

EVOLUTION OF PASSERINE INCUBATION BEHAVIOR: INFLUENCE OF FOOD, TEMPERATURE, AND NEST PREDATION

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Abstract.—Incubation behavior is one component of reproductive effort and thus influences the evolution of life-history strategies. We examined the relative importance of body mass, frequency of mate feeding, food, nest predation, and ambient temperature to explain interspecific variation in incubation behavior (nest attentiveness, on- and off-bout durations, and nest trips per hour) using comparative analyses for North American passerines in which only females incubate. Body mass and frequency of mate feeding explained little variation in incubation behavior. We were also unable to detect any influence of food; diet and foraging strategy explained little interspecific variation in incubation behavior. However, the typical temperature encountered during reproduction explained significant variation in incubation behavior: Species breeding in colder environments take shorter bouts off the nest, which prevents eggs from cooling to temperatures below the physiological zero temperature. These species must compensate for shorter off-bouts by taking more of them (thus shorter on-bouts) to obtain needed energy for incubation. Nest predation also explains significant variation in incubation behavior among passerines: Species that endure high nest predation have evolved an incubation strategy (long on- and off-bouts) that minimizes activity that could attract predators. Nest substrate explained additional variation in incubation behavior (cavity-nesting birds have shorter on-bouts and make more frequent nest trips), presumably because nest predation and/or temperature varies among nest substrates. Thus, nest predation can influence reproductive effort in a way previously not demonstrated—by placing a constraint on parental activity at the nest. Incubating birds face an ecological cost associated with reproductive effort (predation of entire brood) that should be considered in future attempts to explain avian life-history evolution.

Key words.—Ambient temperature, body mass, cost of incubation, food, incubation behavior, incubation rhythm, life-history evolution, life-history strategy, mate feeding, nest attentiveness, nest predation, reproductive effort, Skutch's hypothesis.

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Many hypotheses proposed to explain the evolution of life-history traits rely on an assumed trade-off between current reproduction and future fitness owing to costs associated with reproductive effort (Williams 1966; Bryant 1979; Partridge and Harvey 1988; Reznick 1992; Martin 1995; Martin and Clobert 1996). Studies of reproductive costs in birds focus on the nestling period because energy constraints are commonly assumed to be greatest at this stage (Lack 1954, 1968; Walsberg 1983; Murphy and Haukioja 1986; Nur 1988; Lindén and Møller 1989; Daan et al. 1990; Williams 1996). Previous studies of avian reproductive effort and life-history evolution have ignored incubation because analyses of time-energy budgets suggest it is a period of comparatively low energy expenditure (O'Connor 1978; Walsberg 1983; Murphy and Haukioja 1986). Yet, recent studies of field metabolic rates using doubly labeled water have shown that energy expenditure during incubation is as high or higher than during the nestling period, especially for species with female-only incubation (reviewed in Williams 1996). Consequently, factors that influence reproductive effort during incubation can affect the evolution of other life-history traits (e.g., clutch size, number of broods, probability of renesting).

In many species of temperate-zone passerine birds, only females incubate the eggs (White and Kinney 1974; Ehrlich et al. 1988). Such females face a trade-off in time allocation

between foraging to meet their own nutritional requirements and providing heat for developing embryos (Conway and Martin 2000). Females also must decide how to divide a given amount of foraging time throughout the day. Taking fewer but longer foraging bouts rather than many short ones can reduce the energy cost of incubation to the adult because such a strategy reduces the number of times females must rewarm the clutch (Drent 1975; Vleck 1981b; Williams 1996). However, taking long foraging bouts may slow or impair embryo development because egg temperatures may routinely drop below the physiological zero temperature (temperature below which no embryonic development occurs; Clark and Wilson 1981, Lyon and Montgomerie 1987, Haftorn 1988, Williams 1991). Thus, incubating females must resolve trade-offs between self-maintenance and care of the young by optimizing the length of on- and off-bouts (the incubation rhythm).

Species vary widely in their incubation rhythms (Kendeigh 1952), but the underlying causes of this variation remain obscure. Previous work has focused on proximate ecological factors (e.g., ambient temperature, time of day) that affect variation in incubation behavior within individual birds (Weeden 1966; White and Kinney 1974; Davis et al. 1984; Haftorn 1984; Morton and Pereyra 1985; Thompson and Raveling 1987; Weathers and Sullivan 1989; Conway and Martin 2000). No previous studies have attempted to evaluate the potential ultimate ecological factors that might explain the large interspecific variation in incubation behavior.

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Large variation in incubation behavior across species may be a function of species variation in body mass, frequency of mate feeding, food availability/foraging success, ambient temperature during incubation, and/or nest predation. Most reviews of avian incubation suggest that on-bout duration is dictated by energy needs of adults; hunger level dictates how long a female can stay on the nest before getting off to forage (Nice 1937; Kendeigh 1952; Weeden 1966; White and Kinney 1974; Haftorn 1978; Weathers and Sullivan 1989; Williams 1991). Thus, species that use more energetically expensive foraging strategies or forage on food that is less available or of lower quality may have to take longer or more frequent bouts off the nest (off-bouts) to increase daily foraging time. Although food supplementation has increased nest attentiveness (percent of daylight hours on nest; Nilsson and Smith 1988; Moreno 1989), such results imply food (or time) limitations influence incubation behavior within individuals and do not address whether variation in food availability among species explains interspecific variation in incubation behavior. We tested whether food helps explain variation among species by evaluating whether incubation behaviors differed among species grouped according to diet or foraging categories.

Variation among species in incubation behavior may also reflect evolved differences in behavior in response to the ambient temperatures that a species typically experiences during incubation. Among species that typically breed in colder environments, evolution may have favored shorter off-bouts to decrease the likelihood that egg temperatures would fall below lethal temperatures (*sensu* Haftorn 1984; Weathers and Sullivan 1989). Shorter foraging bouts may require females to take more of them (shorter bouts on the nest) to allow acquisition of needed energy. The selective pressure imposed by ambient temperature on incubation behavior would be relaxed in species that typically breed in warmer environments. We evaluated this hypothesis by testing whether species that typically breed in colder environments have shorter on- and off-bouts (and thus more nest trips per hour) compared to species that typically breed in warmer environments.

Risk of nest predation may help explain differences among species in incubation behavior (Norton 1972; Thompson and Raveling 1987; Weathers and Sullivan 1989; Norment 1995), particularly if common nest predators locate nests by observing adult activity. Short bouts on and off the nest result in more daily trips to and from the nest, which may increase predation risk (Skutch 1949; Prescott 1964; Weathers and Sullivan 1989; Martin 1996; Martin and Ghalambor 1999). If nest predators locate nests by observing adult activity, selection should favor long periods on and off the nest and few trips to and from the nest in species in which risk of nest predation is high. Even if common nest predators locate nests using cues other than adult activity, high nest predation may favor an incubation strategy (e.g., high nest attentiveness) that maximizes the rate of embryonic development and reduces the number of days eggs are exposed to predators (Cody 1966; Ricklefs 1969; Perrins 1977; Bosque and Bosque 1995). We examined whether nest predation has influenced the evolution of passerine incubation behavior by examining

whether incubation behaviors were correlated with the probability of nest predation across species.

