REPRODUCTIVE BIOLOGY OF A NARROWLY ENDEMIC *TACHYCINETA* SWALLOW IN DRY, SEASONAL FOREST IN COASTAL PERU

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Resumen. – **Biología reproductiva de una golondrina *Tachycineta* estrictamente endémica en bosque seco y estacional en la costa de Perú. –** El estado reciente de la especie golondrina de Tumbes (*Tachycineta stolzmanni*) enfatizó nuestra falta de conocimiento básico sobre la historia de vida de dicha especie. Encontrándose sólo en los amenazados bosques tropicales estacionales secos de la región Tumbesina, *T. stolzmanni* puede estar en riesgo. Nosotros estudiamos las aves en estado reproductivo en el noroeste de Perú utilizando cajas nido, lo cual produjo un total de 37 intentos de anidación durante una temporada particularmente seca en 2010–2011. El hábitat cálido y seco plantea desafíos únicos para la fauna que lo habita, este trabajo permitió conocer más sobre la biología de las aves tropicales de ambientes áridos y facilitó el desarrollo de ecología comparativa del género *Tachycineta*. En comparación con otros miembros del género, *T. stolzmanni* mostró un pequeño tamaño de la nidada, un volumen reducido del huevo, períodos largos de incubación y de los polluelos, y una tasa baja de crecimiento del polluelo. Los adultos son más pequeños que sus congéneres y algunos individuos exhiben una superposición en la reproducción y muda. Se argumenta que debido a su área de distribución restringida y preferencia por un hábitat específico, *T. stolzmanni* puede ser menos abundante de lo que se estima en la actualidad por lo que se indica la necesidad de establecer una estimación del tamaño de la población global a la luz de la rápida degradación del hábitat y el cambio climático.

Abstract. – The recent species status of the Tumbes Swallow (*Tachycineta stolzmanni*) emphasized our lack of even basic life history understanding for this species. Found only in the threatened seasonally dry tropical forests of the Tumbesian region, *T. stolzmanni* may be at risk itself. We studied breeding birds in northwestern Peru using nest boxes, which supported 37 total nesting attempts during the particularly arid season of 2010–2011. The hot, dry habitat poses unique challenges for the fauna that inhabit it, allowing for insights into the biology of tropical arid environment birds and developments within the realm of *Tachycineta* comparative ecology. Compared with other members in the genus, *T. stolzmanni* exhibited a smaller clutch size, a reduced egg volume, longer incubation and nestling periods, and a low nestling growth rate. Adults were smaller than their congeners and some individuals exhibited molt-breeding overlap. We argue that due to its restricted range and specific habitat preference, *T. stolzmanni* may be less abundant than is presently recognized and cite the need for establishing an estimate of the global population size in light of rapid habitat degradation and climate change. *Accepted 26 March 2012.*

INTRODUCTION

Avian life histories of tropical species are poorly understood in comparison to those of their temperate counterparts (Martin 1996). This discrepancy is depicted to a greater extent with species from arid regions in contrast to those of the humid tropics (Rodríguez-Ferraro & Blake 2008). Species within the *Tachycineta* genus are increasingly well-studied (Quill 2008), allowing for valuable developments in their comparative ecology. Nonetheless, very little is known regarding the natural history of the Tumbes Swallow (*Tachycineta stolzmanni*). Restricted to the arid regions of northwestern Peru and extreme southwestern Ecuador, *T. stolzmanni* was considered a disjunct subspecies of the Mangrove Swallow (*Tachycineta albilinea*) of Central America until recently (Robbins *et al.* 1997, Remsen *et al.* 2005). Whittingham *et al.* (2002) resolved the phylogeny of the genus, placing *T. stolzmanni* as sister to the *albilinea/ albiventer* clade.

First described in 1880 from specimens collected by M. Stolzmann in 1878 (then *Hirundo leucopygia*), *T. stolzmanni* was not reencountered scientifically until the mid-/to late 1970s (Robbins *et al.* 1997) by expeditions led by the Louisiana State University Museum of Zoology to the departments of Tumbes, Piura, and Lambayeque, Peru (Schulenberg & Parker 1981). The work of Robbins *et al.* (1997) extended the recognized distribution of the species just over the Ecuadorian border. Presently, *T. stolzmanni* has been reported as localized populations within that restricted range (eBird 2011). IUCN currently lists it as a species of least concern; however, the global population has never been quantified (BirdLife International 2011b) and the seasonally dry forests that it inhabits have long been considered a vulnerable ecosystem

(Janzen 1988). Until now, existing natural history information was procured from a single, briefly monitored nesting event (Robbins *et al.* 1997). Here we present the results from the first systematic study of nesting *T. stolzmanni* breeding in northern Peru. In addition, we also examine the role extreme aridity has on its life history traits in order to advance our knowledge of the comparative life-histories within *Tachycineta* and allow comparisons with other arid-environment birds.

