

# Nest attentiveness and egg temperature do not explain the variation in incubation periods in tropical birds

B. I. TIELEMAN,\*† J. B. WILLIAMS‡ and R. E. RICKLEFS\*

\*Department of Biology, University of Missouri – St. Louis, 8001 Natural Bridge Road, St. Louis, MO 63121, USA, and ‡Department of Evolution, Ecology and Organismal Biology, Ohio State University, 318 W 12th Avenue, Columbus, OH 43210, USA

## Summary

1. The wide range in incubation periods among bird species has puzzled biologists for decades, because an extended egg-phase increases time-dependent mortality of the eggs.
2. We investigated a recently proposed mechanistic explanation inspired by life-history theory, suggesting that adults may increase their own survival by reducing nest attentiveness, the percentage of daytime spent incubating eggs, in exchange for reduced offspring (egg) survival due to a longer incubation period. Incubation behaviour and egg temperatures ( $T_{\text{egg}}$ ) of 14 bird species in the humid lowland tropics were studied to test the hypothesis that lower nest attentiveness and reduced  $T_{\text{egg}}$  cause longer incubation periods.
3. Increased nest attentiveness correlated with higher average  $T_{\text{egg}}$ . However, neither nest attentiveness nor average  $T_{\text{egg}}$  was associated with the length of the incubation period. Longer off-bouts resulted in lower  $T_{\text{egg}}$ , but neither number of off-bouts nor off-bout length was associated with incubation period. In addition, we reanalysed a previously published negative association between  $T_{\text{egg}}$  and incubation period based on literature data from temperate passerine birds using a larger data set and found no significant correlation.
4. In conclusion, our results do not support the hypothesis that longer incubation periods are caused by reduced nest attentiveness and corresponding lower  $T_{\text{egg}}$ .

*Key-words:* Incubation behaviour, life-history evolution, tropics

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## Introduction

An effective way for many organisms to increase evolutionary fitness is to decrease the length of the development period that typically is a time of high offspring mortality and intense parental investment (Lack 1968; Kozłowski 1992; Stearns 1992; Roff 1993). Because an extended egg-phase increases time-dependent mortality of the eggs, the wide range in incubation periods among bird species has puzzled biologists for decades (Skutch 1949; Lack 1968; Rahn & Ar 1974; Boersma 1982; Ricklefs 1993; Geffen & Yom-Tov 2000). Life-history theory indicates that parents should accept increased risk to their offspring when this is balanced by an increase in their own survival. Recently, Martin (2002) has suggested that this trade-off might explain the long incubation periods of many tropical and southern hemisphere species, which have low extrinsic adult mortality and experience high rates of nest predation (i.e. predation of eggs and chicks in the nest). Martin's hypothesis is that adults increase their own survival by

reducing nest attentiveness, the percentage of daytime spent incubating eggs, thereby gaining more fitness than they lose through reduced offspring (egg) survival.

Intraspecific studies have shown that birds adjust the time that they spend incubating eggs depending on environmental conditions, including ambient temperature and nest predation, and that nest attentiveness affects egg temperature ( $T_{\text{egg}}$ ) and incubation period (Drent 1975; Webb 1987; Williams 1996; Conway & Martin 2000; Reid, Monaghan & Nager 2002). Lower average  $T_{\text{egg}}$  resulting from reduced attentiveness slows embryonic development and prolongs the period to hatching, presumably increasing egg mortality. Martin (2002) applied this intraspecific mechanism to the interspecific variation in incubation periods and suggested that the low extrinsic mortality of many southern and tropical species favours a shift to higher adult survival (lower nest attentiveness) at the expense of lower chick survival (longer incubation periods). Lower nest attentiveness could lead to higher adult survival through extrinsic factors, such as decreased risk of predation on parents while attending the nest, and through intrinsic factors, such as increased workload (Martin 2002). In his study of nine pairs of closely related species of

passerine birds from Argentina and Arizona, the southern member of each pair had a longer incubation period and lower nest attentiveness than the northern member. In addition, reduced nest attentiveness was associated with lower extrinsic adult mortality, implying that parents might reduce their own mortality by reducing time at the nest in exchange for increased exposure of their eggs to time-dependent mortality. A negative correlation between  $T_{\text{egg}}$  and incubation period, based on literature data from a variety of temperate North American passerines, suggested a mechanism for the longer incubation periods of southern species (Martin 2002).