Species differences in extent of incubation feeding and body mass may also help explain interspecific variation in incubation behavior. Previous studies have suggested an allometric relationship between body mass and incubation behavior, with larger taxa taking longer bouts on the nest (Skutch 1962; Williams 1991; Afton and Paulus 1992). The extent of incubation feeding also has been proposed to influence avian incubation behavior; nest attentiveness is thought to be higher for species in which males feed incubating females (Lyon and Montgomerie 1987). Here, we use comparative analyses to examine the relative influence of body mass, mate feeding, food, temperature, and predation to explain interspecific variation in passerine incubation behavior.

METHODS

Incubation Behavior and Nest Predation

We obtained estimates of mean on- and off-bout duration and nest predation by conducting an exhaustive search of the literature. We used *Absearch* bibliographic software to search all papers published in the *Auk*, *Condor*, *Journal of Field Ornithology*, *Ornithological Monographs*, *Studies in Avian Biology*, and *Wilson Bulletin* from 1955 to 1998; *Conservation Biology* from 1987 to 1998; *Ecological Applications*, *Ecological Monographs*, and *Ecology* from 1945 to 1998; and the *Journal of Wildlife Management*, *Wildlife Monographs*, and *Wildlife Society Bulletin* from 1937 to 1998. We searched for all papers whose abstracts or titles included the words: *life history*, *natural history*, *breeding*, *behavior*, *nest*, *nesting*, *reproduction*, *incubation*, *attentiveness*, *reproductive success*, *nest success*, *productivity*, *nest predation*, or *nest failure*. We also conducted a broader search to locate papers in other journals using *Biological Abstracts* for papers published from 1985 to 1998 whose titles or abstracts contained the words *nest attentiveness* or *incubation rhythm*. We located many additional sources by referencing papers cited in those we obtained in our initial search and in Bent (1942–1968) and *The Birds of North America* (BNA; Poole and Gill 1992–1999) species accounts.

We calculated nest attentiveness (percentage of daylight spent on the nest; *sensu* Kendeigh 1952) as $[\text{mean on-bout duration}/(\text{mean on-bout duration} + \text{mean off-bout duration})]$. We calculated mean nest trips per hour as: $2[60/(\text{mean on-bout duration} + \text{mean off-bout duration})]$, or the number of times the incubating female went to or from the nest per hour. We used estimates of mean bout duration that were based on more than 10 bouts to help ensure that estimates were not based on a few extreme observations. We averaged parameter estimates across studies for species in which we were able to locate multiple data sources. We limited our analysis to North American passerines in which only the female incubates because the evolutionary importance of energy and time constraints during incubation should be greatest for species with female-only incubation (Skutch 1962; Walsberg 1983; Williams 1991, 1996).

Although we were interested in nest predation during incubation, few estimates of nest predation are available for

distinct stages within the nesting cycle. Therefore, we used estimates of nest predation over the entire nesting cycle. We used estimates of nest predation based on exposure (Mayfield 1961, 1975) when possible. If Mayfield estimates were not available, we used the proportion of nests that were depredated. We only used estimates based on more than 15 nests, and we calculated a mean across studies for species ($n = 34$) for which we located multiple estimates of nest predation. We chose not to use a weighted average of studies based on sample size because we did not want to give more weight to a particular population just because it was sampled more intensively. For cavity-nesting birds, we used estimates of nest predation only from studies of natural nests (not nest-box studies) because we were interested in relative risk of nest predation over evolutionary time, and nest predation is lower (and perhaps less variable among species) in nest boxes (Nilsson 1984). We also recorded typical nest substrate of each species (ground, shrub, canopy, cavity; Ehrlich et al. 1988) because rates of nest predation differ among nest substrates (Martin 1993, 1995).

Food Availability

Evaluating whether food availability has influenced the evolution of incubation behavior is difficult because comparative data on relative food availability across species are not available. Therefore, to evaluate the effects of food, we examined whether species grouped according to general foraging strategies or diet categories differ in incubation behavior. Implicit in this approach is the common assumption that food availability (i.e., time and energy needed to obtain food and/or food abundance) differs among species grouped according to general diet or foraging categories (Ettinger and King 1980; Walsberg 1982; Silver et al. 1985; Murphy 1989; Martin 1995). We made no assumptions regarding which diets or foraging strategies were more energetically expensive, we simply asked whether these variables helped explain interspecific variation in incubation behavior. Indeed, Skutch (1962) suggested that variation in diet may help explain interspecific variation in incubation behavior. We obtained information on foraging strategy (ground glean, foliage glean, hover glean, aerial forager) and diet (insectivore, omnivore, granivore) from Ehrlich et al. (1988).

Ambient Temperature

We sought an estimate of the average temperature experienced by incubating females within typical breeding locations of each species. Thus, we used data from the *Breeding Bird Survey* (BBS; Robbins et al. 1986) to obtain average temperature at probable breeding locations. BBS participants record the ambient temperature prior to each survey. We calculated the mean temperature for all BBS routes (1966–1997) that detected at least one individual of a particular species (hereafter, BBS temperature) and repeated the process for each species.

Body Mass and Incubation Feeding

We used estimates of mean body mass (female mass when available) from Dunning (1993). We obtained information

on mate feeding for each species based on information in the papers reporting incubation data and in Bent (1942–1968) and BNA accounts (Poole and Gill 1992–1999). We found few quantitative estimates of actual rates of mate feeding, but many qualitative descriptions, so we categorized the relative frequency of mate-feeding for each species as: (0) seldom or never; (1) infrequent; (2) moderate; and (3) frequent.

Statistics and Comparative Analyses

Prior to analyses, we log-transformed continuous variables (on-bout, off-bout, body mass, and BBS temperature) and arcsine-transformed proportional variables (nest attentiveness, nest predation). We transformed nest trips per hour by log (nest trips per hour + 1) because some raw values were less than 1.0. We performed these data transformations to normalize distributions and to comply with a random-walk model of character evolution; trait changes are measured by *proportion*, rather than amount, across lineages (Felsenstein 1985).

We used several methods to test our hypotheses: raw species means and two sets of phylogenetically independent contrasts (Felsenstein 1985). We used the phylogenetic hypothesis in Martin and Clobert (1996) with modifications suggested by Sheldon and Gill (1996). We used the comparative analysis by independent contrasts program (CAIC; Purvis and Rambaut 1995) to calculate independent contrasts. To overcome potential problems associated with heterogeneity of variance in regressions, contrasts were standardized by dividing each contrast by the square root of its expected variance (sum of its branch lengths).