METHODS

We studied a breeding population of *T. stolzmanni* at Santuario Histórico Bosque de Pomac (SHBP) in the Lambayeque Province of Peru (6°29'S, 79°46'W; 100–200 m a.s.l.) using nest boxes erected in 2008 as part of the Golondrinas de Las Americas network (http:/ /golondrinas.cornell.edu). We attached nest boxes (measuring 12.7 x 12.7 x 21.6 cm on the inside with a 3.8 cm diameter entrance hole) to tree trunks between 1.5 and 2 m above the ground. Field crews arrived 4 December 2010 and monitored all subsequent nesting activity until 10 May 2011 at the 49 boxes present in that season.

SHBP was established in 2001 as a state protected area (5887.4 ha; SERNANP 2011) and is listed as an Important Bird Area (Birdlife International 2011a). SHBP is part of the dry equatorial forest eco-region and is comprised of seasonally dry tropical forest (SDTFs; Brack 1986). SDTFs are loosely defined as tropical forests characterized by high seasonality, with 4 to 6 dry months (rainfall less than 100 mm per month) per year (Mooney *et al.* 1995). In fact, the average annual precipitation within SHBP is only 107.8 mm, concentrated in the months of March and April, making it one of the most arid regions on earth (SERNANP 2011). The

climate is hot and sunny, with temperatures ranging between 11.5–34.4°C throughout the year (SERNANP 2011). The Holdridge life zone is thus classified as a tropical super-arid desert (Holdridge 1967, ONERN 1976). At our study site, located in the northwest region of the sanctuary, *Prosopis pallida* (Fabaceae: Mimosoideae) and *Capparis scabrida* (Capparaceae) comprise the dominant species in the vegetation. Local inhabitants utilize the park to graze their horses, goats, and cows, severely impeding regeneration of undergrowth and therefore the availability of future nesting trees.

Nest boxes were emptied when the crew arrived at the start of the season to remove material from previous seasons and that of other species. We subsequently monitored nest boxes on a daily basis during nest-building, egg-laying, and incubation to determine date of clutch initiation, clutch size, and exact day of hatching. Monitoring continued through to fledging, though we visited nests less frequently during the nestling period to minimize disturbance. We considered a nesting attempt established when the first egg was found. We numbered nesting attempts sequentially for a given box (or female when an individual was known to have relocated), irrespective of the success of each attempt. We considered clutch completion the date that the last egg was laid. We determined incubation period as the duration from clutch completion to first hatch; it therefore does not necessarily reflect the true length of incubation if onset did not occur precisely on the day of clutch completion. Egg survival is defined as the proportion of total eggs that persisted to the end of incubation.

We numbered eggs sequentially; if the order could not be deduced because days passed between nest checks, we labeled them A and B. We measured eggs the day after they were laid, except in the case of A/B eggs, which we measured on the day they were found. We measured egg length (L) and width (W) using dial calipers (± 0.1 mm). We calculated egg volume (V) as $V = 0.077\, L + 0.007\, W^2 - 1.020$ (Winkler 1991). We weighed eggs using a digital scale (+/- 0.01 g). Even though eggs within a clutch are not independent, clutch sizes were sufficiently small that we chose not to use average measures for each clutch. Hatching success is defined as the proportion of eggs present at the end of incubation that then hatched.

Using indelible marker, we uniquely marked nestlings to track individual growth patterns, commencing on day 3 (hatch = day 0). We measured nestling mass on days 3, 6, 9, and 12 using a 10 g Pesola spring scale (+/- 0.25 g). We measured all members in the brood on the above schedule using the first day of hatch in the brood. On days 12 to 15, we gave nestlings numbered aluminum bands from National Band & Tag (size 1242F0). After day 15, we checked nests for fledging non-invasively (to avoid premature fledging) every two to five days. We considered nestling period for a given brood as the time elapsed from first hatch to last fledge.

