

# Enclosed nests may provide greater thermal than nest predation benefits compared with open nests across latitudes

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## Summary

1. Nest structure is thought to provide benefits that have fitness consequences for several taxa. Traditionally, reduced nest predation has been considered the primary benefit underlying evolution of nest structure, whereas thermal benefits have been considered a secondary or even non-existent factor. Yet, the relative roles of these factors on nest structures remain largely unexplored.

2. Enclosed nests have a constructed or natural roof connected to sides that allow a restricted opening or tube entrance that provides cover in all directions except the entrance, whereas open nests are cups or platforms that are open above. We show that construction of enclosed nests is more common among songbirds (Passeriformes) in tropical and southern hemisphere regions than in north temperate regions. This geographic pattern may reflect selection from predation risk, under long-standing assumptions that nest predation rates are higher in southern regions and that enclosed nests reduce predation risk compared with open cup nests. We therefore compared nest predation rates between enclosed vs. open nests in 114 songbird species that do not nest in tree holes among five communities of coexisting birds, and for 205 non-hole-nesting species from the literature, across northern temperate, tropical, and southern hemisphere regions.

3. Among coexisting species, enclosed nests had lower nest predation rates than open nests in two south temperate sites, but not in either of two tropical sites or a north temperate site. Nest predation did not differ between nest types at any latitude based on literature data. Among 319 species from both our field studies and the literature, enclosed nests did not show consistent benefits of reduced predation and, in fact, predation was not consistently higher in the tropics, contrary to long-standing perspectives.

4. Thermal benefits of enclosed nests were indicated based on three indirect results. First, species that built enclosed nests were smaller than species using open nests both among coexisting species and among species from the literature. Smaller species lose heat fastest and thereby may gain important thermal benefits from reduced convective cooling. Second, eggs were warmed by parents for less time in species with enclosed nests, as can be expected if egg cooling rates are slower. Finally, species using enclosed nests exhibited enhanced growth of mass and wings compared with species using open nests, suggesting reduced thermoregulatory costs allowed increased energy for growth.

5. Enclosed nests may therefore provide more consistent thermal than nest predation benefits, counter to long-standing perspectives.

**Key-words:** growth, life history, nest predation, nest structure, temperate, thermal benefits, tropical

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## Introduction

Nests are constructed by diverse taxa, including insects, fish, amphibians, reptiles, mammals and birds, and provide multiple functions that can affect fitness (Collias & Collias 1984; Wells, Lakim & Pfeiffer 2006; Mainwaring *et al.* 2014). Traditionally, protection from predators has been considered the primary benefit of nest structure, whereas protection from harsh microclimates has been considered of secondary importance (Fowler 1979; Gross & MacMillan 1981; Collias & Collias 1984; Magnusson & Hero 1991; Madsen & Shine 1999; Mehlman & Doran 2002; Fast, Gilchrist & Clark 2007; Angilletta, Sears & Pringle 2009). Yet, comparative studies of the relative importance of these two functions are lacking.

Songbirds (Passeriformes) offer an interesting system to compare these two functions because this diverse group of

species (>50% of all bird species) build two major types of nests, open vs. enclosed (Fig. 1), that are expected to differ in their benefits, while reducing broader phylogenetic issues inherent in the inclusion of other orders. Open nests are cups or platforms that are open above and thereby exposed to both climate and predators from above and the sides (Fig. 1a). Enclosed nests have a constructed or natural roof connected to sides that allow a restricted opening or tube entrance that provide protection in all directions except the entrance (Fig. 1b), and do not include holes in trees (Lack 1948; Nice 1957; Collias & Collias 1984). Enclosed nests are used in nearly 50% of passerine families (Collias 1997) and are also used by many small mammals (Dawson & Lang 1973; Shump 1974; Wells, Lakim & Pfeiffer 2006), suggesting a functional importance of enclosed nest construction across taxa. Yet, the functional benefits of this repeated evolution remain unclear.

