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CHILEAN SWALLOWS (*TACHYCINETA MEYENI*) ADJUST THE NUMBER OF FEATHERS ADDED TO THE NEST WITH TIME OF BREEDING

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ABSTRACT.—*Tachycineta* swallows nest in secondary cavities and build nests made of a mat of dry grasses with a nest cup lined with feathers. The insulative quality of feathers may prevent hypothermia of the chicks and increase chick growth, but also may raise the risk of nestling hyperthermia if ambient temperature is high. The number of feathers added to the nest should vary throughout the breeding season according to ambient temperature. We describe nest structure and timing of nest building of Chilean Swallows (*Tachycineta meyeni*) nesting in Tierra del Fuego, Argentina. We analyzed the association between number of feathers in the nest and (1) daily ambient temperature during the period swallows add feathers to the nest, and (2) hatching success of eggs and survival and growth of the chicks. There was a negative association between number of feathers added to the nest and average daily ambient temperature during the nesting cycle. Hatching success was not associated with number of feathers at start of laying or at the end of incubation. There was no association between number of feathers and chick survival or between number of feathers and average weight of the chicks when they were 12 and 15 days of age. Chilean Swallows make temporal adjustments to the number of feathers added to the nest. We suggest these adjustments may help maintain reproductive success throughout the breeding season. *Received 28 January 2009. Accepted 3 May 2009.*

An important characteristic of nests, which generally has an effect on reproductive success, is amount of insulating material placed within them. Many bird species use feathers, hair or other materials with good insulating properties as nest lining material. Differences in type and amount of insulation may affect timing of breeding (O'Connor 1978), incubation rhythms (White and Kinney 1974, Møller 1991), incubation energetics (Skowron and Kern 1980), incubation time (Lombardo et al. 1995), nestling growth (Møller 1991, Winkler 1993, Lombardo et al. 1995), brood thermoenergetics (Mertens 1977), and risk of nestling hyperthermia (Lombardo 1994).

Tachycineta swallows nest in secondary cavities and build nests of a mat of dry grasses with a nest cup lined with feathers (Dyrcz 1984, Brown et al. 1992, Winkler 1993, Allen 1996, Bulit and Massoni 2004, Townsend et al. 2008). The effect of nest feathers on reproductive success has been experimentally examined in Tree Swallows (*T. bicolor*), where removal of feathers reduces chick growth, possibly as a result of chicks' hypothermia before they become fully homoeothermic (Winkler 1993, Lombardo et al. 1995). Similarly, Dawson et al. (2005) experimentally demonstrated the importance of ambient temperature during this period. These authors showed that raising the nest temperature by 5° C when nestlings of Tree Swallows are 4 days of age enhances nestling survival, and results in heavier nestlings with longer primary feathers at 16 days of age compared to nestlings in control nests.

The benefit of adding feathers to the nest may vary temporally throughout the breeding season. Well-insulated nests of Tree Swallows may be advantageous early in the season, when ambient temperatures are low and eggs and chicks are vulnerable to hypothermia, but may become disadvantageous late in the season, when higher ambient temperatures increase risk of nestling hyperthermia (Lombardo 1994).

Within *Tachycineta* swallows, the Chilean Swallow (*T. meyeni*) has the southernmost breeding range. This species experiences low ambient temperatures during the temperate breeding season and the effect of nest feathers on reproductive success should be important. We describe the nest structure and timing of nest building of Chilean Swallows nesting in nest boxes in Tierra del Fuego, Argentina, the southern limit of the species' range. To date, the reproductive biology of this species has not been studied. Our objectives were to: (1) analyze the association between number of feathers added to the nest and ambient temperature throughout the breeding season, and (2) analyze if the number of feathers

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is associated with hatching success of eggs and survival and growth of chicks. We expected the number of feathers to be negatively correlated with temperature without any detrimental effect on reproductive success if Chilean Swallows adjust the number of feathers in the nest according to ambient temperature.

METHODS

Study Site.—The study was conducted at two sites near the city of Ushuaia, Tierra del Fuego, Argentina. Site A (54° 44′ S, 61° 13′ W) was 11 km northeast of Ushuaia, while site B (54° 53′ S, 67° 20′ W) was at Harberton Ranch, 85 km east of Ushuaia. The study area is part of the biogeographic region of the Andean-Patagonic Woodland. Monthly average ambient temperature during the breeding season ranges between 5.9° C in October and 9.6° C in January, while monthly average precipitation ranges from 33.1 mm in October and 54.1 mm in December.