We captured adults in the first week after the chicks hatched, at which time we determined their sex (based on presence or absence of brood patch), gave them a numbered aluminum band and measured their body mass (± 0.25 g), using a 30 g Pesola spring scale; flattened wing length, using a ruler with a wing stop (± 0.5 mm); and head-bill length as the maximal distance between the back of the head and the bill tip, using dial or digital calipers (± 0.1 mm). If we captured individuals more than once during the season, we only included initial measurements in analyses. Because adults of both sexes are identical in plumage, we marked rump feathers and undertail coverts with indelible markers to differentiate between the two. Whenever possible, food boluses were collected from the

mouths of adults or nestlings and examined to determine diet contents.

We conducted observations of parental provisioning behavior from a distance of 50 m for 60 consecutive minutes between the hours of 06:30 and 10:00 h on nestling days 7 and 10. We recorded number and duration of nest visits for each individual within the pair to determine feeding rates. For one nest, we instead performed feeding observations on days 8 and 11; we pooled these with day 7 and 10 observations, respectively.

At the conclusion of the season we cleaned all nest boxes, excepting three nests with continued activity. We photographed nests then dissected the contents, counting any feathers with length greater than 1 cm and identifying other materials present in the nest structure.

Statistical methods. We report means with standard errors. We performed Welch's *t*-tests to determine the effect of nesting attempt and lay order on clutch size and egg measures (width, length and mass). Eggs missing any of the three measures were excluded from the egg measurement analysis; eggs whose lay order could not be determined (those labeled A and B) were excluded from the lay order analysis only. Welch's *t*-tests were also performed to determine the effect of sex on adult morphology, as well as the effect of both age of chicks and adult sex on feeding rates.

We calculated growth curves for individual nestling measurements of mass using an iterative, non-linear mixed effects procedure (nlme) with the software R (ver. 2.13.0). This function approximates the likelihood function of the model with the methods described by Lindstrom and Bates (1990) but allows for nested random effects and is commonly applied to repeated measures data (Pinheiro & Bates 2000). For Tree Swallows, logistic models are most appropriate for growth in

nestling mass (Zach & Mayoh 1982). We therefore employed the logistic formula $M_x = M_\infty/(1 + (M_\infty - M_i)/M_i) * e^{(-K*x)}$ where M_x is the mass at age x, M_8 is the asymptotic measure, M_i is the initial mass, and K is the growth constant (Ricklefs 1983). The model only included nests in which all nestlings in the brood fledged. We began by including nest and chick as random effects for all model parameters and then examined the model fits to determine which terms could be excluded. We simplified the model through hierarchical model selection, opting to eliminate a term only when the p-value of the proportional log-likelihood test was greater than 0.05. We followed an identical procedure for a separate model fixing M_∞ as the average adult mean mass. The fixed M_∞ model was compared to the floating M_∞ model (where M_∞ estimated by model) using Akaike information criterion.

RESULTS

Nesting activity. Upon our arrival on 4 December 2010, nesting activity had commenced, though no clutches had yet been initiated. In the 49 nest boxes, there were 37 clutches before our departure on 10 May 2011. These were composed of 18 first attempts, 15 second attempts, 3 third attempts, and 1 fourth attempt. One nest that contained a single egg was excluded from the analysis because the egg was never incubated and thus may represent an instance of egg-dumping or interrupted-laying. Pairs stayed in the same nest box for successive nesting attempts (n = 12 pairs, excluding three failed attempts for which the pair could not be identified) with the exception of one pair which moved to a nearby box for their second attempt, and then back to the original nest box for their third attempt.

Nest materials. Adults filled nest boxes with 2–15 cm of nesting material before initiating

clutches. The nest volume was largely made up of feathers (mean = 367 ± 23.5 feathers, n = 16 nests) and included a shallow, circular cup. Feathers that could be identified came from Long-Tailed Mockingbird (*Mimus longicaudatus*), West Peruvian Dove (*Zenaida meloda*), Variable Hawk (*Buteo polyosoma*), Pacific Parrotlet (*Forpus coelestis*), Tropical Kingbird (*Tyrannus melancholicus*), Cattle Egret (*Bubulcus ibis*), Pacific Hornero (*Furnarius leucopus cinnamomeus*), Lesser Nighthawk (*Chordeiles acutipennis*), and domestic Muscovy (*Cairina moschata*). Additionally, rump feathers from female *T. stolzmanni* were commonly located in the nest, recognized by our indelible marker. Most of the remaining nesting material was comprised of dried grasses though other materials included dried leaves, bark, fur, plastic bags, black plastic, tissue, nylon string, seed casings, *Capparis* inflorescences, and reptile skin.