Estimates of distances between nodes (branch lengths) were not available, so we conducted two separate sets of independent contrasts that make different assumptions about the mode of character evolution. One model assumed that all branch lengths were equal, thus reflecting a speciation model of evolution (Rohlf et al. 1990; Martins and Garland 1991). This model is equivalent to a Brownian motion model with all branch lengths set equal to unity (Harvey and Purvis 1991; Díaz-Uriarte and Garland 1996). The other model assumed a gradual evolutionary process of character change and used a maximum-likelihood algorithm to estimate branch lengths from our topology in units of expected variance of character change (Grafen 1989; Purvis and Rambaut 1995). Results from both sets of independent contrasts were very similar, so we only present those from the speciation model. To examine the robustness of our major results, we performed analyses on the entire clade and on two subclades.

We performed analysis of covariance (ANCOVA) on both raw species means and independent contrasts. Nest substrate, foraging strategy, and diet were fixed factors and body mass, mate feeding, nest predation, and BBS temperature were covariates in ANCOVA models using raw species means. We excluded the intercept from ANCOVA models using independent contrasts. We created $n - 1$ dummy variables for each nominal variable (diet, nest substrate, foraging strategy), where n is the number of categories in the original variable. Each dummy variable was used as a continuous variable in CAIC to calculate independent contrasts. We calculated the overall sum-of-squares for each nominal variable by sub-

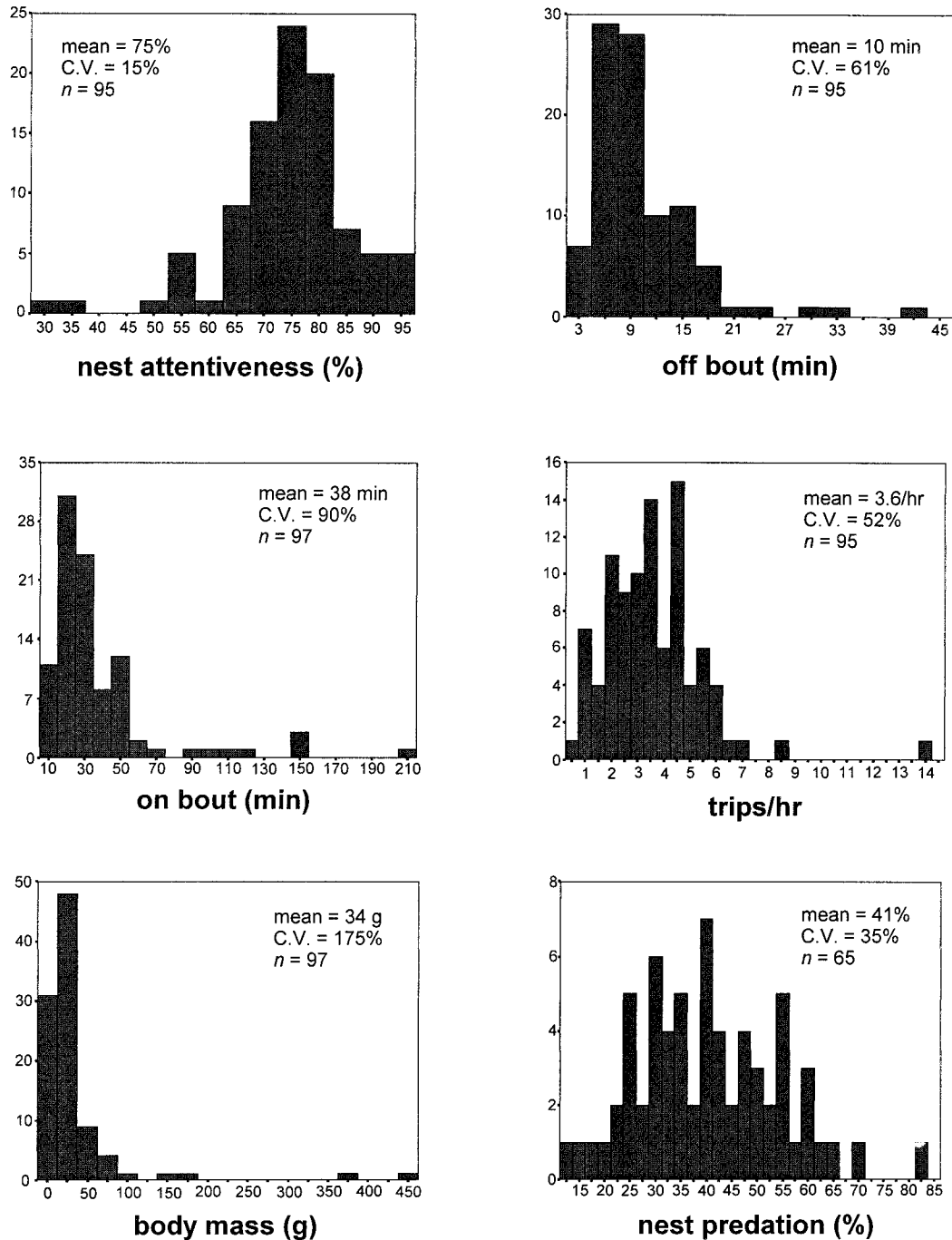


FIG. 1. Variation among species in incubation behaviors, nest predation, and female body mass for North American passerines with single-sex incubation (from Appendix 1). Numbers on the vertical axes represent number of species.

tracting sum-of-squares of an ANCOVA model without the $n - 1$ dummy variables from the sum-of-squares in the overall ANCOVA model. We then calculated the F -value for each nominal variable by dividing its sum-of-squares by the appropriate degrees of freedom and by the error mean square of the overall model. This approach is the standard method used by traditional ANOVA/ANCOVA to evaluate the proportion of variance in a dependent variable explained by a categorical factor.

We addressed the assumptions (linearity, homoscedasticity, normality of error variance) of using a linear regression model on our contrast data. We evaluated the linearity assumption by examining plots of absolute values of unstandardized regression residuals versus the dependent variable; no systematic departures from zero suggested that the relationships were linear. We examined plots of residuals versus predicted values for heteroscedasticity of the error variances; we found none. We examined normal probability plots and

TABLE 1. Univariate correlations (r) among off-bout duration, on-bout duration, nest trips per hour, percent nest attentiveness, female body mass, frequency of mate feeding, ambient temperature at breeding locations (BBS temp.), and probability of nest predation among 97 species of North American passerines.

	Off-bout	On-bout	Nest trips per hr	Attentive	Body mass	Mate feed	BBS temp.
On-bout	0.188						
Nest trips per hr	-0.451**	-0.648**					
Attentive	-0.442**	0.545**	-0.346**				
Body mass	-0.172	0.159	-0.165	0.271**			
Mate feed	-0.110	0.118	-0.049	0.210*	0.193		
BBS temp.	0.259*	0.002	-0.186	-0.051	-0.030	0.022	
Nest predation	0.262*	0.273*	-0.358**	0.151	-0.134	-0.130	0.104

* $P < 0.05$; ** $P < 0.01$.

histograms of the residuals; we could detect no obvious departures from normality of error terms.

Distributions of all standardized linear contrasts were unimodal and approximated normal distributions. Correlation coefficients between absolute values of standardized linear contrasts and standard deviations of the raw contrasts were

TABLE 2. ANCOVA results using Type III sums-of-squares to examine factors that explain interspecific variation in incubation behaviors for North American passerines with female-only incubation using species means ($n = 62$) and independent contrasts ($n = 59$). Significant P -values are shown in bold.