Although there are conflicting claims about the relative incubation periods of tropical/southern latitude and northern temperate species (Ricklefs 1992; Geffen & Yom-Tov 2000; Martin 2002), it is evident that incubation periods vary widely among birds of similar size and development type within the tropics (Skutch 1954, 1960, 1969). Mechanisms proposed to explain differences in incubation period between tropical and temperate birds should also apply to variation within the tropics. In addition, studies addressing mechanistic explanations for the variation in incubation periods would benefit from reducing differences in environmental conditions between species to exclude environment as a confounding factor.

We studied incubation behaviour and egg temperatures of birds in the humid lowland tropics to test the hypothesis that lower nest attentiveness and reduced  $T_{\text{egg}}$  cause longer incubation periods. Our study included species with incubation periods ranging from 12 to 19 days, a 40% greater range than that available in the study of Martin (2002). In addition, unlike analyses based on a variety of literature sources, our analyses were not confounded by variation in thermal environment or field methods.

### Materials and methods

We conducted our study during May and June 2003 in and around Soberania National Park in the Republic of Panama (9° N 79° W). The area is characterized by humid lowland tropical forest with average annual temperatures of about 25 °C and a rainy season from late April until December. We measured egg temperatures ( $T_{\text{egg}}$ ) and nest attentiveness in 13 species of passerine birds and one dove in both residential/park-like and inner forest habitats (Table 1). Incubation strategies included 12 female-only incubators and two biparental incubators. Incubation periods were obtained from literature, as indicated in Table 1.

For a wide variety of avian orders, incubation period increases with egg size (Rahn & Ar 1974; Ricklefs & Starck 1998). However, within orders the allometric regression slope of incubation period on egg size (0–11) is low and relatively little of the variation in incubation period among birds can be explained by size (Ricklefs & Starck 1998). Among 97 species of small (<100 g) North American passerines, Martin (2002) found no effect of body or egg mass on incubation period. We restricted

our study to mainly passerine birds of small body size (8–80 g), which greatly reduces the influence of egg size on incubation period.

To measure egg temperature ( $T_{\text{egg}}$ ), we briefly removed an egg from a nest, drilled a small hole in its side, inserted a 40-gauge copper–constantan thermocouple and glued it in place with superglue and dental cement (Davis *et al.* 1984). The tip of the thermocouple was placed about 1–2 mm from the top of the egg, to measure the temperature experienced by the embryo. Extending the thermocouple wire through the nest-bottom, we fixed the egg in the middle of the nest among the rest of the clutch.  $T_{\text{egg}}$  was recorded every minute using a Campbell Scientific datalogger (model CR23X or CR10X, Campbell Scientific Inc., Logan, Utah, USA) or an Omega handheld digital thermometer (model HH21, Omega Engineering, Inc., Stamford, Connecticut, USA). We calibrated the dataloggers and thermometer in a Neslab water bath (Thermo Electron, Waltham, MA, USA) against an ERTCO mercury thermometer (Ever Ready Thermometer Co., Inc., Dubuque, IA, USA) with a calibration certificate traceable to the National Institute for Standards and Technology. The eggs with the thermocouples were used for 1–4 days, periods short enough to avoid effects of rotten eggs on attentiveness. We only used nests with completed clutches for measurements of  $T_{\text{egg}}$ . The behaviour of incubating parents and the patterns of attentiveness at nests with thermocouple-eggs appeared typical of non-manipulated nests.

We used the records of  $T_{\text{egg}}$  to identify the lengths of on and off-bouts to the nearest minute, after verifying our on and off-bout assignments for five nests at which we made behavioural observations and measurements of  $T_{\text{egg}}$  simultaneously. Nest attentiveness was calculated as the percentage of time that a parent attended the nest over the entire 13.5 h (810 min) daylight period (05.30–18.59 h) for 44 days, and over a part of the daylight period for 15 days (mean  $\pm$  SD: 405  $\pm$  194 min, range 114–737 min). Number of nests and number of measurement days for each species are given in Table 1.