Phenology. The first egg was laid on 16 December 2010 (Fig. 1). Median lay date for first nesting attempts was 1 January, whereas it was 17 January for all nesting attempts combined, excluding four nests for which clutch initiation could not be ascertained with sufficient certainty (± 3 days). The last clutch initiation of the season occurred after 23 April, though the exact date cannot be deduced because unused boxes were no longer being checked on a regular basis thus the nest was not encountered until 10 May, at which time incubation was in progress. No first attempts were initiated after 5 February (n = 18). The median clutch completion date was 2 January for first attempts only and 19 January for all attempts, excluding the same four nests. The first hatching event occurred on 4 January. The first chick fledged on 31 January and the last known fledging occurred on 20 April, though it is possible that chicks from three other nests fledged after 10 May, when our monitoring ceased. During the second week

of April, numbers of *T. stolzmanni* present at the site dropped from ∼ 50–60 individuals to less than 10 individuals. We concurrently observed *T. stolzmanni* over adjacent irrigated, agricultural land for the first time that season.

Eggs and incubation. Egg mass and length did not differ among nesting attempts (see Appendix 1), but average egg widths in first clutches were significantly smaller than those of successive clutches. There was no effect of laying order on egg mass, length, or width. Measurements for all eggs were thus combined in the analysis (Table 1).

Mean clutch size was 2.68 ± 0.10 and did not differ significantly between first (n = 18; mean = 2.61 ± 0.14) and second nesting attempts (n = 15; mean = 2.67 ± 0.16), though it did increase significantly for third clutches (n = 3; mean = 3.00 ± 0, t = 2.7, df = 17, P = 0.01). The incubation period was between 15 and 18 days with a mean of 16.11 ± 0.14 days, excluding six nests for which the clutch completion date could not be determined accurately (± 2 days). For the 37 nesting attempts followed to hatch, egg survival was 84.38%. No predation of eggs was recorded; egg loss was chiefly caused by abandonment.

Hatching and fledging success. Hatching success was 92.11 %, excluding three clutches associated with a predation event shortly after hatch before the hatching success of the entire clutch could truly be deduced. In nests persisting until hatching (n = 29 clutches, excluding the three aforementioned clutches), four clutches contained one egg and one clutch contained two eggs that did not hatch. Because we checked nests once per day, we were unable to determine times of hatching at intervals less than 24 h. Often nestlings that were not present at first hatch were present on subsequent nest checks; a hatch period in excess of 24 h was discerned once.
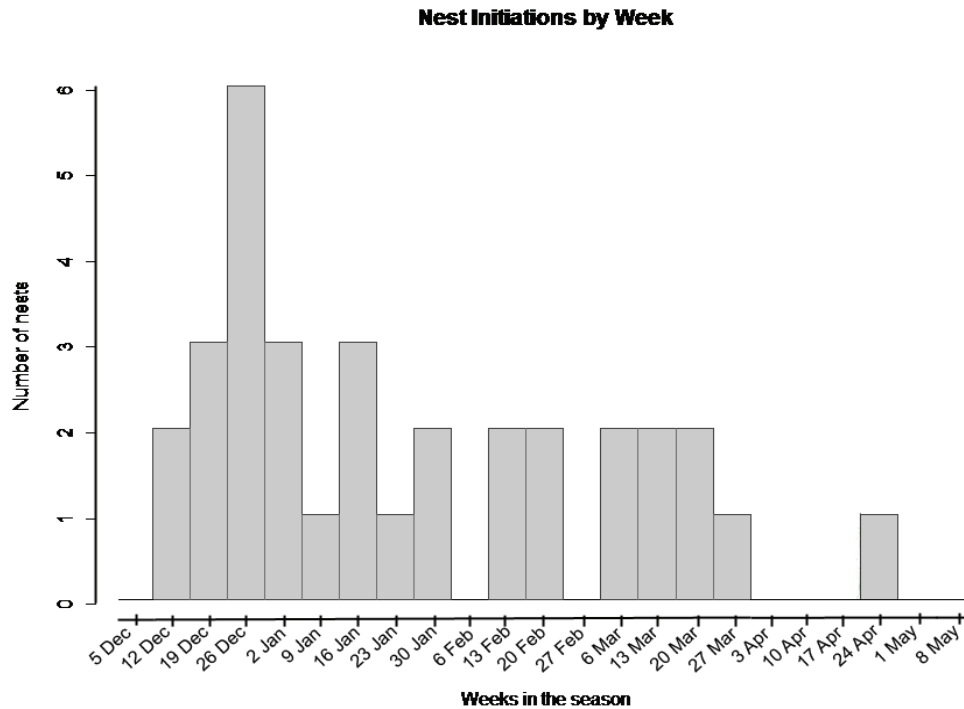
FIG. 1. Number of nests of the Tumbes Swallow (*Tachycineta stolzmanni*) initiated weekly from 4 December to 10 May at Santuario Histórico Bosque de Pomac (SHBP) in the Lambayeque Province, Peru.