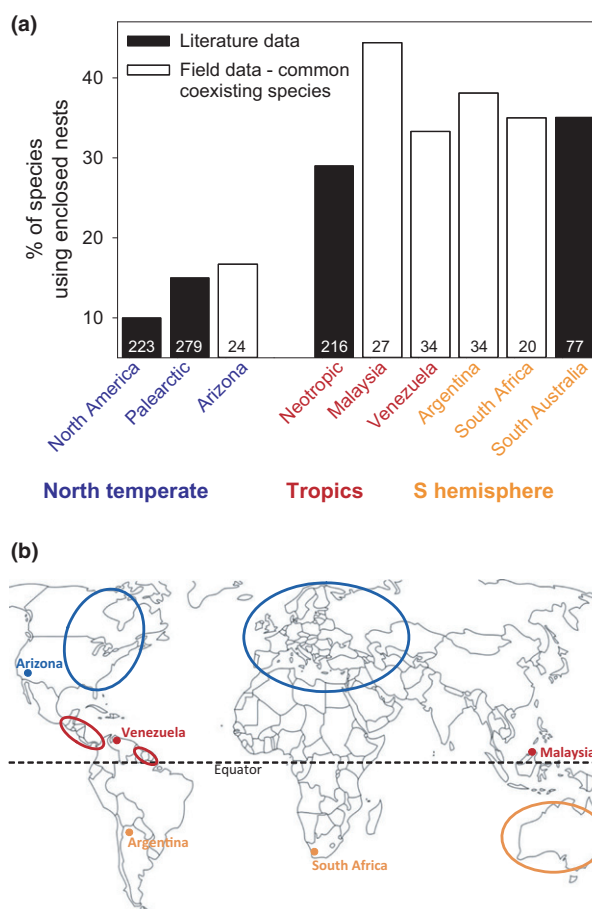


**Fig. 1.** Example photos of (a) open (species down vertically are: *Catharus guttatus*, *Zosterops pallidus*, *Rhipidura albicollis*) vs. (b) enclosed (*Ficedula hyperythra*, *Seiurus montis*, *Chlorophonia cyanea*) nests (photos by T.E. Martin).

Enclosed nests are widely thought to reduce the risk of predation (Nice 1957; Oniki 1985; Hall *et al.* 2015). They may also provide thermal benefits of reduced heat loss and protection from rain or sun, but these benefits are generally considered to be of secondary importance (Snow 1978; Collias & Collias 1984; Skutch 1985). Of course, these two benefits are not mutually exclusive, but their relative importance has not been broadly tested across diverse species and geographical locations in any taxa.

Reduced nest predation risk is the prevailing and most commonly invoked hypothesis for benefits of enclosed nests across taxa (Nice 1957; Snow 1978; Fowler 1979; Oniki 1979, 1985; Gross & MacMillan 1981; Magnusson & Hero 1991; Spencer & Thompson 2003; Hall *et al.* 2015). Yet, broad tests of predation differences between open and enclosed nests are lacking (but see Auer *et al.* 2007), especially across large spatial scales. Tests across geographical regions are important because the percentage of passerine species using enclosed nests in the tropics and southern hemisphere is roughly double to triple the percentage in north temperate regions (Fig. 2). At the same time, nest predation is commonly assumed to be greater in tropical and southern hemisphere regions compared with the north temperate region (Skutch 1949, 1966; Willis 1974; Snow 1978; Major 1991). Thus, the latitudinal pattern in nest structure could reflect responses to higher predation in these regions (Snow 1978; Oniki 1985; Hall *et al.* 2015). However, some evidence suggests that nest predation may not be higher in the tropics (Oniki 1979; Martin 1996), raising the possibility that other functional benefits of nest structure may play a more important role.

The role of other functional benefits, like reducing thermal costs, has received little attention or support. For example, Heenan & Seymour (2011) argued that open cup nests merely provide structural support for breeding rather than any insulation benefits. Similarly, thermal benefits of reduced heat loss and protection from rain or sun in enclosed nests, while acknowledged as a possibility (Snow 1978; Collias & Collias 1984; Skutch 1985), have received little attention. Indeed, Oniki (1985) specifically argued that enclosed nests are not a response to weather or thermal conditions, and only reflect an adaptation to reduce nest predation. In contrast to these arguments, reduced thermal costs via reduced heat loss could be an important benefit of enclosed nests across taxa (e.g. Madsen & Shine 1999; Mehlman & Doran 2002; Angilletta, Sears & Pringle 2009). Offspring may be particularly vulnerable to thermal costs because bird and mammal juveniles have higher conductance to heat loss, especially from wetting, due to poorer insulation than adults (Nye 1964; Webb, Porter & McClure 1990). In addition, exposure to the sun can cause heat stress, and wetting can increase heat loss, each of which can cause offspring mortality (White & Kinney 1974; Salzman 1982; Öberg *et al.* 2015). Both weather impacts may be reduced in enclosed nests with their shielding roofs and sides. Moreover, enclosed nests are thought to reduce convective and radiative avenues of heat loss



**Fig. 2.** (a) Percentage of songbird species of all nest types (open, enclosed and hole nests) that construct enclosed nests based on regional data from the literature (solid bars) for North America (von Haartman 1957), Palearctic (von Haartman 1957), Neotropics (Skutch 1985) and south Australia (Remeš, Matysioková & Cockburn 2012), and for our field studies (open bars) of the common species coexisting in five communities across latitudinal regions. Enclosed nests are defined as those that have a constructed or natural roof connected to sides that allow a restricted opening or tube entrance that provide protection in all directions except the entrance (Fig. 1), and are not in holes in trees. Numbers at the base of columns indicate the total number of species. (b) Map of the locations of our intensive field studies are indicated by points, and the ellipses represent the areas covered by literature sources.

even in dry conditions (Buttemer *et al.* 1987; Lamprecht & Schmolz 2004). All of these potential thermal benefits may be important for offspring because their growth is energetically demanding, such that reduction in thermoregulatory costs in enclosed nests could thereby benefit growth.