Study Species.—Chilean Swallows are austral migrants that remain in our study area from mid October to mid March. Egg laying occurs from late October to early January and the last chicks fledge in early February. This species lays from two to five eggs (modal clutch size = 4 eggs), which are incubated for 17.5 days on average. Chicks fledge at 21–29 days of age (modal time: 26.5 days) with a weight of 20–21 g. Adult weight is 17 g for males and 19 g for females (M. Liljesthröm, unpubl. data).

Data Collection.—The study was conducted during the breeding seasons of 2006–2007 and 2007–2008. We placed 88 and 62 nest boxes at sites A and B, respectively to facilitate data collection. Nest boxes were in trees or on fence poles at a height of 1.5 m and separated by at least 20 m. The external dimensions of the boxes were 25.4 × 16.5 × 17.8 cm (height, width, depth), while the internal dimensions were 23.8 × 12.7 × 12.7 cm. Boxes had a 3.5 cm diameter entrance hole and a lateral opening that allowed us to monitor progress of the nest.

We recorded 71 breeding attempts (i.e., nests in which eggs were laid), 30 in 2006–2007, and 41 in 2007–2008. We analyzed data from 63 breeding attempts for which we could measure all variables (26 in 2006–2007 and 37 in 2007–2008).

We started monitoring nest boxes in mid October. Nest boxes were visited every other day until start of nest building (the day the first nesting material was observed inside the nest box). We checked nest boxes daily during nest building, and recorded the height of the nest (from the floor of the nest box to the top of the nest border), and the number of feathers inside and outside the nest cup. We counted the number of feathers until start of laying and then after the last chick fledged or the nest failed. We estimated the number of feathers added during laying and incubation (we did not observe adding of feathers during the nestling period) as the number of feathers after the chicks fledged minus the number of feathers when laying started. We calculated the total number of feathers in the nest as the sum of the number of feathers inside and outside the nest cup.

We checked nests daily during laying and every other day during incubation, except near the expected hatching date, when we visited nests daily. We checked nests every second or third day during the nestling period until chicks were 15 days of age (to avoid premature fledgling induced by the investigator). All chicks were weighed to the nearest 0.1 g with a Pesola spring balance during these visits. We recorded clutch size, number of eggs before hatching, number of chicks hatched, number of chicks fledged, and if the nest was successful (fledged at least 1 chick) or failed. We estimated hatching success as the number of hatched chicks divided by the number of eggs at the time of hatching, and chick survival as the number of fledged chicks divided by the number of chicks that hatched. We used brood mean weights for analysis of the association between number of feathers and weight of the chicks. We considered 1 October as the first day of the breeding season and all dates are reported relative to that day.

Data for ambient temperature were provided by the Environmental and Geographic Information Service of the Austral Center of Scientific Research (Servicio de Información Ambiental y Geográfica, Centro Austral de Investigaciones Científicas, CADIC-CONICET) in Ushuaia. We used data from two weather stations; one near site A, and the other near site B. These stations recorded ambient temperatures every hour. We calculated mean daily temperatures for our analyses and then, for each nest, the average temperatures during nest building and during laying and incubation.

Statistical Analysis.—We used nonparametric statistics for analyses due to lack of normality of the data and small sample sizes of the groups. We

TABLE 1. Number of feathers added inside and outside the nest cup from start of nest building until the first egg, and during laying and incubation. Values indicate mean ± SE. Range is indicated between parentheses. Number of nests analyzed was 63 for nest building and 43 for laying and incubation.

Number of feathers added to nest	Inside nest cup	Outside nest cup	Totals
Nest building	18.4 ± 1.1 (5–45)	10.3 ± 0.9 (0–30)	28.7 ± 1.9 (6–75)
Laying and incubation	114.4 ± 6.2 (20–202)	32 ± 2.5 (27–93)	146.4 ± 6.8 (33–261)
Entire nesting cycle	133 ± 6.5 (35–237)	42.3 ± 2.7 (15–108)	175.3 ± 7.4 (53–290)

did not find differences between years (Mann Whitney *U* test, $z = 0.20$, $P = 0.84$) or sites (Mann Whitney *U* test, $z = -1.0$, $P = 0.30$) in number of feathers added to the nest and pooled the data. Statistical analyses were performed using StatView Version 5.0 statistical software (SAS Institute 1998). All *P*-values are two-tailed with alpha (*P*) set at 0.05. Data are presented as means ± standard errors.