	Raw species means		Independent contrasts	
	F	P	F	P
Nest attentiveness				
Diet	0.9	0.422	0.3	0.766
Foraging strategy	2.8	0.053	0.7	0.596
Nest substrate	2.2	0.096	1.0	0.440
Body mass	0.2	0.692	0.7	0.418
Mate feeding	1.6	0.212	0.8	0.368
BBS temperature	0.1	0.711	0.1	0.846
Nest predation	0.9	0.359	0.1	0.823
	$r^2 = 0.411$		$r^2 = 0.205$	
Off-bout duration				
Diet	1.6	0.209	1.7	0.216
Foraging strategy	0.6	0.626	0.2	0.919
Nest substrate	1.0	0.384	1.1	0.379
Body mass	0.1	0.906	0.7	0.406
Mate feeding	0.1	0.802	0.3	0.594
BBS temperature	9.1	0.004	9.8	0.003
Nest predation	4.2	0.046	3.2	0.079
	$r^2 = 0.361$		$r^2 = 0.304$	
On-bout duration				
Diet	0.9	0.414	0.0	1.000
Foraging strategy	2.5	0.067	1.0	0.420
Nest substrate	2.5	0.068	3.0	0.041
Body mass	0.2	0.667	4.9	0.032
Mate feeding	0.5	0.499	1.8	0.182
BBS temperature	9.3	0.004	12.5	0.001
Nest predation	6.5	0.014	3.7	0.059
	$r^2 = 0.443$		$r^2 = 0.414$	
Nest trips per hr				
Diet	0.6	0.567	0.8	0.481
Foraging strategy	2.1	0.112	0.9	0.458
Nest substrate	2.6	0.061	3.4	0.024
Body mass	0.2	0.697	3.5	0.068
Mate feeding	1.5	0.219	0.1	0.840
BBS temperature	9.6	0.003	12.9	0.001
Nest predation	9.6	0.003	7.0	0.011
	$r^2 = 0.456$		$r^2 = 0.398$	

low ($|r| < 0.34$). Correlation coefficients between absolute values of standardized linear contrasts and estimated nodal values were also low ($|r| < 0.39$). We analyzed two equal-sized subsets of our contrast data based on both age of node and location in our phylogeny. Results were similar to those from the complete analysis, with patterns being stronger at lower taxonomic levels. We also reanalyzed our data after removing potential outliers; results were similar to those using the complete dataset.

RESULTS

We located incubation data for 97 North American passerine species and found extensive interspecific variation in incubation behavior (Fig. 1; Appendix 1). We located estimates of nest predation for 65 of these species and also found large interspecific variation (Fig. 1; Appendix 1). Among the four incubation behaviors, on-bout duration was most variable and nest attentiveness was least variable among species (Fig. 1). Interspecific variation in on- and off-bout durations translated into substantial species differences in parental activity around the nest; species vary from less than one trip per hour to 14 trips per hour (Fig. 1).

Off-bout duration and on-bout duration were not correlated among species (Table 1). Nest attentiveness and number of nest trips per hour were both calculated from on- and off-bout durations and thus were correlated with these parameters. Frequency of mate feeding and body mass were both positively correlated with nest attentiveness, but not correlated with the other three incubation behaviors. In univariate analyses, BBS temperature was positively correlated with off-bout duration and nest predation was positively correlated with both off- and on-bout duration and negatively correlated with nest trips per hour (Table 1).

In multivariate analyses, nest predation and temperature at breeding locations both explained significant variation in incubation behavior based on both raw species means and independent contrasts in ANCOVA analyses (Table 2). Off-bout duration ($r_p = 0.29$, $P = 0.022$) and on-bout duration ($r_p = 0.26$, $P = 0.039$) were both positively correlated with nest predation, and nest trips per hour ($r_p = -0.35$, $P = 0.006$) was negatively correlated with nest predation (Fig. 2). Nest predation did not explain interspecific variation in nest attentiveness (Table 2). Off-bout duration ($r_p = 0.34$, $P = 0.007$) and on-bout duration ($r_p = 0.34$, $P = 0.008$) were both positively correlated with BBS temperature, and nest trips per hour ($r_p = -0.35$, $P = 0.006$) was negatively cor-

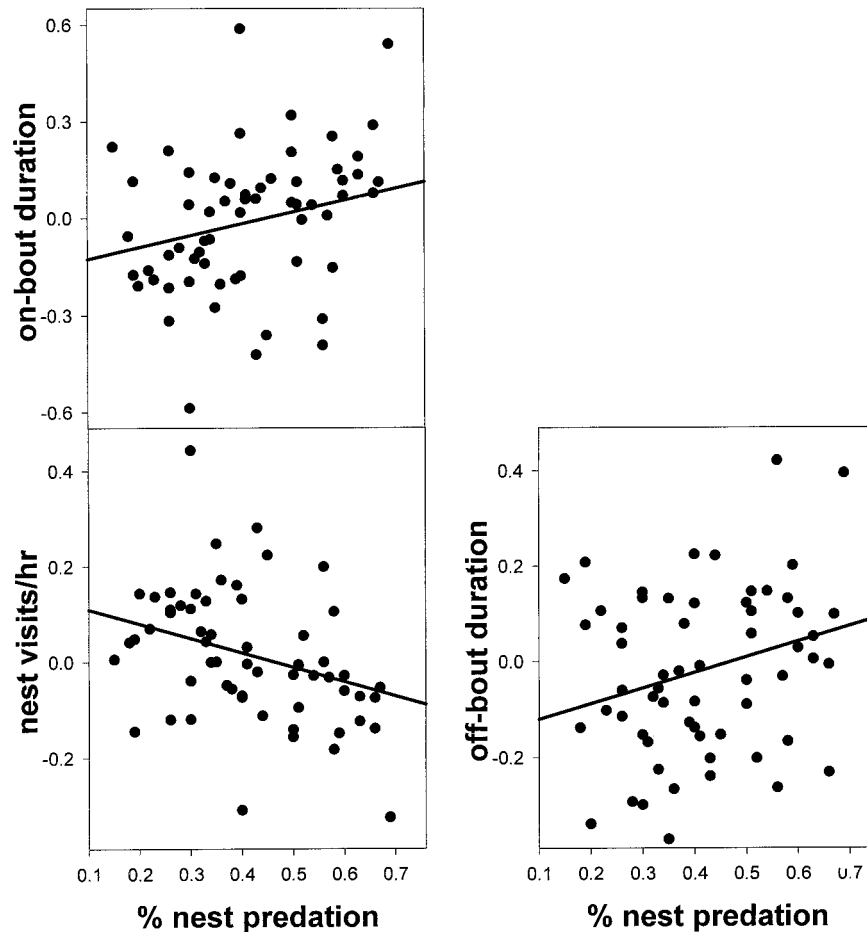


FIG. 2. Scatter plot of nest predation versus unstandardized residuals (partial regressions) of incubation behaviors (on- and off-bout duration and nest trips per hour) corrected for diet, foraging strategy, nest substrate, body mass, mate feeding frequency, and BBS temperature. We arcsine-transformed nest predation and log-transformed body mass and BBS temperature prior to calculating residuals. Lines represent slopes of significant linear regressions.

related with BBS temperature (Fig. 3). Scatter plots suggested more interspecific variation in incubation behavior at higher temperatures (Fig. 3). BBS temperature did not explain interspecific variation in nest attentiveness (Table 2). Nest substrate explained additional variation in on-bout duration and nest trips per hour in phylogenetic analyses (Table 2); cavity-nesting birds take shorter on-bouts and make more frequent nest trips compared to birds nesting in other substrates (Fig. 4). Body mass explained additional variation only in on-bout duration in phylogenetic analyses (Table 2); larger species took slightly longer on-bouts. Mate feeding, diet, and foraging strategy explained little variation in any of the four incubation behaviors (Table 2).