### PHYLOGENETIC CONSIDERATIONS AND STATISTICAL ANALYSIS

Sister taxa may have similar trait values as a result of common ancestry, biasing analyses in which all species values are weighted equally (Felsenstein 1985; Harvey & Pagel 1991). We used the test for serial independence (Abouheif 1999; Reeve & Abouheif 1999) to determine whether a phylogenetic effect (*sensu* Grafen 1989 and Harvey & Pagel 1991) existed in our data, with a phylogenetic hypothesis based on Sibley & Ahlquist (1990). In each simulation the topology was randomly rotated 1000 times per iteration and the original data were shuffled 1000 times to provide a sampling distribution for the null hypothesis (Reeve & Abouheif 1999). We found a significant phylogenetic effect for incubation period ( $P = 0.008$ ), a marginally insignificant effect for

**Table 1.** Number of nests, number of measurement days, incubation period, clutch size and incubation strategy for the 14 species included in this study

Species	Scientific name	Number of nests	Number of days	Incubation period (days)	Clutch size	Incubating parent	Reference*
Clay-coloured Robin	<i>Turdus grayi</i>	4	10	12	3	Female only	Skutch (1960)
Common Tody-flycatcher	<i>Todirostrum cinereum</i>	3	8	17.7	(2) 3	Female only	Skutch (1960)
Social Flycatcher	<i>Myiozetetes similis</i>	2	5	15.5	3 or 4	Female only	Skutch (1960)
Thick-billed Euphonia	<i>Euphonia laniirostris</i>	2	5	14.5	4	Female only	Geffen & Yom-Tov (2000)
Red-throated Anti-tanager	<i>Habia fuscicauda</i>	1	2	13	3	Female only	Geffen & Yom-Tov (2000), Willis (1961)
House Wren	<i>Troglodytes aedon</i>	1	2	15	3–5	Female only	Skutch (1960)
Yellow-green Vireo	<i>Vireo flavoviridis</i>	1	3	13.7	(2) 3	Female only	Skutch (1960)
Red-capped Manakin <sup>a</sup>	<i>Pipra mentalis</i>	2	7	19	2	Female only	Skutch (1969)
Spotted Antbird	<i>Hylophylax naevioides</i>	2	6	18	2	Male and female	Skutch (1969), Robinson <i>et al.</i> (2000)
Tropical Kingbird	<i>Tyrannus melancholicus</i>	1	2	15.5	2	Female only	Skutch (1960)
Variable Seedeater	<i>Sporophila americana</i>	1	2	12.5	2	Female only	Skutch (1954)
Yellow-bellied Seedeater <sup>b</sup>	<i>Sporophila nigricollis</i>	1	2	12.5	2	Female only	
Ruddy Ground-dove <sup>c</sup>	<i>Columbina talpacoti</i>	2	4	13	2	Male and female	
White-lined Tanager	<i>Tachyphonus rufus</i>	1	1	14.5	2	Female only	Geffen & Yom-Tov (2000)

<sup>a</sup>Incubation period estimated as average of three other *Pipra* species (Skutch 1969).

<sup>b</sup>Incubation period assumed to be the same as Variable Seedeater.

<sup>c</sup>Incubation period based on Common Ground-dove (Bowman 2002).

nest attentiveness ( $P = 0.06$ ), and no significant effects for average 24-h  $T_{\text{egg}}$  ( $P = 0.46$ ), daytime  $T_{\text{egg}}$  ( $P = 0.23$ ), night-time  $T_{\text{egg}}$  ( $P = 0.50$ ), off-bout number ( $P = 0.12$ ), off-bout length ( $P = 0.14$ ), on-bout length ( $P = 0.46$ ), minimum  $T_{\text{egg}}$  ( $P = 0.29$ ) and maximum  $T_{\text{egg}}$  ( $P = 0.35$ ). When no phylogenetic effect exists, incorporating phylogeny in statistical analyses is unnecessary (Gittleman & Kot 1990; Björklund 1997; Abouheif 1999). If a phylogenetic effect does exist, it may be due to phylogenetic constraint or to ecological factors and incorporating phylogenetic relatedness may or may not be appropriate (Westoby, Leishman & Lord 1995).

We used SPSS 11.5 to calculate conventional parametric or non-parametric correlations of species-values. Analyses that included incubation period or nest attentiveness were also performed with phylogenetic independent contrasts (Felsenstein 1985), calculated with the PDTREE module of the program PDAP (Garland, Harvey & Ives 1992).

