2% failing to support the hypothesis; Table 4).

Discussion

Each of our analyses provided broadly consistent results: FDs were tendentially positively associated with clutch size, positively associated with female age and air temperature, and negatively associated with overhead vegetation density. FDs were not associated with six additional variables that we considered in any analysis. Our last findings from our review of the literature revealed substantial inconsistency in risk-taking relative to a variety of explanatory variables. While these and other results provide some support for nest defense hypotheses, overall, the evidence is not as compelling as our reading of the literature had suggested it would be (also see Caro 2005, pp. 335–379). Thus, we emphasize the number of results that do not support hypotheses.

We found no support for the prediction that nests initiated earlier in the year would be more vigorously defended. This prediction is based on the observation that earlier nesting is associated with both large clutch sizes (Winkler et al. 2014) and a higher likelihood of recruitment (e.g., Shutler et al. 2006), presumably making these nests more valuable to parents. Nests initiated earlier hatch earlier, and, by chance, have more FDs recorded when temperatures are apt to be cooler; although we observed no significant association with initiation date, we did observe the predicted relationship of greater FD with warmer temperatures. We also found no support for the prediction that nests later in incubation would be more vigorously defended. This prediction arises because nests later in the nesting cycle have a higher probability of producing fledglings, assuming predators destroy nests at a relatively constant rate throughout the nesting cycle (a pattern that is by no means universal; e.g., Grant et al. 2005; Bulluck and
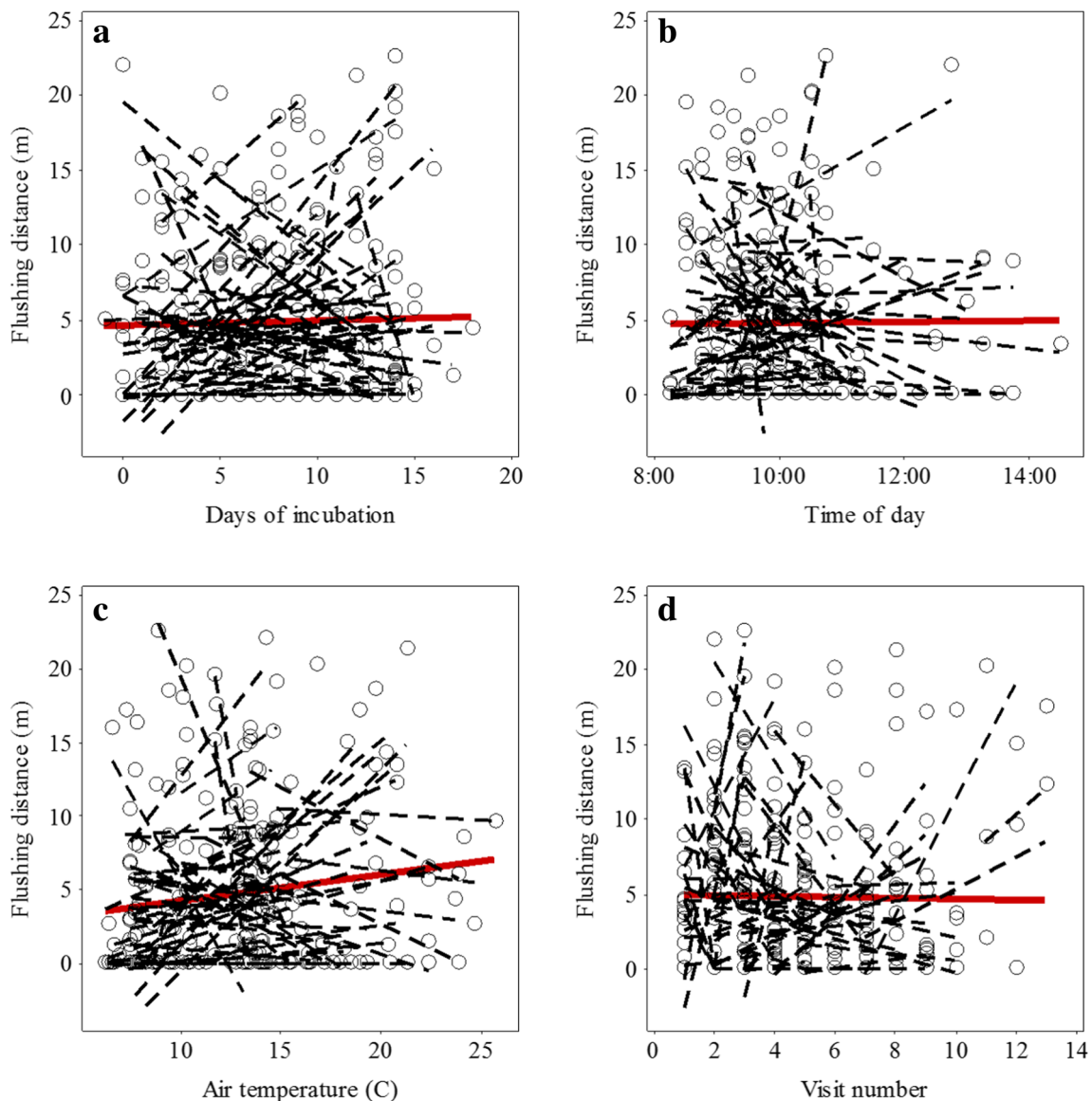
Fig. 2 Overall (solid bold red lines) and individual nest (dashed black lines) linear regressions of flush distances relative to **a** days of incubation, **b** minute of the day, **b** air temperature, and **d** visit number