RESULTS

Nest Structure and Timing of Nest Building.—Chilean Swallow nests consist of a base of dry grasses with woven feathers and a nest cup lined with feathers. Nest building occurred from late October to early December ($n = 11$ nests in October, $n = 44$ nests in November, $n = 8$ nests in December). Nest height was 5.2 ± 0.1 cm (range: 3–7 cm, $n = 63$ nests). The addition of feathers to the nest in all nest cups began before egg laying. Feathers used as lining were mostly from Upland Goose (*Chloephaga picta*). The number of days elapsed between start of nest building and the first egg was 19.1 ± 1.1 (median: 18 days, range: 5–39 days, $n = 63$ nests). Construction of the nest cup started 5.1 ± 0.8 days (median: 2 days, range: 0–27 days, $n = 63$ nests) after start of nest building.

The number of feathers inside and outside the nest cup at time of laying was 18.4 ± 1.1 and 10 ± 0.9, respectively (Table 1). These values represented only 16% of the total number of feathers. The remaining 84% were added during the incubation period (swallows were not observed adding feathers to nests during the nestling period). The final number of feathers inside and outside the nest cup was 133 ± 6.5 and 42.3 ± 2.7, respectively (Table 1).

Number of Feathers, Time of Breeding, and Ambient Temperature.—The total number of feathers added before egg laying decreased with date at which nest building started (Spearman rank correlation: $\rho = -0.33$, $z = -2.58$, $P = 0.01$, $n = 63$, Fig. 1A). Total time spent building nests decreased with date of nest building (Spearman rank correlation: $\rho = -0.49$, $z = -3.82$, $P = 0.0001$, $n = 63$). However, the number of feathers added per day before egg laying did not vary with date of nest building (Spearman rank correlation $\rho = 0.14$, $z = 1.09$, $P = 0.28$, $n = 63$). The number of feathers added during laying and incubation decreased with date

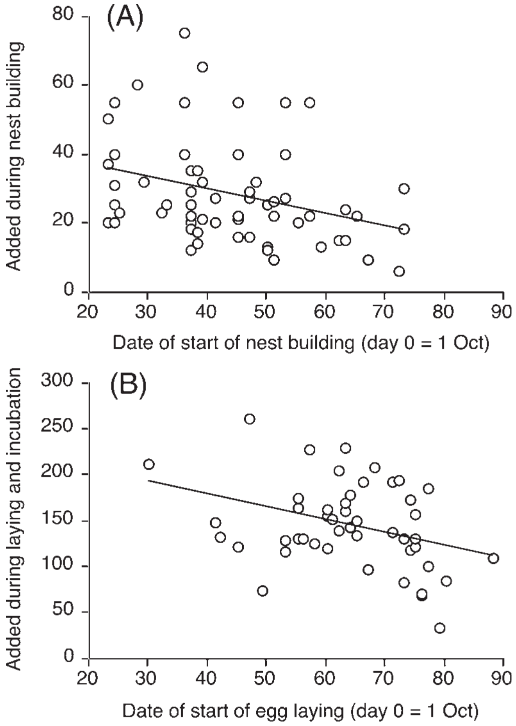

FIG. 1. (A) Number of feathers added to the nest from start of nest building until the first egg, and (B) number of feathers added to the nest during laying and incubation. The X axis (A) indicates the day the first nest material was added to the nest box while (B) indicates the day the first egg was laid. Number of nests in (A) and (B) are 63 and 48, respectively.

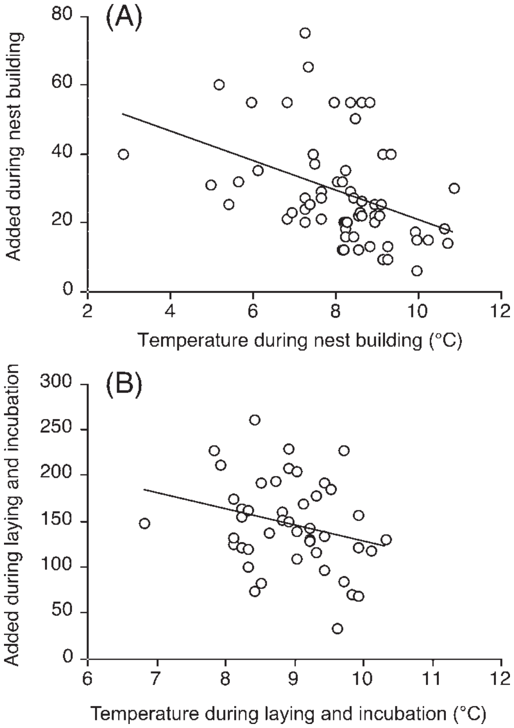

FIG. 2. (A) Number of feathers added to the nest from start of nest building until the first egg, and (B) number of feathers added to the nest during laying and incubation. The X axis (A) indicates the daily average temperature during nest building while (B) indicates the daily average temperature during laying and incubation. Number of nests in (A) and (B) are 63 and 48, respectively.