Potential thermal benefits of enclosed nests also may be important to adult energy expenditure (e.g. Madsen & Shine 1999; Redman, Selman & Speakman 1999; Fast, Gilchrist & Clark 2007). Enclosed nests can reduce adult energy expenditure when temperatures are below the thermoneutral zone of birds (Buttemer *et al.* 1987) and mammals (Redman, Selman & Speakman 1999). In addition, lab tests showed that egg cooling rates were slowed in enclosed compared with open cup nests of birds

(Lamprecht & Schmolz 2004), and slower egg cooling rates could allow parents to spend more time off the nest during incubation. Time off the nest is beneficial to parent birds because it allows them to obtain food for self-maintenance (White & Kinney 1974). Thus, enclosed nests may provide thermal benefits for offspring and parents, as well as protection from rain in the wet tropics, and from the sun in open and arid environments.

We investigate these alternative functions for enclosed nests via a series of predictions. The most fundamental prediction of the nest predation hypothesis is that predation rates should be lower in enclosed than open nests. It further predicts that enclosed nesting should be more common in regions where nest predation rates are higher. Finally, large species often experience higher nest predation rates than small species (Biancucci & Martin 2010; Remeš, Matysioková & Cockburn 2012), which predicts that enclosed nests should be used more commonly by large species. Meanwhile, the thermal benefits hypothesis has three testable predictions. First, heat loss is a larger problem for smaller species (Calder 1984), so enclosed nests should be more common in smaller species if they provide a thermal benefit. Note this prediction directly contrasts with the nest predation hypothesis. Second, tropical and southern hemisphere parents commonly spend less time on the nest (Chalfoun & Martin 2007; Martin *et al.* 2007, 2015a; Martin & Schwabl 2008), increasing exposure of their offspring to weather. If enclosed nesting provides a thermal benefit and slower egg cooling rates, it should allow species to spend less time on the nest than in open nests. Third, growth of mass and especially wing development can be critical to juvenile survival, but may be energy-limited (Martin 2014, 2015a). Experimental warming to reduce thermoregulatory costs yielded larger mass and longer wings at nest departure in a cavity-nesting passerine, demonstrating thermal constraints on growth (Dawson, Lawrie & O'Brien 2005). Thus, if enclosed nests provide thermal benefits, we might expect relatively larger offspring with more developed wings at fledging (nest departure).

We examine predation vs. thermal hypotheses across latitudes based on data from the literature and intensive studies of 17–31 coexisting species in each of five sites on four continents. Comparisons between nest types among coexisting species provide a particularly strong test because they are exposed to the same macroclimate and community of predators.

## Materials and methods

### STUDY AREAS, SPECIES AND NEST TYPES

Species that build nests of all types were included for the examination of geographical variation in the frequency of enclosed nests (i.e. Fig. 2). This included 139 passerine species that we intensively studied in five sites on four continents and 795 passerine species among regions from the literature (Fig. 2, Fig. S1, Supporting

Information). However, nests in tree holes are not included in the remainder of the paper because this is considered a different nest type and strategy (e.g. von Haartman 1957), and we have data on few such species at any site except the north temperate site. Consequently, 114 songbird species on our study sites and 205 species from the literature with nest predation data did not nest in tree holes and are the focus of tests here. We studied nests of coexisting birds of a mid-elevation (2300 m elevation) mixed forest in Arizona (34° N) for 28 years as our north temperate site. The two tropical sites included mid-elevation sites (1400–2000 m elevation) in rain forests in large national parks; Kinabalu Park in Malaysian Borneo (6° N) and Yacambu National Park in Venezuela (9° N), each studied for 7 years. The two southern hemisphere sites included a mid-elevation (1000–2000 m elevation) subtropical forest in El Rey National Park in Argentina (24° S) studied for 3 years and a large nature reserve of coastal shrubland in South Africa (34° S) studied for 5 years (Martin *et al.* 2015a).

We classified nests into open vs. enclosed (Fig. 1) based on general definitions (i.e. Nice 1957; Collias & Collias 1984) that open nests are cups or platforms that are open above and thereby exposed to both climate and predators from above and the sides (Fig. 1a). In contrast, enclosed nests have a constructed or natural roof connected to sides that allow a restricted opening or tube entrance that provides cover in all directions except the entrance (Fig. 1b). In practice, nest structures vary extensively among species and this dichotomy does not fully capture the variation. For example, open nests may be placed in thick vegetation in some species, which may restrict air flow or detectability to predators. Similarly, enclosed nests can vary extensively in the size of their opening, again affecting air flow and detectability to predators. Ultimately, we believe the dichotomy describes general differences that are relevant to nest predation and thermal costs.

### NEST PREDATION RATES

We found and monitored 26 437 nests of the 114 species in the field sites following standardized protocols to provide robust estimates of nest predation rates (Martin *et al.* 2015a). Nests were checked every 2–4 days to determine their status and predation events, but were checked daily or twice daily during egg laying, near hatching and near fledging to obtain exact period durations. Nest predation was assumed when all nestlings disappeared more than 2 days prior to average fledging age, and parents could not be found in the area feeding fledglings.

We used already-compiled nest predation data from the literature for North American (Martin 1995), tropical (Skutch 1985; Remeš, Matysioková & Cockburn 2012), and southern hemisphere (Remeš, Matysioková & Cockburn 2012) regions for another 205 species (Fig. S2). The literature data for the Neotropical site (Skutch 1985) provided nesting success, and we classified all failures as nest predation. This may slightly overestimate nest predation, but the vast majority of nest failures are due to predation (Skutch 1985; Martin 1992). Data for species in the North American data set that were based solely on our Arizona site were removed to eliminate overlap with the Arizona comparisons. Finally, the southern hemisphere data for Australia was separated into southeastern and southwestern locations by the original authors because predation rates differed between these two regions (Remeš, Matysioková & Cockburn 2012).