## Results

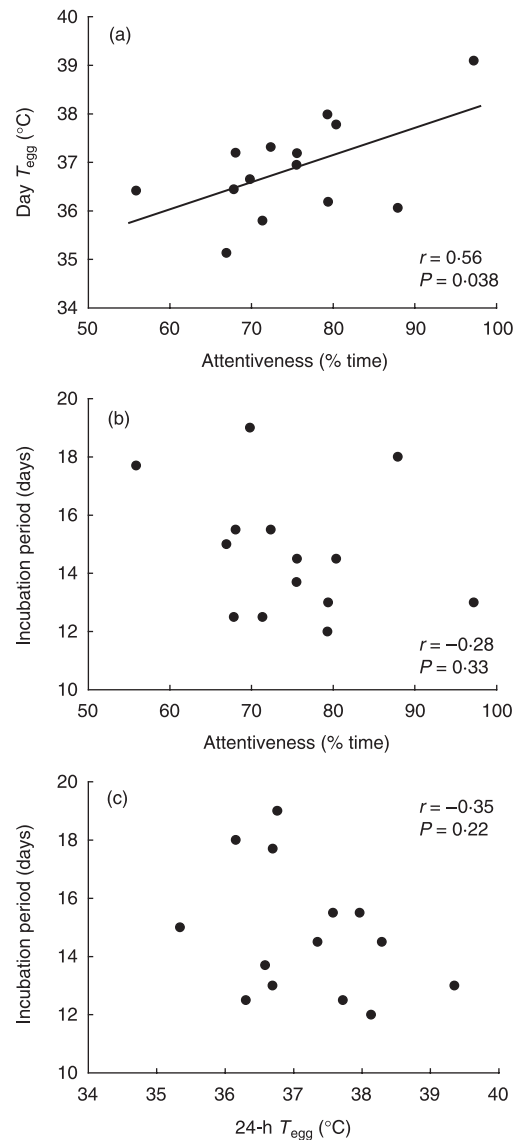
### NEST ATTENTIVENESS, $T_{\text{egg}}$ AND INCUBATION PERIOD

Nest attentiveness was significantly and positively associated with daytime  $T_{\text{egg}}$  using conventional analysis (species  $r = 0.56$ ,  $n = 14$ ,  $P = 0.04$ , Fig. 1a), but this trend was not significant with independent contrasts (contrasts  $r = 0.33$ ,  $n = 13$ ,  $P = 0.26$ ). Neither nest attentiveness nor average  $T_{\text{egg}}$  over the 24-h period was related to incubation period (Table 2; attentiveness: species  $r = -0.28$ ,  $n = 14$ ,  $P = 0.33$ , contrasts  $r = -0.15$ ,  $n = 13$ ,  $P = 0.61$ , Fig. 1b;  $T_{\text{egg}}$ : species  $r = -0.35$ ,  $n = 14$ ,  $P = 0.22$ , contrasts  $r = -0.24$ ,  $n = 13$ ,  $P = 0.42$ , Fig. 1c). To evaluate the robustness of these patterns in light of the small sample sizes for a number of the species, we randomly selected two measurement days per species for the six species that we measured for 5 or more days (Table 1), and reanalysed the correlations. These analyses confirmed the insignificance of the relationships between nest attentiveness or  $T_{\text{egg}}$  and incubation period (attentiveness: species  $r = -0.29$ ,  $n = 14$ ,  $P = 0.32$ ;  $T_{\text{egg}}$ : species  $r = -0.29$ ,  $n = 14$ ,  $P = 0.31$ ).