Buehler 2008; Grant and Shaffer 2012). Thus, it was perhaps surprising that none of these associations were significant.

We found weak support (tendency) for an association between risk-taking and clutch size, but larger clutches were actually associated with lower risk-taking, contrary to prediction. Winkler (1992) found no effect of clutch size on nest defense in tree swallows, and > 80.0% of other tests with different species did not find a relationship between risk-taking and clutch size, although those finding significant associations did find a positive association more often (Table 4). In our case, a possible explanation for the negative association between risk-taking and clutch size may relate to female age; younger females took greater risks (contrary to a general pattern that younger birds and mammals are generally more vigilant; reviewed in Caro 2005, pp. 166–170). Younger tree

swallows initiate nests later and have smaller clutches (Stutchbury and Robertson 1988); for our study, 18 second-year birds had average initiation dates $\pm$ SD of 143.6 ($\sim$ 24 May) $\pm$ 5.4 whereas 13 after-second-year birds initiated on 138.5 ($\sim$ 19 May) $\pm$ 2.7 ($R^2 = 0.26$, $F_{1,\,29} = 10.1$, $P = 0.004$); equivalent results for clutch size were 5.1 $\pm$ 0.8 and 5.8 $\pm$ 0.6 ($R^2 = 0.20$, $F_{1,\,29} = 7.3$, $P = 0.01$). We lacked power to simultaneously control for initiation date, clutch size, and female age in analyses of FD. It is unclear why younger females would take greater risks particularly because they have smaller clutches. We can exclude the possibility that females later in the year have lower re-nesting potential (e.g., Pavel and Bureš 2008) because tree swallows rarely have second clutches especially at the latitude of our study site (Winkler et al. 2011). One possibility is that older females have learned to leave

Table 2 Results of controlling for multiple flushing distance (FD) observations for the same nests. For variables that changed during the year, we used mixed models with nest coded as a random variable. For variables that did not change, we randomly selected a single observation for each nest and repeated analyses 1000 times, reporting here average statistics. A "+" before F statistics indicates a positive relationship between FD and the explanatory variable, a "−"indicates a negative relationship. Significant results italicized

	N	Test statistic	P
Variables that changed with each visit		F	
Days of incubation when FD measured	246	− 0.5	0.47
Time	238	− 1.0	0.33
Air temperature	238	+ 4.0	*0.05*
Visit number	246	− < 0.1	0.89
Variables that were constant with each visit		r	
Initiation date	66	− 0.01	0.93
Clutch size	66	+ 0.10	0.44
Hatch date	62	+ 0.02	0.86
Female parent age	41	+ 0.30	0.06
Overhead vegetation density	64	− 0.10	0.44
Lateral vegetation density	64	− 0.09	0.47

boxes based on previous experience with our visits. We had insufficient data to undertake this analysis, or to control for females that were monitored in each of the 2 years of the study. A related question is whether females captured in nest boxes are more likely to flush sooner the next time an observer approaches. We tested this and found no support for this hypothesis (mean flush distance the visit after being captured = 4.5 ± 5.6 m, after escaping without being captured = 5.0 ± 5.6 m; $R^2 < 0.01$, $F_{1, 243} = 0.6$, $P = 0.44$). Thus, the explanation must lie elsewhere. One possibility is "personal"

differences among females in phenotypic proclivity to flush (e.g., Bötsch et al. 2018); more data will be needed to test this.