### ADULT BODY MASS, NEST ATTENTIVENESS AND NESTLING SIZE AT FLEDGING

Body mass was obtained in the field studies from birds captured in capture/recapture efforts as part of estimating adult survival (Martin *et al.* 2015a). Body mass of adults and nestlings was

obtained with GemPro 250 portable electronic scales (MyWeigh, Phoenix, AZ, USA) with an accuracy of  $\pm 0.001$  g.

Nest attentiveness was measured throughout the entire incubation period of each species and was calculated as the percent of time that parents spent on the nest incubating based on video samples, following standardized protocols (Martin *et al.* 2007, 2015a). Nests were video-taped during incubation for the first 6–8 h of the day, beginning within 30 min after sunrise, from 1993 to 2014 in Arizona and in all study years in the other sites. This protocol standardized both time of day and sampling duration (Martin 2002; Martin *et al.* 2015a). We controlled for age of the embryo in the estimates of nest attentiveness using a linear mixed model to provide age-independent mean estimates of attentiveness for each species (Martin *et al.* 2015a).

Nestlings were measured every day for the first 3 days starting on hatch day and then every other day throughout the nestling period (Martin 2014, 2015a). Some nests were simply measured every other day beginning at hatch or the day after hatch. Wing chord length was measured using Mitutoyo (Kingsport, TN, USA) digital calipers with a precision of 0.01 mm. Measurements are difficult to obtain on fledge day (the day young leave the nest) because young often fledged before we returned to the nest and so measurements often ended the day before fledging. In the last few years, we actively sought to measure young on fledge day, even chasing them after they left the nest to obtain fledge day measurements. However, these measurements were not available for the South Africa and Argentina sites, where we worked prior to the focus on fledge day measurements. In addition, insufficient numbers of species used enclosed nests in Arizona ( $n = 4$ ) for comparisons. Thus, we only examined differences in wing length at fledging between nest types in the two tropical sites.

#### STATISTICAL ANALYSES

Daily nest predation rates were estimated for our coexisting species using the logistic exposure method (Shaffer 2004) using R v3.0.3, as reported in Martin (2015a). Literature data provided estimates of the percentage of nests lost to predators.

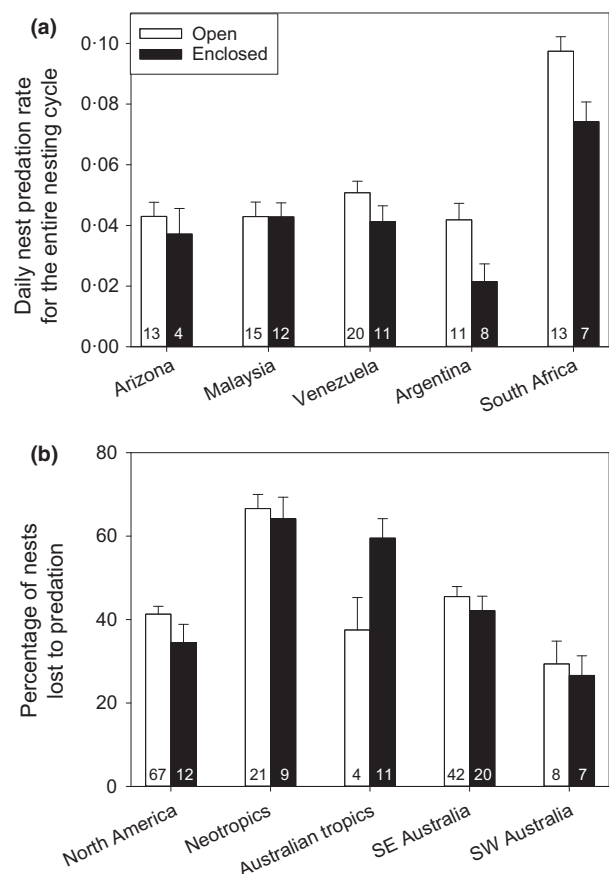
We corrected for possible phylogenetic effects (Felsenstein 1985) using the Ape (Paradis, Claude & Strimmer 2004) package in R v3.0.3 (R Development Core Team, Vienna, Austria). Phylogenetic trees were obtained from www.birdtree.org (Jetz *et al.* 2012) using the Hackett *et al.* (2008) backbone and imported into program Mesquite (Maddison & Maddison 2011) where a majority rules consensus tree was constructed based on 1000 trees (Fig. S1 and S2). This consensus tree was then used in phylogenetic generalized least squares (PGLS) analyses of daily nest predation rates, body mass, nest attentiveness and wing length.