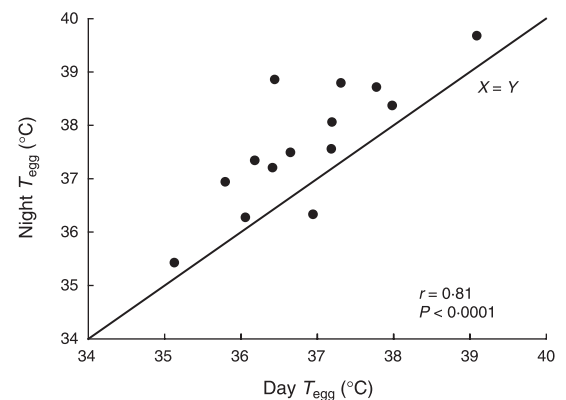
$T_{\text{egg}}$  during the night-time period was positively correlated with  $T_{\text{egg}}$  during the daytime period (species  $r = 0.81$ ,  $n = 14$ ,  $P < 0.0001$ , Fig. 2). Minimum  $T_{\text{egg}}$ , measured as the last reading of each off-bout and averaged over all off-bouts per species, and maximum  $T_{\text{egg}}$ , measured as the average last reading of each on-bout, were not correlated with incubation period (Table 2; minimum  $T_{\text{egg}}$ : species  $r = -0.18$ ,  $n = 12$ ,  $P = 0.57$ ; maximum  $T_{\text{egg}}$ : species  $r = -0.11$ ,  $n = 12$ ,  $P = 0.72$ ).

### NUMBER AND LENGTH OF BOUTS IN RELATION TO INCUBATION PERIOD AND $T_{\text{egg}}$

We restricted the analyses of off-bout length and number to the 12 species with female-only incubation



**Fig. 1.** (a) The relationship between (a) average nest attentiveness (% time) and average daytime egg temperature ( $^{\circ}\text{C}$ ); (b) average nest attentiveness (% time) and incubation period (days); and (c) average 24-h egg temperature ( $^{\circ}\text{C}$ ) and incubation period for 14 species of small tropical birds.



**Fig. 2.** The correlation between egg temperature ( $^{\circ}\text{C}$ ) during day and night for 14 species of small tropical birds. The line depicts day  $T_{\text{egg}} = \text{night } T_{\text{egg}}$ .

**Table 2.** Average, standard deviation and sample size for 24-h  $T_{\text{egg}}$  (°C), minimum  $T_{\text{egg}}$  (°C), maximum  $T_{\text{egg}}$  (°C), and nest attentiveness (% daytime) for the species included in this study

Species	24-h $T_{\text{egg}}$			Maximum $T_{\text{egg}}$			Minimum $T_{\text{egg}}$			Nest attentiveness		
	Average	SD	<i>n</i>	Average	SD	<i>n</i>	Average	SD	<i>n</i>	Average	SD	<i>n</i>
Clay-coloured Robin	38.1	0.21	7	38.7	0.93	141	35.8	1.79	138	79.3	5.63	10
Common Tody-flycatcher	36.7	0.52	7	38.4	1.11	164	33.3	1.95	164	55.9	5.19	8
Social Flycatcher	37.6	2.05	4	38.8	2.28	82	33.0	2.50	80	68.0	4.25	5
Thick-billed Euphonia	37.3	0.87	5	38.5	1.29	70	33.1	1.55	70	75.6	3.41	5
Red-throated Ant-tanager	36.7	0.01	2	38.4	0.56	8	27.9	1.03	8	79.4	5.64	2
House Wren	35.3	0.23	2	35.9	0.63	24	33.4	0.72	24	66.9	0.37	2
Yellow-green Vireo	36.6	–	1	37.8	1.20	28	34.9	1.47	28	75.5	6.91	3
Red-capped Manakin	36.8	1.78	5	37.8	2.78	59	30.7	2.28	57	69.8	9.96	7
Spotted Antbird	36.2	0.57	6	–	–	–	–	–	–	87.9	6.05	6
Tropical Kingbird	38.0	0.73	2	39.0	1.53	41	32.0	2.31	41	72.4	5.74	2
Variable Seedeater	36.3	0.71	2	37.4	0.94	41	31.4	1.86	41	71.4	1.12	2
Yellow-bellied Seedeater	37.7	0.43	2	39.0	1.46	39	33.6	3.82	38	67.8	4.48	2
Ruddy Ground-dove	39.4	1.93	4	–	–	–	–	–	–	97.2	5.56	4
White-lined Tanager	38.3	–	1	38.4	0.71	11	34.5	1.40	11	80.4	–	1