Predictions for relationships between risk-taking and nest vegetation density are difficult to make because the risks imposed by denser vegetation are unknown (also see Caro 2005, pp. 265–303). Thus, the nature of presumed tradeoffs among being able to detect approaching predators, the security of concealment, risks of tipping off a predator of a nest's location by flushing, and having easy escape routes (Götmark et al. 1995; Burhans and Thompson 2001; Miller et al. 2013) are unclear and apt to be complex. Moreover, concealment is measured in different ways among studies, making comparisons difficult; we separated vertical and lateral concealment and only found that vertical concealment was important, despite the fact that we approached nests laterally. However, the predator community is often an important unknown in evaluating the importance of visual concealment; despite our study site having 20–30 nests depredated (which we based on missing and/or broken eggs, disturbed nest bowls, and adult remains in ~ 2 nests/year) each year, and despite capturing over 70,000 images with trail cameras at our nests, only one image was that of a predator (a raccoon, *Procyon lotor*; Obomsawin 2017). Raccoons are probably less influenced by visual than olfactory cues in finding nests (Conover 2007; Shutler 2019), so the importance of vegetation density to our populations of tree swallows is unknown. Based on limited visual evidence, we suspect deer mice, *Peromyscus maniculatus*, are the most important predators in this system and they too are largely nocturnal and rely on olfaction; house sparrows (*Passer domesticus*) are also suspected in a few instances of nest predation. We speculate that tree swallows have limited capacity to defend against raccoons, mice, or house sparrows. However, each of these predators also approaches boxes

Table 3 Medians and means of explanatory variables for females that did not flush and those that did, and results of Wilcoxon tests for differences in explanatory variables between birds that did not ($N = 171$ maximum) or did ($N = 85$ maximum) flush when their nest was approached. A "+" before test statistic indicates higher mean values for females that flushed; a "−" indicates the opposite. Significant results italicized

Variable	Did not flush median	Flushed median	Did not flush mean	Flushed mean	Test statistic	z approximation	P
Initiation date	140.0	140.0	140.7	140.6	− 10,190.5	0.4	0.72
Clutch size	6.0	6.0	5.5	5.6	+ 9183.0	1.7	0.08
Days of incubation	8.0	8.0	7.9	7.8	− 10,037.5	0.1	0.95
Hatch date	160.0	160.0	160.1	160.1	− 9256.5	0.1	0.91
Female age	1.0	2.0	1.7	2.5	*+ 4156.0*	*2.4*	*0.01*
Overhead vegetation density (%)	1.6	0.3	16.9	10.2	*− 10,597.0*	*2.0*	*0.05*
Lateral vegetation density (trees/100 m²)	0.6	0.5	1.5	1.3	− 9040.5	0.6	0.58
Time of day	585.0	585.0	597.1	593.2	− 9642.0	0.6	0.52
Air temperature (°C)	11.1	13.3	12.0	13.1	+ 8420.0	1.8	0.07
Visit number	5.0	5.0	5.0	5.0	− 10,150.5	0.3	0.78

Table 4 Results of the current study alongside data from other studies (summarized from Graham 2018). Note that higher flush distances are associated with lower risk-taking, i.e., results from Tables 1, 2, and 3 will appear contrary to what is reported in the "increased" and "decreased" columns. Numbers are the number of tests done on each explanatory variable; some studies conducted multiple tests and some tested multiple species. Each test and tests on separate species were treated as independent. Where samples sizes warranted, binomial tests evaluate whether among significant results there was a tendency for either increased or decreased risk-taking among continuous variables, and whether there was a tendency for either non-significance or significance for categorical variables. Significant results italicized