We included log-transformed body mass as a covariate in the models of nest predation because nest predation can be higher in larger species (Bianucci & Martin 2010; Remeš, Matysioková & Cockburn 2012), but dropped it when it was not significant ( $P > 0.10$ ). Analyses of body mass differences between enclosed vs. open nests were based on log-transformed body mass. The maximum likelihood estimate of Pagel's lambda (Pagel 1992) exceeded 1.0 for body mass, which reflects highly structured phylogenetic relationships (Blomberg, Garland & Ives 2003). In the literature data, seven species exceeded 150 g (up to 928 g) and strongly increased variances, but did not change significance of differences in mass between nest types. Thus, we report analyses of body mass differences between nest types for species  $< 150$  g ( $n = 198$ ) to maintain equal variances among regions and to maintain the same range of mass as in the field data. We also included log-transformed mass as a covariate in analyses of nest attentiveness. Finally, we included both log-transformed adult mass and

length of the nestling developmental period on relative (% of adult size) wing length and nestling mass at fledging between nest types.

## Results

The percentages of species using enclosed nests in tropical and southern hemisphere regions were nearly triple the north temperate percentage both among coexisting species and among diverse songbird species from the literature (Fig. 2a). Predation benefits of enclosed nesting were not broadly supported (Fig. 3). In our field studies, daily nest predation rates were reduced in enclosed compared with open nests (Table 1a), but only because of differences in our two southern hemisphere sites (South Africa, Argentina; Fig. 3a). Nest predation rates did not differ between nest types in either of the two tropical sites nor in the north temperate field site (Fig. 3a). Similarly, nest predation was not reduced in enclosed nests in any region based



**Fig. 3.** Mean ( $\pm 1$  SE) differences in nest predation rates between open vs. enclosed nests (Table 1). (a) Daily nest predation rates of coexisting species in five bird communities in north temperate (Arizona), tropical (Malaysia and Venezuela) and southern hemisphere (Argentina and South Africa). (b) Percentage of nests lost to predation based on data from the literature for north temperate (North America), tropical (Neotropical and Tropical Australia) and southern hemisphere (Southeast and Southwest Australia) sites. Numbers at the base of columns indicate the number of species.

**Table 1.** Nest predation variation among songbird species using open vs. enclosed nests (nest type) across latitudinal regions and in relation to body mass based on (a) field data from our studies and (b) literature data. Nest type effects are in comparison to open nests and site effects are in comparison to the north temperate reference [Arizona in (a) or North America in (b)]. We show coefficients and standard errors [ $B$  (SE)],  $t$ -values, and significance from PGLS using the ape package (Paradis, Claude & Strimmer 2004)

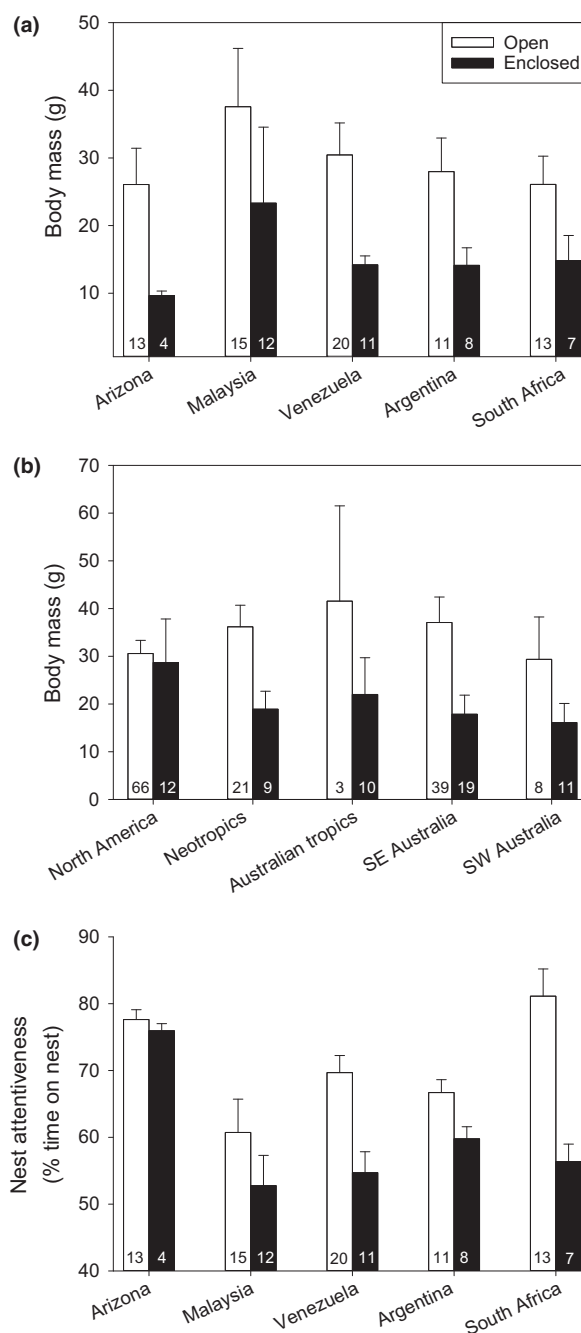
Variable	$B$ (SE)	$t$	d.f.	$P$ -value
(a) Daily nest predation rates in field sites ( $\lambda = 0.764$ )				
Nest type	-0.007 (0.004)	-1.95	1	0.054
log Mass				ns
Site (Malaysia)	-0.005 (0.007)	-0.79	1	0.43
Site (Venezuela)	0.006 (0.005)	1.26	1	0.21
Site (Argentina)	-0.006 (0.005)	-1.25	1	0.21
Site (South Africa)	0.044 (0.007)	6.55	1	<0.001
Error			108	
(b) Percentage of nests lost to predation from literature data ( $\lambda = 0.500$ )				
Nest type	-2.252 (3.070)	-0.73	1	0.46
log Mass	-8.761 (3.547)	-2.47	1	0.014
Site (Neotropics)	23.57 (3.853)	6.12	1	<0.001
Site (Tropical Australia)	15.70 (5.700)	2.75	1	0.006
Site (SE Australia)	7.480 (4.133)	1.81	1	0.07
Site (SW Australia)	-9.99 (5.427)	-1.84	1	0.06
Error			199	