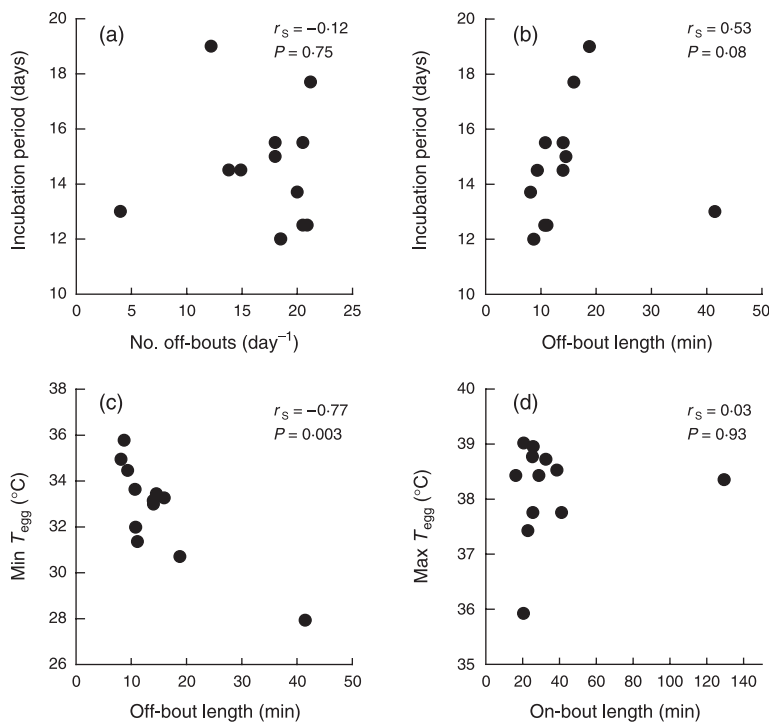
(Table 1). Neither number of off-bouts nor off-bout length was associated with incubation period (off-bout number: species  $r_s = -0.12$ ,  $n = 12$ ,  $P = 0.75$ , contrasts  $r = -0.11$ ,  $n = 11$ ,  $P = 0.74$ , Fig. 3a; off-bout length: species  $r_s = 0.53$ ,  $n = 12$ ,  $P = 0.08$ , contrasts  $r = -0.08$ ,  $n = 11$ ,  $P = 0.80$ , Fig. 3b). Minimum  $T_{\text{egg}}$  was negatively correlated with the average length of the off-bouts (species  $r_s = -0.77$ ,  $n = 12$ ,  $P = 0.003$ , Fig. 3c). That is,

longer off-bouts resulted in lower  $T_{\text{egg}}$ . Maximum  $T_{\text{egg}}$  was not related to the length of the preceding on-bout (species  $r_s = 0.03$ ,  $n = 12$ ,  $P = 0.93$ , Fig. 3d).

## Discussion

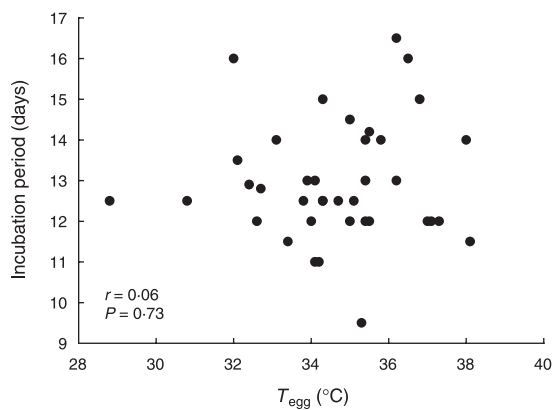
Our results do not support the hypothesis that longer incubation periods in some tropical birds are caused by reduced nest attentiveness and corresponding lower average  $T_{\text{egg}}$ . Similar conclusions have been reached in studies concerning the long incubation period of pelagic seabirds, which incubate their eggs at temperatures within the range of coastal species having much shorter embryo development times (Ricklefs 1984; Williams & Ricklefs 1984). Our findings on tropical birds are consistent with Ricklefs's (1993) analysis of data from Skutch (1976) for which there was no association between attentiveness and egg-size corrected incubation period in a sample of primarily small tropical birds. However, our results differ from those of Martin (2002), who reported lower attentiveness and reduced  $T_{\text{egg}}$  in passerines with longer incubation periods.