When we removed nest predation from the analyses, which allowed us to include all species for which we had estimates of incubation behaviors, diet and foraging strategy explained some of the variation in incubation behavior using raw species means, but still failed to explain variation after controlling for phylogeny (Table 3). Body mass, mate feeding, and nest substrate explained even less of the variation in incubation behavior in this broader analysis, but BBS temperature explained significant variation in both phylogenetic and nonphylogenetic analyses (Table 3).

DISCUSSION

The frequency with which females alternate incubation with other activities varies greatly among passerines. On- and off-bout durations are often assumed to reflect a trade-off between energy needs of the adult (food limitation) and thermal needs of the developing embryos (temperature) (Nice 1937, 1943; Kendeigh 1952; Davis 1960; White and Kinney 1974; Drent 1975; Nolan 1978; Vleck 1981a,b; Drent et al. 1985). Our results support the notion that nesting temperature explains some of the interspecific variation in incubation behavior. However, we were unable to demonstrate that variation in food availability is important; diet and foraging strategy did not help explain the large interspecific variation in incubation behavior. Reviews of avian incubation fail to emphasize the role of nest predation (White and Kinney 1974; Drent 1975; Grant 1982; Webb and King 1983; Davis et al. 1984; Williams 1991). Yet, our results suggest that risk of nest predation may explain more of the interspecific variation in incubation behavior than does food availability.

Nest predation appears to have affected the evolution of passerine incubation behavior by placing constraints on activity at the nest (Table 2, Fig. 2). Skutch (1949) first sug-

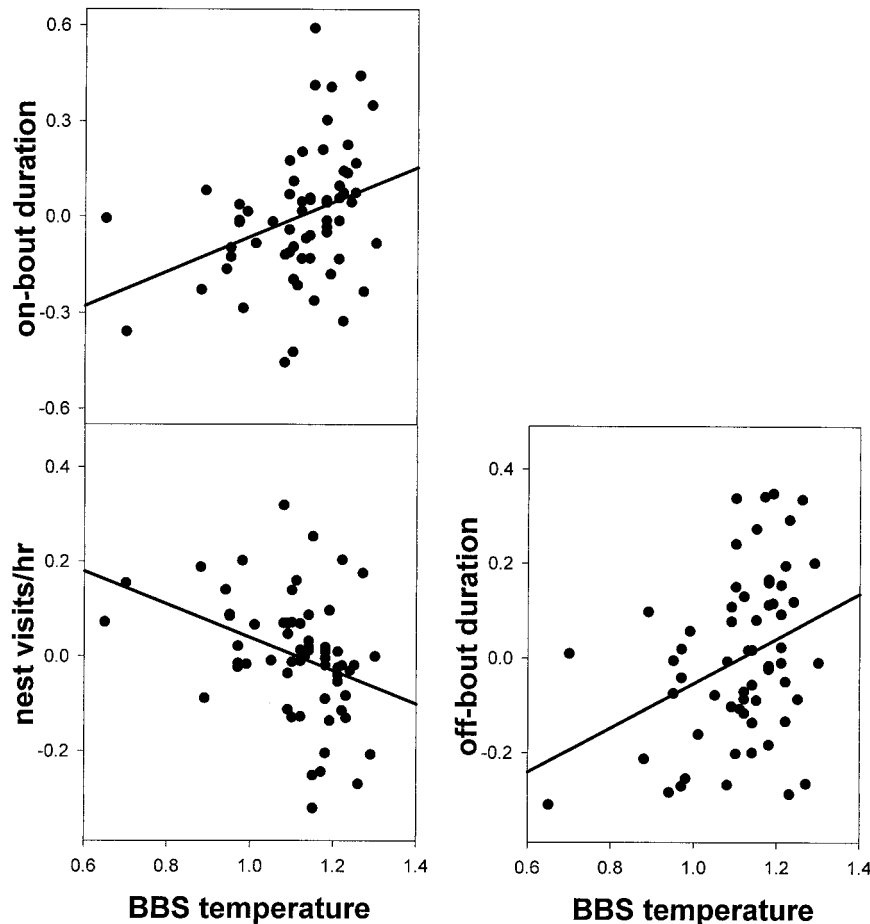


FIG. 3. Scatter plot of BBS temperature versus unstandardized residuals (partial regressions) of incubation behaviors (on- and off-bout duration and nest trips per hour) corrected for diet, foraging strategy, nest substrate, body mass, mate feeding frequency, and nest predation. We arcsine-transformed nest predation and log-transformed body mass and BBS temperature prior to calculating residuals. Lines represent slopes of significant linear regressions.

gested that parental activity at the nest may influence the risk of nest predation in passerines, but explicit tests of his hypothesis are lacking. We found that species that nest in substrates or environments with high nest predation have evolved incubation behavior that minimizes parental activity at the nest. Reduced activity at the nest is largely achieved by increased duration of on-bouts (Fig. 2). Species with high nest predation also take longer off-bouts (Fig. 2), despite the fact that increased time off the nest may lengthen the incubation period, which would increase the exposure to nest predation. Nest predation also did not help explain species variation in nest attentiveness (Table 2). These results suggest that the risk of nest predation affects current passerine incubation strategies primarily by limiting nest activity.

Thompson and Raveling (1987) suggested that heightened risk of nest predation selects for increased nest attentiveness in geese; however, we found that increased nest predation did not affect nest attentiveness, but rather selected for reduced activity at the nest. Differences may reflect different nest defense strategies. Geese construct visible nests and rely on their large size to physically repel potential nest predators (Thompson and Raveling 1987). Indeed, nest predation is lower at goose nests with high nest attentiveness (Inglis

1977). Geese rely on endogenous resources for incubation and prevent nest predation by maximizing daily nest attentiveness. In contrast, passerines are probably less able to physically repel potential nest predators, but typically have well-concealed nests (Martin 1992). Passerines rely on exogenous resources for incubation and the higher frequency at which passerines get on and off their nest may serve as a cue to nest predators. Therefore, we might expect high nest predation to select for different behaviors in geese (increased nest attentiveness) and passerines (fewer nest trips per hour). Future attempts to explain interspecific variation in incubation behavior in other taxa should consider the extent to which incubating parents rely on exogenous resources and the parents' ability to repel or distract predators.