on the literature data (Fig. 3b, Table 1b). Nest predation decreased in larger species in the literature data, but not our field data (Table 1).

Nest predation rates did not differ among latitudes among the four mid-elevation field sites, and were higher only on the lowland South Africa site (Fig. 3a, Table 1a). Nest predation rates of species in tropical regions, but not southern hemisphere regions, were higher than for north temperate species based on literature data (Fig. 3b, Table 1b). Nest predation in the southwestern Australia site was lower than in the north temperate site, opposite to conventional wisdom (Fig. 3b, Table 1b). Thus, nest predation did not show a consistent latitudinal pattern.

Adult mass was consistently smaller among coexisting species using enclosed than open nests across the field sites (Fig. 4a, Table 2a) and in the literature data (Fig. 4b, Table 2b). Nest attentiveness (percent time spent warming eggs during incubation) also was lower in species that built enclosed nests, and lower in tropical and Argentina sites than in the north temperate site (Fig. 4c, Table 2c), but body mass did not contribute to differences in nest attentiveness (Table 2c).

Relative (% of adult size) wing length at fledging was longer in species using enclosed nests, while controlling for length of development time (Fig. 5a, Table 2d). Nestling mass at fledging also was greater in these species with enclosed nests, while controlling for nestling period and adult mass (Fig. 5b, Table 2e). However, differences in nestling mass between nest types were not as strong as for wing length (Fig. 5; compare Table 2d,e).



**Fig. 4.** Mean ( $\pm 1$  SE) differences in body mass and nest attentiveness between open vs. enclosed nests (Table 2a–c). (a) Body mass of coexisting species in five bird communities in north temperate (Arizona), tropical (Malaysia and Venezuela) and southern hemisphere (Argentina and South Africa) sites. (b) Body mass of species <150 g in varied habitats and locations based on data from the literature for north temperate (North America), tropical (Neotropical and Tropical Australia) and southern hemisphere (Southeast and Southwest Australia) sites. (c) Nest attentiveness among the five bird communities of coexisting species. Numbers at the base of columns indicate the number of species.

## Discussion

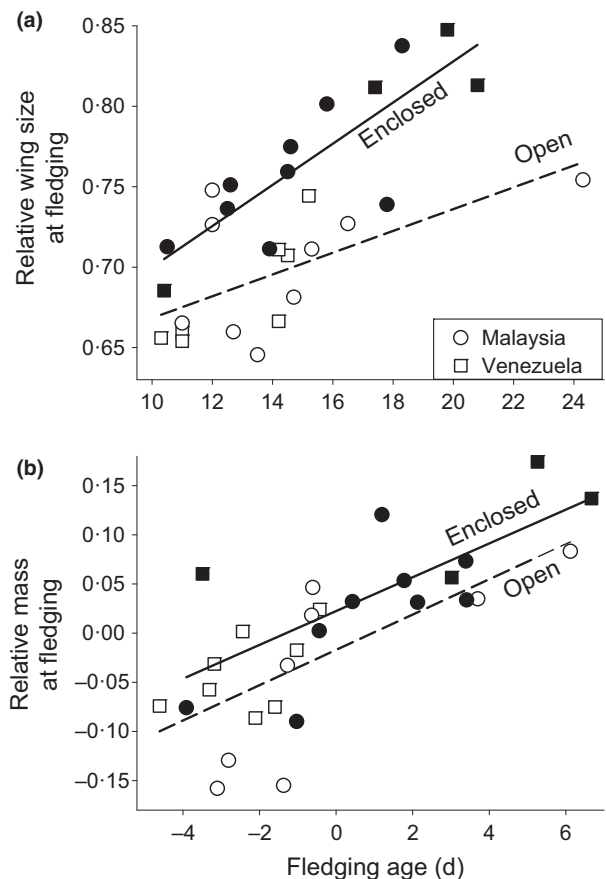
In contrast to conventional wisdom (Skutch 1966, 1985; Willis 1974; Snow 1978; Major 1991), nest predation was

**Table 2.** Life-history variation among songbird species using open vs. enclosed nests (nest type) across latitudinal regions with respect to: (a) body mass from field data from our studies, (b) body mass from the literature data, (c) nest attentiveness, (d) relative wing length (% of adult size) corrected for mass and length of the nestling period and (e) relative nestling mass (% of adult size) at fledging corrected for mass and length of the nestling period. Nest type effects are in comparison to open nests and site effects are in comparison to the north temperate reference (Arizona or North America). We show coefficients and standard errors [ $B$  (SE)],  $t$ -values, and significance from PGLS using the ape package (Paradis, Claude & Strimmer 2004)