The relationship between incubation period and  $T_{\text{egg}}$  reported by Martin (2002) was based on data for  $T_{\text{egg}}$  from 23 North American species, which comprised a subset of the 38 North American and European passerines listed in the appendix of Williams (1996). We reanalysed the association between incubation period and  $T_{\text{egg}}$  using the complete data set from Williams (1996), after correcting three typographical errors from the original literature (for the species *Progne subis*, *Spizella passerina* and *Melospiza melodia*), and data for incubation periods from the *Birds of North America* series (Poole, Stettenheim & Gill 1992–93; Poole & Gill 1993–2002) and the *Handbook of the Birds of Europe, the Middle East and North Africa* (Cramp 1988–93; Cramp & Perrins 1994). We found no significant association between  $T_{\text{egg}}$  and incubation period (species  $r = 0.06$ ,  $n = 38$ ,  $P = 0.73$ , Fig. 4).



**Fig. 3.** The relationship between incubation period and number of off-bouts (a) and average off-bout length (b) for 12 species of small tropical birds with female-only incubation. (c) The correlation between off-bout duration and egg temperature at the end of the off-bout for 12 tropical birds with female-only incubation. (d) The association between on-bout duration and egg temperature at the end of the on-bout for 12 tropical birds with female-only incubation.





**Fig. 4.** The association between  $T_{\text{egg}}$  and incubation period based on literature data for North American and European passerines.

The behaviour of incubating parents has been related to the risk of nest predation (Skutch 1949, 1985; Martin 1996; Martin, Scott & Menge 2000) and to the risk of adult mortality (Martin 2002), and has been shown to influence the rate of development of the embryo in intraspecific studies (Drent 1975; Reid *et al.* 2002). High predation risk at the nest, either for the clutch or for the parent, presumably selects for less activity around the nest, resulting in fewer and longer off-bouts that cause lower minimum  $T_{\text{egg}}$  than short off-bouts and potentially slow embryonic development. Although longer off-bouts resulted in lower minimum  $T_{\text{egg}}$  (Fig. 3c), we found no support for an association between number or length of off-bouts and incubation period (Fig. 3a,b). Correlations between incubation period and daily mortality rates of nests have varied among studies from absent or weak (Ricklefs 1993) to strong (Conway & Martin 2000; Martin *et al.* 2000; Ghalambor & Martin 2002). Where correlations exist, they might reflect an indirect effect of nest attentiveness on  $T_{\text{egg}}$  or a more direct effect of time-dependent mortality on the evolved rate of embryonic growth. The absence of a  $T_{\text{egg}}$  effect on incubation period in our study discounts the first hypothesis.

If interspecific variation in incubation period reflected  $T_{\text{egg}}$ , the cause of this variation would be primarily non-genetic. In contrast, our finding that variation in the incubation period is independent of  $T_{\text{egg}}$  implies that the rate of embryonic growth is adaptively modified in a manner that enhances the fitness of the hatchling. Many species exhibit substantial variation in incubation periods – up to 100% – usually related to environmental conditions (Drent 1975; Boersma & Wheelwright 1979; Moreno 1989; Reid *et al.* 2002). However, the average or minimum incubation periods of species appear to be evolutionarily conservative, with most of the variation explained at the levels of orders and families within orders, and less at the levels of genera within families and species within genera (Ricklefs 1993; Ricklefs & Starck 1998). Two species have been subject to cross-fostering experiments of eggs to distinguish environmental from genetic effects on incubation periods. Dividing the

genetic standard deviation of incubation period within populations by the mean gives coefficients of variation smaller than 1% in starling and chicken, indicating that the genetic variance in incubation period is small (Crittenden & Bohren 1961; Ricklefs & Smeraski 1983). These patterns suggest constraints on embryonic development, but their nature and extent are as yet unclear. Prolonged incubation has been associated with long life span and well-developed immune system responsiveness (Ricklefs 1992, 1993; Martin 2002), and could be part of a set of life-history characteristics typified as ‘slow pace of life’ (Ricklefs & Wikelski 2002). If we assume that long incubation periods result from a uniform slowing of embryonic growth throughout the development period (Ricklefs 1987), possible physiological mechanisms determining incubation period include rate of protein turnover for embryonic growth, and potential for embryonic gas exchange, which can be a function of eggshell structure (Carey 2002).

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