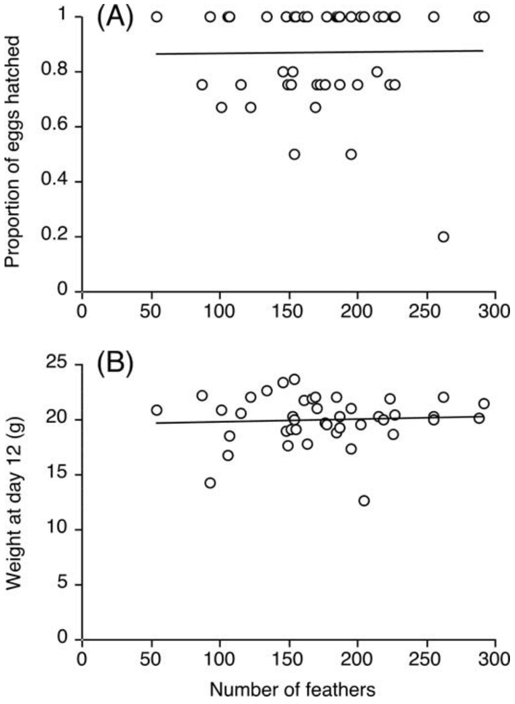

FIG. 3. (A) Proportion of eggs present in the nest at end of incubation period that hatched and (B) weight of chicks (brood averages) at day 12 of age (day 0 of age = day chicks hatched) in nests with different number of feathers (i.e., total number of feathers added during nest building, laying and incubation). Number of nests in (A) and (B) are 51 and 46, respectively.

of egg laying (Spearman rank correlation $\rho = -0.3$, $z = -2.06$, $P = 0.04$, $n = 48$, Fig. 1B).

There was a significant negative correlation between number of feathers added to the nest during nest building and mean daily ambient temperature during this period (Spearman rank correlation $\rho = -0.46$, $z = -3.65$, $P = 0.0003$, $n = 63$, Fig. 2A). There was a non-significant negative association between number of feathers added to the nest during laying and incubation, and mean daily ambient temperature during this period (Spearman rank correlation $\rho = -0.28$, $z = -1.9$, $P = 0.06$, $n = 48$, Fig. 2B).

Number of Feathers and Reproductive Success.—We did not detect an association between number of feathers in the nest and different components of the reproductive success of the breeding pair. Twelve of 63 nests were deserted during incubation and five of 51 nests were deserted during the nestling period. There were no differences in total number of feathers between nests that fledged chicks and those that failed during the nestling stage (Mann Whitney U test, $z = -1.13$, $P = 0.26$). Hatching success was 0.86 ± 0.03 ($n = 51$) and was not associated with total number of feathers either at the start of laying (Spearman rank correlation $\rho = 0.02$, $z = 0.17$, $P = 0.87$, $n = 51$), or at the end of the incubation period (Spearman rank correlation $\rho = 0.13$, $z = 0.91$, $P = 0.36$, $n = 46$, Fig. 3A). Chick survival was 0.98 ± 0.01 and was not associated with total number of feathers (Spearman rank correlation $\rho = 0.02$, $z = 0.15$, $P = 0.88$, $n = 45$, Fig. 3B). There was no association between total number of feathers and weight of chicks when they were 12 days of age (20.0 ± 0.34 g, Spearman rank correlation $\rho = -0.03$, $z = -0.17$, $P = 0.87$, $n = 42$, Fig. 3B) or when they were 15 days of age (21.2 ± 0.36 g, Spearman rank correlation $\rho = -0.15$, $z = -0.86$, $P = 0.39$, $n = 34$).

DISCUSSION

Nest Structure and Timing of Nest Building.—The general structure of Chilean Swallow nests was similar to that described for other species of the genus (*T. albilinea*: Dyrcz 1984, *T. thalassina*: Brown et al. 1992, *T. bicolor*: Winkler 1993, *T. cyaneoviridis*: Allen 1996, *T. leucorrhoa*: Bulit and Massoni 2004, and *T. euchrysea*: Townsend et al. 2008). Some of these species use other materials in addition to feathers for nest lining (i.e., cow and horse hair, lamb's wool, soft plant material), but they all build nests that consist of a base of dry grasses or pine needles and a cup lined with feathers. Nest building time for Chilean Swallows was similar to that of White-rumped Swallows (19.1 ± 1.1 versus 15.8 ± 1.6 days, Bulit and Massoni 2004) and both species, as well as Tree Swallows (Winkler 1993), began adding feathers to the nest cup before egg laying.