Variable	$B$ (SE)	$t$	d.f.	$P$ -value
<b>(a) Adult body mass from field data (<math>\lambda = 1.020</math>)</b>				
Nest type	-0.157 (0.052)	-3.01	1	0.003
Site (Malaysia)	0.120 (0.101)	1.19	1	0.24
Site (Venezuela)	0.055 (0.055)	0.98	1	0.33
Site (Argentina)	0.033 (0.055)	0.59	1	0.56
Site (South Africa)	0.147 (0.100)	1.46	1	0.15
Error			108	
<b>(b) Adult body mass from literature data (<math>\lambda = 1.212</math>)</b>				
Nest type	-0.029 (0.011)	-2.73	1	0.007
Site (Neotropics)	-0.011 (0.013)	-0.83	1	0.40
Site (Tropical Australia)	-0.010 (0.020)	-0.49	1	0.63
Site (SE Australia)	0.004 (0.016)	0.23	1	0.82
Site (SW Australia)	0.013 (0.019)	0.71	1	0.48
Error			192	
<b>(c) Nest attentiveness (% time on nest) from field data (<math>\lambda = 0.744</math>)</b>				
Nest type	-6.311 (2.678)	-2.36	1	0.020
log mass				ns
Site (Malaysia)	-15.17 (5.123)	-2.96	1	0.004
Site (Venezuela)	-11.87 (3.019)	-3.93	1	<0.001
Site (Argentina)	-11.45 (2.985)	-3.84	1	<0.001
Site (South Africa)	0.385 (5.082)	0.08	1	0.94
Error			106	
<b>(d) Relative wing size at fledging from field data (<math>\lambda = 0.005</math>)</b>				
Nest type	0.060 (0.012)	4.85	1	<0.001
log mass				ns
Nestling period	0.009 (0.002)	5.13	1	<0.001
Site (Venezuela)	-0.003 (0.012)	-0.23	1	0.82
Error			25	
<b>(e) Relative nestling body mass from field data (<math>\lambda = 0.819</math>)</b>				
Nest type	0.055 (0.023)	2.44	1	0.022
log mass	-0.234 (0.044)	-5.29	1	<0.001
Nestling period	0.013 (0.004)	3.75	1	0.001
Site (Venezuela)	-0.035 (0.026)	-1.32	1	0.19
Error			24	

not consistently higher in tropical and southern hemisphere regions than north temperate regions, even among open nests (Fig. 3). This result was true for nests from lowland sites in the literature (Fig. 3b) as well as our mid-elevation sites (Fig. 3a). Nest predation can change among elevations in the tropics (Skutch 1985; Boyle 2008; Jankowski *et al.* 2013), which reinforces the fact that nest predation does not change predictably with latitude. Thus, the greater incidence of enclosed nesting in tropical and southern regions (i.e. Fig. 2) does not seem to reflect a response to geographic patterns of nest predation.

The fact that predation rates did not generally differ between nest types among coexisting species at tropical and north temperate sites (Fig. 3a) as well as regional



**Fig. 5.** Relative sizes (% of adult size) of (a) wings and (b) nestling mass at fledging (nest-departure) in the two tropical sites between species in open vs. enclosed nests relative to the age at fledging. The nestling mass plot was also corrected for adult mass (Table 2e). Solid symbols reflect enclosed nests, and open symbols reflect open nests.

data from the literature (Fig. 3b) suggests a weak role of nest predation. The lack of differences among coexisting species is a particularly powerful result because coexisting species are exposed to the same community of predators. Of course, enclosed nests experience lower predation in some cases, as seen among the coexisting species at our Argentina and South Africa sites (Fig. 3a), suggesting that enclosed nesting can provide predation benefits in some situations. Yet, even in the latter case, general predation benefits of enclosed nests are not always clear. For example, the general difference in nest predation rates between open and enclosed nesting species at our South Africa site (Fig. 3a) was strongly influenced by *Anthoscopus minutus* which experiences quite low predation ( $0.009 \pm 0.002\%$  per day) due to an unusually strong enclosed nest (Lloyd *et al.* 2017). In contrast, three of the enclosed nesting species at this site (*Apalis thoracica*, *Prinia maculosa* and *Nectarinia chalybea*) had nest predation rates ( $0.104 \pm 0.006$ ,  $0.101 \pm 0.003$  and  $0.099 \pm 0.005$ ) that were as high or higher than the average rate ( $0.097 \pm 0.005$ ) for open-nesting species at this site (Fig. 3a). Such results are not unusual as nest

predation commonly can be quite high in enclosed nesting species (e.g. Magrath & Yezerinac 1997; Van Bael & Pruett-Jones 2000; Hatchwell *et al.* 2013), again emphasizing that enclosed nests often do not provide nest predation benefits. Ultimately, the broad absence of differences in nest predation rates between nest types (Fig. 3) demonstrates that enclosed nests do not provide consistent nest predation benefits, counter to long-standing perspectives (Nice 1957; Snow 1978; Fowler 1979; Oniki 1979, 1985; Gross & MacMillan 1981; Magnusson & Hero 1991; Spencer & Thompson 2003; Hall *et al.* 2015).