The nestling period ranged from 26 to 32 days (n = 15 nests, excluding one nest for which fledge could not be ascertained with sufficient certainty (± 4 days)). Thirty-six nestlings fledged from 16 nests with a success rate of 50.0% (mean = 1.20 ± 0.23 nestlings per brood, n = 30). Nine of 18 first nesting attempts successfully fledged offspring. Of these, seven pairs attempted second broods, three of which also successfully fledged. Of the eight additional second attempts (replacement clutches), three fledged successfully. Two of the three third attempts successfully fledged offspring, though neither pair was successful in either of its first two attempts. The sole fourth nesting attempt came from a pair that was successful in its first attempt but failed in both the second and third attempts.

Our field crews left before the fate of this fourth attempt could be determined.

The period between a new clutch initiation following an unsuccessful nesting attempt ranged from 10–19 days (mean = 15.4 ± 1.2; n = 10). The period between a new clutch initiation following a successfully fledged brood ranged from 7–47 days (mean = 23.5 ± 4.48; n = 8). However, fledglings were not monitored after leaving the nest so it is not known whether they were successful as juveniles or the degree of post-fledging parental care exhibited.

We observed vigilant protection of nests by the adults, yet predation was the cause of 13 nest failures. Adults showed perceptible signs of agitation when individuals of Bicolored Hawk (*Accipiter bicolor*), Peregrine Falcon

TABLE 1. Average measured brood parameters of the Tumbes Swallow (*Tachycineta stolzmanni*) at Santuario Histórico Bosque de Pomac (SHBP) in the Lambayeque Province, Peru.

	n	$\mu \pm$ SE	Range
Egg length (mm)	82	16.69 ± 0.06	15.55–17.90
Egg width (mm)	82	12.06 ± 0.04	11.30–12.89
Egg mass (g)	82	1.30 ± 0.01	1.11–1.48
Clutch size	37	2.68 ± 0.10	2–4
Egg survival	96	84.38%	
Incubation period (d)	27	16.11 ± 0.14	15–18
Hatching success	76	92.11%	
Brood size	32	2.25 ± 0.14	1–4
Nestling success	72	50.00%	
Nestling period (d)	15	28.27 ± 0.42	26–32

(*Falco peregrinus*), American Kestrel (*Falco sparverius*), or the diurnal Peruvian Pygmy-owl (*Glaucidium peruanum*) were in the area, though there is no reason to believe that any of these – most certainly not the first three – were the source of nestling predation. Though acts of predation were not witnessed, some evidence points towards a diurnal predator. Rats are a likely candidate predator; rats were seen in the vicinity and are known to prey upon nestlings in nest boxes (Snetsinger *et al.* 2005, Tweed *et al.* 2006). An additional 6 nests were abandoned, some of which were likely researcher-influenced. Two of these are thought to be related to capture of the females too early in the breeding cycle and one was linked to neophobia from the addition of a supplemental data logger on the outside of the box. The other three abandonments are assumed to be due to natural causes, perhaps due to food limitation, as we observed evidence of starvation in the nestlings (see below).

Three broods this season suffered ectoparasitism by a *Philornis* sp. (Diptera, Muscidae). In two broods infected, the chicks (n = 3) did not survive to fledging, though we cannot say with certainty that the parasites caused or contributed to the deaths. In the other instance, we observed a lesion on a fledgling representing a current or previous infection;

however it had successfully fledged by the time of the observation. This may represent the first *Philornis* parasitism event documented on a Peruvian bird (Martin Quiroga, pers. comm.) as previous collections of the genus in Peru were found in Vespid wasp nests (Dodge 1968 and we can find no recent mentions). *P. downsi* recently established on the Galapagos Islands, Ecuador and is a conservation concern as it inflicts high levels of mortality on several rare endemic species (O'Connor *et al.* 2010).