Number of Feathers, Time of Breeding and Ambient Temperature.—Our results support the prediction that Chilean Swallows add fewer feathers to their nests with time of breeding, likely taking into account ambient temperature during the period when they add the feathers. This negative association could also be the result of competition between breeding pairs for a limited number of feathers (i.e., as more pairs start building nests, there are less feathers available). However, this is an unlikely explanation as we observed the daily number of feathers added to the nest did not vary with time of breeding, which indicates that breeding pairs were able to obtain feathers at the same rate throughout the breeding season.

Chilean Swallows that started nest building late in the season spent less time building the nest and began laying with fewer feathers than those which started nest building early in the season. This pattern was similar to that reported for White-rumped Swallows (Bulit and Massoni 2004). However, White-rumped Swallows increase the total number of feathers added to the nest with time of breeding, suggesting that in this species other factors besides ambient temperature may influence the number of feathers added to the nest.

Nest linings are usually thicker in cold climates (Collias and Collias 1984), and variations in insulative qualities of nests among different populations or subspecies are correlated with local temperatures (Schaefer 1980). We expected those species within *Tachycineta* nesting in colder areas would add more feathers to their nest than those nesting in warmer areas. Accordingly, the number of feathers at the start of laying was almost six times larger for Chilean Swallows than for Tree Swallows (Winkler 1993). Mean daily ambient temperature during the breeding season of Tree Swallows in Winkler's study area (Ithaca, NY, USA; 42° 30′ N, 76° 27′ W) is ~17° C (NRCC 2000) whereas temperature during the breeding season of Chilean Swallows in our study area is ~9° C. However, the number of feathers in nests of Chilean Swallows at start of laying was similar to that of White-Rumped Swallows, which experience mean daily ambient temperatures during the breeding season similar to those of Tree Swallows (18° C, SMN 2000). A similar pattern was observed when we compared the total number of feathers at the end of the breeding attempt among these three species. These results indicate the insulative quality of swallow nests could depend not only on the number of feathers, but also on their size, the tightness with which the nest material is woven, the thickness of the nest wall, or other structural characteristics of the nest. Studies measuring variation in the insulative qualities of nests under controlled laboratory conditions, or quantifying the insulation of the nest in physical terms may provide a better understanding of the interspecific variation in feather numbers of *Tachycineta* swallows.

Variation in the number of feathers may also reflect age-related differences between females. Subadult female Tree Swallows build nests with fewer feathers than adult females (Lombardo 1994). However, because subadult females began clutches later than adults (Lombardo 1994), it is not clear if these differences are related to age of the female or time of breeding. Nest feathers may also serve as a barrier between nestlings and nest ectoparasites (Winkler 1993, but see Lombardo et al. 1995), and variation in number of feathers between species or populations may also reflect differences in nest ectoparasites. Comparative studies of *Tachycineta* species nesting under different ambient temperatures that quantify nest ectoparasites and age of females should provide a more complete understanding of the function of feather lining and possible causes of the temporal variation in number of feathers.

Number of Feathers and Reproductive Success.—Nestlings of altricial birds have a trade-off between devoting energy to growth or to thermoregulation, and it is likely the thermal environment of the nest influences this trade-off (Dawson et al. 2005). Changes in the environmental conditions for Tree Swallows explain a significant amount of the variation in nestling growth (McCarty and Winkler 1999) and nestlings in experimentally heated nests have enhanced survival, are heavier, and have longer ninth primary feathers (Dawson et al. 2005). Experimental removal of feathers reduces growth and survival of nestlings (Winkler 1993, Lombardo 1994, Lombardo et al. 1995).

Our results support the hypothesis that Chilean Swallows reduce the number of feathers they add to the nest as ambient temperature increases without any noticeable effect on hatching success or growth and chick survival. This suggests these adjustments may help maintain reproductive success throughout the breeding season avoiding risks of hypothermia or hyperthermia. However, we cannot rule out indirect effects of ambient temperature on reproductive success through its influence on food availability (McCarty and Winkler 1999). Additional experiments involving manipulation of nest insulation and nest microclimate are needed to separate direct and indirect effects of ambient temperature and the insulating effect of feathers on reproductive success of Chilean Swallows.

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