Environments with a high risk of nest predation may favor long on-bouts and few foraging trips, but such an incubation strategy may prevent frequent feeding by adults and thus compromise future reproductive attempts (Williams 1966; Bryant 1979; Partridge and Harvey 1988; Reznick 1992). Therefore, nest predation may influence the evolution of avian life-history traits in several ways. High nest predation favors a bet-hedging strategy of holding back reproductive effort for renesting attempts and survival (Cody 1966; Slatkin

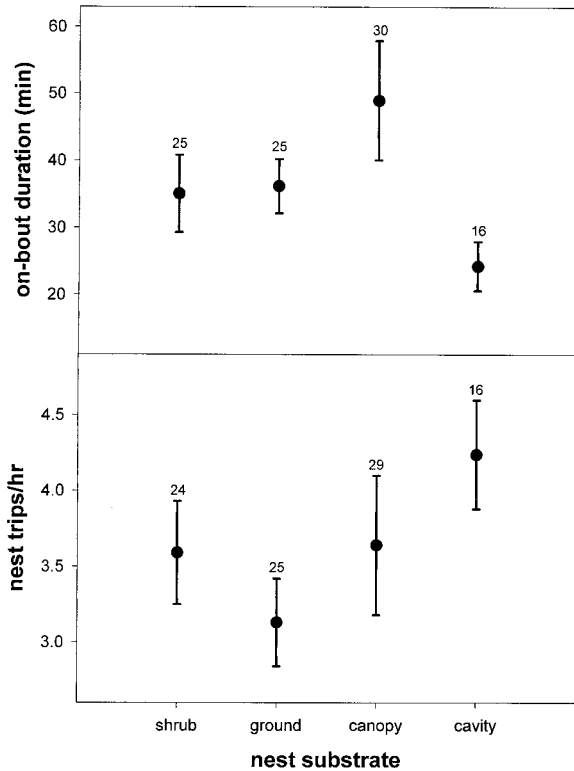


FIG. 4. Mean (± 1 SE) on-bout duration and nest trips per hour among North American passerines (with female-only incubation) nesting in different substrates. Numbers above error bars represent number of species (see Appendix 1 for raw data).

1974; Perrins 1977; Slagsvold 1982, 1984; Lundberg 1985; Milinoff 1989; Martin 1995), a short nesting cycle to minimize the time nests are susceptible to predation (Cody 1966; Ricklefs 1969; Perrins 1977; Bosque and Bosque 1995), and small brood size to minimize noise of begging young (Perrins 1977). Yet, our results suggest that nest predation may influence passerine life-history evolution in a way that has been largely ignored (Skutch 1949; Slagsvold 1982; Martin 1996; Martin and Ghalambor 1999) by placing constraints on parental activity and the way an incubating female allocates her time between incubation and foraging. Thus, in environments with high nest predation, natural selection simultaneously favors infrequent nest trips (to reduce the probability of predator detection) and short off-bout duration (to maximize development rates and reduce time of exposure to predators). These somewhat opposing constraints limit the range of effective incubation strategies available to females in environments with high nest predation. High nest predation may even favor slightly larger clutch volume in some environments because larger clutches cool more slowly (C. J. Conway, unpubl. ms.) which may allow incubating females to take fewer, longer foraging bouts (thus reducing nest activity without increasing incubation period).

The typical ambient temperature within species' breeding distributions also appears to have influenced the evolution of incubation behavior. Within species, numerous studies have reported a relationship between air temperature and incubation behavior (see review in Conway and Martin 2000),

TABLE 3. ANCOVA results (Type III sums-of-squares) when we excluded nest predation from the analyses, using species means ($n = 92$) and independent contrasts ($n = 87$). Significant P -values are shown in bold.

	Raw species means		Independent contrasts	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Nest attentiveness				
Diet	4.6	0.013	0.4	0.700
Foraging strategy	2.9	0.040	1.1	0.395
Nest substrate	2.1	0.114	0.5	0.712
Body mass	0.5	0.488	2.0	0.159
Mate feeding	1.0	0.325	0.1	0.896
BBS temperature	0.1	0.845	1.3	0.263
	$r^2 = 0.433$		$r^2 = 0.127$	
Off-bout duration				
Diet	0.3	0.752	0.7	0.494
Foraging strategy	0.6	0.615	0.3	0.802
Nest substrate	1.0	0.378	0.8	0.487
Body mass	0.8	0.381	0.5	0.490
Mate feeding	2.2	0.145	0.2	0.682
BBS temperature	6.9	0.010	6.3	0.015
	$r^2 = 0.251$		$r^2 = 0.154$	
On-bout duration				
Diet	12.5	0.00002	0.7	0.505
Foraging strategy	2.8	0.046	0.8	0.518
Nest substrate	1.9	0.144	1.8	0.161
Body mass	0.2	0.631	3.6	0.063
Mate feeding	0.6	0.446	2.1	0.156
BBS temperature	6.8	0.011	19.2	0.00004
	$r^2 = 0.434$		$r^2 = 0.320$	
Nest trips per hr				
Diet	6.8	0.002	1.2	0.324
Foraging strategy	2.4	0.079	0.3	0.826
Nest substrate	1.5	0.213	1.7	0.194
Body mass	0.1	0.716	0.3	0.586
Mate feeding	0.1	0.872	0.1	0.955
BBS temperature	7.0	0.010	18.0	0.00006
	$r^2 = 0.364$		$r^2 = 0.266$	

but our results are the first to demonstrate a correlation across species. Species that breed in colder environments are forced to take shorter off-bouts and shorter on-bouts, which results in more frequent nest trips per hour (Table 2; Fig. 3), but frequent nest trips may increase the risk of nest predation (Skutch 1949, Prescott 1964, Weathers and Sullivan 1989). Thus, low breeding temperature and high nest predation can place opposing selective pressures on incubating females. Cold environments with an abundance of visual nest predators probably pose severe challenges for breeding passerines. In addition to altering incubation behavior, birds may also adapt to nesting in cold environments by building thicker, more insulated nests or nesting in more protected microclimates to reduce the rate of egg cooling during foraging bouts (Skutch 1962; Calder 1973; Walsberg 1981; Collias and Collias 1984; Kern and van Riper 1984; Kern et al. 1993).

We found little evidence to suggest that food constraints help to explain observed species differences in incubation behavior (Table 2). Ultimately, our ability to adequately examine the influence of food availability on species variation in incubation behavior is hampered by the lack of a direct quantitative measure of relative food availability across species. Moreover, food availability may have influenced evo-

lution of incubation behavior primarily at higher taxonomic levels (e.g., among orders or families).