	Association with risk-taking				Binomial test P
	Current study	Decreased	Was unrelated	Increased	
Continuous variables					
Initiation or hatch date	Unrelated	16	41	4	*0.007*
Clutch size	Weakly decreased	3	97	19	*0.0006*
Days of incubation	Unrelated	3	85	57	*< 0.0001*
Age of parent	Decreased	0	9	1	
Vegetation density	Increased / unrelated	1	3	6	0.06
Time of day	Unrelated	1	3	1	
Air temperature	Decreased	2	4	0	
Visit number	Unrelated	6	55	18	*0.01*
			Significant?		
Categorical variables (not tested in current study)			No	Yes	
Sex of parent			7	14	0.13
Individual			3	6	0.32
Condition of parent or young			4	2	0.41
Presence of other birds including mate			3	5	0.48
Predator type			4	6	0.53
Habitat type			4	1	0.18

Sources include those cited in text as well as Andersen, 1990; D'Orazio and Neudorf, 2008; Forbes et al. 1994; Mallory et al. 1998; Palestis, 2005; Redondo and Carranza, 1989; Weatherhead, 1979; Westneat, 1989; Wilson-Aggarwal et al. 2016

laterally, making the association between FD and overhead vegetation enigmatic. Based on our zero-inflated FD data that suggested many birds did not perceive risk, a reviewer raised an interesting point about diurnal versus nocturnal risks of flushing that we had not considered. We are unaware of any rigorous comparisons that have been made between FDs at these times, likely in part because accurate data on the latter interval would be difficult to obtain. In any case, one relevant issue is likely differences in the predator community, and how this would change risk between these two time intervals. We speculate that flushing at night would entail additional risks for birds with diurnal habits, so we suspect that FDs would more often be zero at night, but we leave this to others to investigate.

We found no evidence that FD was associated with time of day, but we did find some evidence (tendency) for higher FDs with warmer air temperatures. The latter variable is a better proxy for risks that eggs may face if a female ceases incubation (White and Kinney 1974; Olson et al. 2006; Bicudo et al. 2010), and the association we detected makes sense; surprisingly, we found few tests for this association in the literature, where 2 of 6 studies found a similar relationship (Table 4).

Finally, we found no support for Knight and Temple's (1986) prediction that learning (the revisitation hypothesis;

Caro 2005, p 367) would lead to greater risk-taking with later visits; some studies do find this relationship (Gunness and Weatherhead 2002 and other citations in Caro 2005), whereas others do not (Weatherhead 1989 and other citations in Caro 2005).

Given the large numbers of results that find no support or find evidence contrary to expectations for risk-taking at nests, it is surprising that support for a body of hypotheses is so widely assumed. We submit that the logic is sound, so why is the empirical evidence less than compelling? First, there may be insufficient data to generate meaningful values for all of the costs and benefits associated with various behaviors, brood values, parental values, and other variables that are considered. As an example, the average tree swallow that makes it to breeding age has approximately a 50% chance of breeding again (Shutler et al. 2006). The benefits of successfully fledging young are obvious, but to what extent do costs change once incubation begins or as a bird ages? Senescence is difficult to detect in most wild organisms unless enormous sample sizes are collected (see Promislow 1991; Carey et al. 1992; Robertson and Rendell 2001; Nussey et al. 2013), and most individuals perish for reasons other than senescence; most causes of mortality are therefore likely to be

unpredictable. Thus, the optimal strategy for tree swallows and many other species may be to take very high risks at all times (also see Winkler 1992), which will obscure relationships with most or all explanatory variables. Second, there may be many other variables that affect risk-taking such as predator type, nearest neighbor distance, energetic condition of parent, condition of young, personality differences, and sex ratio of offspring (Regelmann and Curio 1983; Radford and Blakey 2000; Redmond et al. 2009). Moreover, there may be interactions among the variables we measured and those we did not, such that sample sizes for proper analysis may be difficult to achieve. Third, life histories vary both inter- and intra-specifically (e.g., tree swallows further south are more likely to have second broods; Winkler et al. 2011; M. Stanback pers. comm.), which will shift optimal responses to risk. We conclude that relationships between risk-taking behaviors and logically connected explanatory variables should not be taken for granted, that more research is required, and that new ideas and approaches are needed.

Compliance with ethical standards

Ethical statement Our tree swallows occupy an anthropogenically modified landscape where interactions with humans and vehicles are commonplace, and we would have approached nests for routine monitoring even had we not measured flush initiation distances. When handling birds for sexing and banding, we worked as quickly and as quietly as possible to minimize stress. All procedures were approved by the Acadia University Animal Care Committee (Protocol 03-16R#1). All applicable guidelines for the care and use of animals were followed.

Conflict of interest The authors declare that they have no conflict of interest.

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