Fledging did not always occur synchronously within a brood. Again, due to the frequency with which we checked nests, precise measures of asynchrony cannot be made. It is also possible that fledglings returned to the nest box to roost post-fledge. Fledglings were observed in the vicinity for a short period following their departure from the nest. They were uniformly dark grey on the head, back, wings and tail, with white rumps and pale grey under parts.

Nestling development. Thirty-one nestlings in 13 nests were included in the analysis of nestling development. Two broods contained a single chick each found dead in the nest; subsequently these broods (5 nestlings in all) were not included in the analysis. Both nestlings
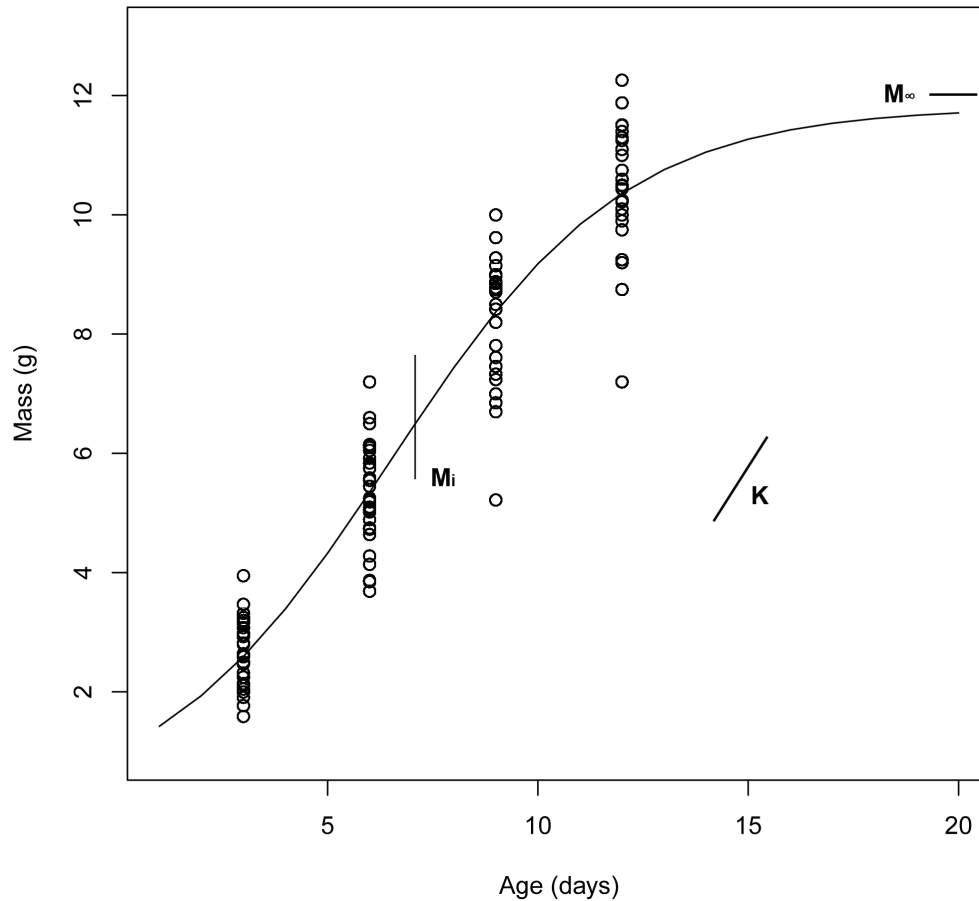
FIG. 2. Body mass of 31 nestlings of the Tumbes Swallow (*Tachycineta stolzmanni*) on days 3, 6, 9, and 12 with fitted growth curve representing the parameters M_∞, M_i, and K.

were visibly smaller than their brood mates, suggesting starvation as the cause of death.

Growth in body mass exhibited a sigmoidal curve, as is typical of other passerines (Fig. 2). The best fit model was one where M_∞ was estimated by the model rather than fixed at the adult mean mass (10.87 g, see below; delta AIC [Δi] = 63.50). It included chick as a random effect applied to M_∞ and M_i; K was not significant to the random part ($L_{7,115}$ = 2.96, P = 0.40) nor was nest as a random effect ($L_{7,115}$ = 3.53, P = 0.32). The model estimated the parameters at the following values: M_∞ = 11.80 ± 0.25; M_i = 1.03 ± 0.06; and K = 0.36 ± 0.01. M_∞ exceeds that of the observed adult mass suggesting that weight recession occurs before fledging, though the model does not depict this.