Nest substrate explained additional variation in on-bout duration and nest trips per hour in addition to the variance explained by nest predation and breeding temperature in phylogenetic analyses (Table 2). Cavity-nesting birds have shorter on-bouts and thus make more frequent trips to and from their nest (Fig. 4). Species nesting in different substrates vary in risk of nest predation; cavity-nesting birds have comparatively lower predation risk (Martin 1993, 1995). However, nest temperature may also differ among nest substrates, so the causal factor responsible for observed differences in incubation behavior among nest substrates awaits further study. We found only very limited evidence suggesting that incubation behavior varies with body mass in passerines (Table 2). One previous study that reported a strong allometric relationship between on-bout duration and body mass included an uneven distribution of species among several taxonomic orders and failed to control for phylogeny (Williams 1991). Thus, body mass may help explain variation in incubation behavior among higher taxonomic levels (e.g., orders), but does not explain the large variation among passerines.

All attempts to control for phylogeny make assumptions about the true model of how traits evolve (e.g., speciation, punctuational, gradual) and the true phylogeny. We calculated independent contrasts using two different models of trait evolution, and these analytical approaches produced very similar results. Moreover, our results using independent contrasts are concordant with our major results from nonphylogenetic analyses: Nest predation and temperature explain a significant amount of the interspecific variation in passerine incubation behavior.

In summary, passerines vary widely in the behaviors used to incubate their eggs, and some of this interspecific variation in incubation behavior can be explained by risk of nest predation and temperature of typical breeding locations. Our results indicate that species with high rates of nest predation are under selection to reduce the level of activity at their nest. Consequently, nest predation places constraints on reproductive effort because incubation behavior influences the energy cost of incubation (Vleck 1981a). Therefore, our results suggest that nest predation can influence the evolution of passerine life-history traits in a way that has been overlooked by placing constraints on parental activity at the nest and how females allocate their time between incubating and foraging (also see Martin 1995). Studies of avian life-history evolution have focused on the costs of rearing young through the nestling period, based on the assumption that the energy cost of incubation is relatively low. Regardless of the energy cost of incubation, incubating birds face an ecological fitness cost (predation of entire brood) associated with incubation behavior that must be considered in future attempts to explain avian life-history evolution.

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APPENDIX 1

Species means of female body mass (BM; g); on-bout (ON; min) and off-bout duration (OFF; min); nest attentiveness (%); nest trips per hour (TRIP); frequency of mate feeding (M; 0, none; 1, infrequent; 2, moderate; 3, frequent); diet (D; i, insectivore; o, omnivore; g, granivore/frugivore); foraging strategy (FS; ha, hawking; hg, hover glean; fg, foliage glean; gg, ground glean); nest substrate (NS; gr, ground; sh, shrub; cp, canopy; cv, cavity); BBS temperature (°C); and % nest predation (PR) for North American passerines with female-only incubation. Full references to the sources of data on incubation behavior and nest predation are given in Appendix 2.

Species	BM	ON	OFF	%	TRIP	M	D	FS	NS	°C	PR	Reference
<i>Myiarchus crinitus</i>	34	21	18	62	3.5	2	i	ha	cv	16		18, 46
<i>Tyrannus tyrannus</i>	44	23	11	69	3.6	0	i	ha	cp	15	39	18, 97
<i>Sayornis phoebe</i>	20	34	17	64	4.7	0	i	ha	cv	16	15	18, 21
<i>Empidonax difficilis</i>	10	29	8	79	3.3	2	i	ha	sh	9	59	24, 98
<i>Empidonax hammondi</i>	10	15	4	78	6.2	0	i	ha	cp	9	50	22, 98
<i>Empidonax oberholseri</i>	10	20	7	75	4.5	3	i	ha	sh	9	57	69
<i>Empidonax fulvifrons</i>	8	25	9	74	3.6	0	i	ha	cp		51	12
<i>Empidonax virescens</i>	13	22	5	78	4.8	1	i	ha	sh	18	28	72
<i>Empidonax minimus</i>	10	17	5	78	5.4	2	i	hg	sh	13	55	18, 71, 100
<i>Contopus virens</i>	14	20	7	74	4.6	3	i	ha	cp	16		18
<i>Corvus caurinus</i>	368	34	6	86	3.0	3	o	gg	cp	10	22	16
<i>Corvus brachyrhynchos</i>	438	94	4	96	1.2	3	o	gg	cp	15		18, 48
<i>Perisoreus canadensis</i>	73	210	6	97	0.6	1	o	gg	cp	9		23
<i>Pica nuttalli</i>	144	49	4	92	2.3	3	o	gg	cp	13	18	61
<i>Pica pica</i>	166	27	5	84	3.8	3	o	gg	cp	11		28
<i>Aphelocoma c. coerulescens</i>	80	34	5	88	3.1	3	o	gg	cp	12	39	1
<i>Vireo olivaceus</i>	17	27	10	72	4.0	0	i	hg	cp	15	49	18, 33, 100, 104
<i>Vireo philadelphicus</i>	12	25	8	77	3.7	0	i	hg	cp	11		36
<i>Bombycilla cedrorum</i>	33	37	6	87	2.9	3	g	fg	cp	14	36	1 (18) 8, 88
<i>Sialia sialis</i>	32	14	12	53	4.5	3	i	ha	cv	16	12	18, 99
<i>Sialia currucoides</i>	30	26	7	79	3.7	3	i	ha	cv	9		86
<i>Sialia mexicana</i>	27	19	7	72	4.7	3	i	ha	cv	10	61	73, 102
<i>Hylocichla mustelina</i>	47	30	10	75	3.3	1	i	gg	sh	16	34	13, 18, 104
<i>Catharus minimus</i>	33	13	10	56	5.3	0	i	gg	sh	8		74
<i>Catharus fuscescens</i>	31	53	16	77	1.8	0	i	gg	gr	12	55	4, 100
<i>Turdus migratorius</i>	77	29	8	81	3.6	2	i	gg	sh	14	40	18, 41, 101
<i>Dumetella carolinensis</i>	37	21	9	71	4.0	1	i	gg	sh	15	31	18, 83, 84, 101
<i>Mimus polyglottos</i>	49	13	8	63	6.0	1	i	gg	sh	17	44	25
<i>Sitta carolinensis</i>	21	31	4	88	3.4	3	i	cv		15	40	89, 101
<i>Salpinctes obsoletus</i>	17	18	15	55	3.6	2	i	gg	gr	11		44
<i>Troglodytes aedon</i>	11	13	7	65	5.9	1	i	gg	cv	14	33	7, 18, 101, 102
<i>Troglodytes troglodytes</i>	9	20	4	85	5.2	2	i	gg	cv	11		35
<i>Campylorhynchus brunneicapillus</i>	39	15	13	53	4.4	0	i	gg		17	29	3
<i>Thryomanes bewickii</i>	10	18	30	37	2.6	3	i	gg	cv	16		52
<i>Thryothorus ludovicianus</i>	19	72	32	68	1.2	2	i	gg	cv	18	64	44, 53
<i>Parus inornatus</i>	16	29	9	77	3.2	2	i	fg	cv	11	36	45, 102
<i>Parus bicolor</i>	22	31	12	73	3.0	3	i	fg	cv	17		14
<i>Parus atricapillus</i>	11	22	8	74	4.2	3	i	fg	cv	12	33	15, 49, 101
<i>Parus carolinensis</i>	10	17	5	76	5.5	3	i	fg	cv	19	34	15, 37
<i>Tachycineta bicolor</i>	20	11	9	54	5.9	3	i	ha	cv	13	24	50, 101
<i>Stelgidopteryx serripennis</i>	16	13	5	71	6.8	3	i	ha	cv	15	19	95
<i>Regulus satrapa</i>	6	6	2	74	14.0	2	i	fg	cp	10		31
<i>Eremophila alpestris</i>	31	20	6	67	6.3	2	g	gg	gr	14	30	60
<i>Anthus rubescens</i>	20	15	6	73	5.7	2	i	gg	gr	8	31	58
<i>Carduelis psaltria</i>	10	99	42	70	0.9	2	g	fg	cp	13		59
<i>Carduelis lawrencei</i>	11	119	4	97	1.0	3	g	fg	cp	12		59