The importance of thermal benefits from nest sites has been documented in ectotherms (e.g. Shine, Elphick & Harlow 1997b; Shine *et al.* 1997a; Madsen & Shine 1999; Angilletta, Sears & Pringle 2009; Booth, Feeney & Shibata 2013), and also has been suggested for mammals (e.g. Dawson & Lang 1973; Redman, Selman & Speakman 1999; Mehlman & Doran 2002). However, such benefits have been documented based more on location than on nest structure. In a few avian species, such as the megapodes, thermal benefits of nest sites have been demonstrated (Göth & Booth 2005). However, a more consistent role of thermal benefits over nest predation benefits for enclosed nests of songbirds is suggested by the broad differences in body size across all regions. Species using enclosed nests are consistently smaller than species using open nests (Fig. 4a,b). Large species often experience higher predation than small species (Table 2b, Biancucci & Martin 2010; Remeš, Matysioková & Cockburn 2012), which yields the expectation that larger species should use enclosed nests if such nests were being used for predation risk benefits. Instead, the greater use of enclosed nests by smaller species (Fig. 4a,b) clearly fits better with the thermal benefits hypothesis given that smaller species are subject to greater heat loss (Calder 1984).

The potential importance of thermal benefits of enclosed nests is further suggested by the fact that species using enclosed nests spend more time off the nest (Fig. 4c). Of course, increased time on the nest among open-nesters may alternatively reflect a need to cover eggs to reduce their conspicuousness. Yet, eggs in open nests are more cryptically coloured than in enclosed nests and predators may search more for nests and incubating adults than for eggs (Weidinger 2001). Thus, eggs may not be more conspicuous compared with a bird sitting on them. Moreover, reduced nest attentiveness (time on the nest) has been linked to greater insulation properties of nests (Deeming & Gray 2016). Even more pertinently, egg cooling rates were slowed in enclosed compared with open cup nests in the lab (Lamprecht & Schmolz 2004) which could facilitate the reduced time and parental effort in warming eggs in enclosed nests (Fig. 4c). Consequently, the higher frequency of enclosed nesting species in tropical and southern hemisphere latitudes (Fig. 2) may reflect a functional response to their reduced attentiveness in these regions compared with north temperate birds, even

when comparing the same nest type (Table 2c; Martin *et al.* 2007; Chalfoun & Martin 2007; Martin & Schwabl 2008).

Finally, evidence of thermal benefits that can enhance fitness is indicated by larger mass and wings at fledging in enclosed nests while controlling for fledging age (Fig. 5). Both body mass and wing size have been associated with substantial improvements in offspring survival after leaving the nest (Martin 2014; Lloyd & Martin 2016). Similarly, thermally beneficial nest locations can enhance offspring size and locomotor traits in other taxa that also increase subsequent survival (Shine, Elphick & Harlow 1997b; Shine *et al.* 1997a; Booth, Feeney & Shibata 2013). Thus, thermal benefits of enclosed nests (i.e. Buttemer *et al.* 1987) may be much more consistent than the long-assumed predation benefits. Thermal benefits of enclosed nests may be particularly beneficial in tropical and southern hemisphere latitudes where life histories are slower (Skutch 1949, 1985; Martin 1996; Martin *et al.* 2000) and include parents spending less time on the nest, and selection favours larger body and wing size of offspring at fledging (Martin *et al.* 2007, 2015a; Martin 2014, 2015a).

Ultimately, thermal benefits of enclosed nests may trade-off with the length of time and energy it takes to construct such nests, although comparative data on nest construction times are not available. On the other hand, nest mass may provide an alternative measure of time and energy expenditure (e.g. Mainwaring & Hartley 2008) and such data may be more readily available. If enclosed nests take substantially more time and energy to construct than open nests, such effects may explain why they are less common in north temperate regions where time may be more constrained due to shorter breeding seasons. Yet, such possibilities need study. Moreover, the possible survival and energetic consequences of nest structure deserve more explicit study in harsh (both cold, rainy and hot, sunny) environments where thermal benefits of enclosed vs. open nests may be particularly important.

### Author contributions

T.E.M. conceived the study, designed the field work, collected field data, performed all statistical analyses and wrote the initial draft. All co-authors collected field data and contributed to manuscript writing and revisions.

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## Data accessibility

Data for mass and wing length at fledging are available in Dryad: <https://doi.org/10.5061/dryad.2m15n>; data files: Life\_history\_data (Martin 2015b). Data for nest predation, adult mass and nest attentiveness during incubation for species on the field sites are available in Dryad: <https://doi.org/10.5061/dryad.km646> (Martin *et al.* 2015b), and <https://doi.org/10.5061/dryad.ks62j> (Martin *et al.* 2015c). Data from the literature are detailed in Methods.

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## Supporting Information

Details of electronic Supporting Information are provided below.

**Fig. S1.** Phylogenetic relationships of species on the field sites.

**Fig. S2.** Phylogenetic relationships of species from the literature.