APPENDIX 1. Continued.

Species	BM	ON	OFF	%	TRIP	M	D	FS	NS	°C	PR	Reference
<i>Carduelis tristis</i>	13	152	9	95	0.8	3	g	fg	sh	14	48	18, 35, 54, 107
<i>Loxia curvirostra</i>	37	148	7	95	0.8	3	g	fg	cp	10		56
<i>Loxia leucoptera</i>	25	150				2	g	fg	cp	9		10
<i>Leucosticte arctoa</i>	27	48	15	76	1.9	0	g	gg	gr	4		42
<i>Coccothraustes vespertinus</i>	59	27	10	73	3.3	2	g	gg	cp			96
<i>Zonotrichia leucophrys</i>	26	21	11	68	3.9	2	i	gg	sh	9	51	35, 82
<i>Zonotrichia querula</i>	34	32	13	72	2.7	0	i	gg	gr	8	30	81, 82
<i>Junco phaeonotus</i>	20	50	14	78	1.9	1	i	gg	gr	15	26	77
<i>Melospiza lincolnii</i>	17	28	6	83	3.3	0	i	gg	gr	9	42	2
<i>Melospiza georgiana</i>	17	11	23	32	3.6	3	i	gg	sh	13	53	35, 103
<i>Melospiza melodia</i>	21	28	9	77	3.2	0	i	gg	sh	13	40	18, 76, 100
<i>Ammodramus henslowii</i>	13	44	19	70	1.9	0	i	gg	gr	15		90
<i>Passerculus sandwichensis</i>	20	19	10	63	4.7	0	i	gg	gr	12	34	17, 108
<i>Spizella passerina</i>	12	18	9	67	4.6	2	i	gg	sh	14	26	18, 67
<i>Spizella pusilla</i>	13	33	14	70	2.6	2	i	gg	sh	16	56	20, 107, 108
<i>Spizella arborea</i>	20	17	9	65	4.7	0	i	gg	gr	7		9
<i>Aimophila aestivalis</i>	19	40	10	80	2.4	0	g	gg	gr	20	53	66
<i>Aimophila botterii</i>	20	35	18	66	2.3	2	i	gg	gr	17	29	78
<i>Pipilo erythrophthalmus</i>	39	37	10	78	2.6	2	i	gg	sh	17	59	8, 105
<i>Calcarius pictus</i>	24	11	10	52	5.7	0	i	gg	gr	5	25	43
<i>Plectrophenax nivalis</i>	42	28	5	86	3.7	3	i	gg	gr	4	39	5
<i>Seiurus aurocapillus</i>	19	110	19	85	0.9	2	i	gg	gr	14	39	38, 100, 104
<i>Limnithlypis swainsonii</i>	19	59	16	78	1.6	2	i	gg	sh	20	48	57, 65
<i>Dendroica petechia</i>	9	36	10	92	3.1	3	i	fg	cp	13	34	18, 94, 100
<i>Parula americana</i>	9	21	6	79	4.5	2	i	fg	cp	16		32
<i>Oporornis philadelphia</i>	12	39	13	75	2.3	2	i	fg	gr	12		19, 70
<i>Geothlypis trichas</i>	10	49	16	80	1.6	2	i	fg	sh	15	26	40
<i>Vermivora celata</i>	9	49	12	80	2.0	0	i	fg	gr	9	48	85, 106
<i>Vermivora ruficapilla</i>	9	39	14	73	2.2	2	i	fg	gr	12		55
<i>Setophaga ruticilla</i>	8	23	5	82	4.6	3	i	hg	cp	14	40	6, 18, 47, 100
<i>Seiurus noveboracensis</i>	18	30	10	75	3.0	0	i	gg	gr	11		27
<i>Seiurus motacilla</i>	21	35	9	79	2.7	1	i	gg	gr	17		91
<i>Dendroica fusca</i>	10	21	8	72	4.2	1	i	fg	cp	12		47, 57
<i>Dendroica kirtlandii</i>	14	51	11	82	2.1	3	i	fg	gr	12	43	35, 64, 106
<i>Dendroica discolor</i>	7	55	15	77	1.9	1	i	fg	sh	18	62	80
<i>Dendroica striata</i>	13	19	6	77	5.0	2	i	fg	cp	10		35
<i>Dendroica castanea</i>	12	18	5	80	5.5	2	i	fg	cp	11		34
<i>Dendroica virens</i>	9	50	15	78	1.9	0	i	fg	cp	13		75
<i>Dendroica pensylvanica</i>	9	23	7	75	4.5	2	i	fg	sh	13	38	26, 47, 55, 100
<i>Dendroica magnolia</i>	9	17	7	70	4.9	0	i	hg	cp	12		57
<i>Dendroica caerulescens</i>	10	31	12	72	2.9	2	i	hg	sh	12	43	47, 70, 109
<i>Wilsonia citrina</i>	10	60				0	i	fg	sh	18	45	29, 106
<i>Wilsonia pusilla</i>	8	22	5	81	4.5	2	i	fg	gr	9	35	93
<i>Piranga olivacea</i>	29	20	6	77	4.7	2	i	hg	cp	15	33	87, 105
<i>Quiscalus quiscula</i>	100	47	15	76	1.9	0	o	gg	cp	15	83	63
<i>Sturnella magna</i>	76	51	20	72	1.7	0	i	gg	gr	17	56	92
<i>Icterus galbula</i>	34	30	8	80	3.2	1	i	fg	cp	15		18
<i>Xanthocephalus xanthocephalus</i>	49	9	5	63	8.3	1	i	gg	sh	12	42	30
<i>Dolichonyx oryzivorus</i>	37	20	8	70	4.3	0	i	gg	gr	13	30	62
<i>Cardinalis cardinalis</i>	44	54	6	90	2.0	2	i	gg	sh	17	69	51, 79
<i>Passerina cyanea</i>	14	45	11	80	2.2	0	i	fg	sh	16	54	68, 79

APPENDIX 2

Sources of incubation behavior and nest predation data in Appendix 1.

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