Parental care and diet. Both members of the pair attended nestlings. During the 42 provisioning observations, chicks received an average of 11.00 ± 1.00 provisioning visits per hour. There was no difference in provisioning rates between nestling day 7 (mean = 11.35 ± 1.21 visits/hour) and day 10 (mean = 10.59 ± 1.65

visits/hour, t = 0.4, df = 36, P = 0.71), nor a difference between male (mean = 4.88 ± 0.72 visits/hour) and female provisioning rates (mean = 5.3 ± 0.51 visits/hour, t = 0.5, df = 74, P = 0.61).

We analyzed the contents of seven food boluses collected incidentally while trapping adults. We identified insects to order; spiders were identified as Araneae (Table 2). Four specimens became mangled either in the parents' mouths or while collecting/processing, and thus could not be identified. Prey items had an average length of 2.64 mm (*n* = 63). Additionally, individuals were observed feeding on swarms of winged reproductive termites (Isoptera).

Adults. We measured a total of 33 adults throughout the course of the season, comprised of 18 females and 15 males. Males and females did not differ significantly in morphological measurements (Table 3). Sexes are similar in plumage: blue-brown above with white rumps, brown flight feathers and streaky, light gray under parts. We observed some individuals of both sexes initiating flight feather molt in early March, starting with the innermost primary (P1) and progressing outward, as is typical of *Tachycineta* swallows (Stuchbury & Rowher 1990). During their final nesting attempts, 70.6% of captured adults exhibited primary molt (n = 17).

DISCUSSION

Here we report the first systematic natural history observations of *Tachycineta stolzmanni*. Our observations reveal considerable natural history features characteristic of the genus, as well as many unique adaptations to a seasonally arid, tropical environment.

Similar to other *Tachycineta*, *T. stolzmanni* is a secondary cavity nester that construct its nests primarily of dried grasses or herbaceous vegetation with a feather-lined cup (*T. albi-*

linea: Dyrcz 1984; *T. thalassina*: Brown *et al.* 1992; *T. bicolor*: Winkler 1993; *T. cyaneoviridis*: Allen 1996; *T. leucorrhoa*: Bulit & Massoni 2004; *T. meyeni*: Liljesthrom *et al.* 2009; *T. euchrysea*: Townsend et al. 2008). Unlike Robbins *et al.* (1997), we did not witness the use of pebbles within the nest structure though no pebbles existed near the study site; our findings instead paralleled the typical *Tachycineta* nest though they differed in their heavy use of feathers. Grass did not grow within the study site during the study period, suggesting that the birds may have traveled > 1 km to acquire this material. It is therefore possible that due to the limited amount of available vegetative material, the birds utilized a more abundant material: feathers.

The use of feathers in the nest lining is commonly associated with their insulating properties (Collias & Collias 1984, Windsor *et al.* in review), which can both reduce the risk of hypothermia and increase the risk of hyperthermia in nestlings, depending on the environmental conditions (Mertens 1977, Møller 1984). Contrary to the theory that other *Tachycineta* species utilize feathers principally for insulation (Winkler 1993, Lombardo *et al.* 1995, Liljesthrom 2009, Stephenson *et al.* 2009), we observed high feather numbers in the presence of warm temperatures (never below 15.5°C and daily fluctuations did not exceed 11°C), suggesting that the risk of hyperthermia may be great (Lombardo 1994). However, we noted that in comparison to *T. bicolor* nests, the construction of *T. stolzmanni* nests was much looser and less tidy. A bulky nest construction may retain external radiation on the surface of the nest and in so doing maintains a cooler interior (Schaefer 1980); however, it is not clear how this finding may relate to nests within an (artificial) nest cavity. Feathers influence the bacterial environmental conditions within the nest, thereby affecting hatching success (Soler *et al.* 2010, Peralta-

TABLE 2. Summary of nestling diet samples from food boluses (n = 7) retrieved from the mouths of nestlings and adults of the Tumbes Swallow (*Tachycineta stolzmanni*), identified to order at Santuario Histórico Bosque de Pomac (SHBP) in the Lambayeque Province, Peru.

Taxa	n	% of total	Average length (mm)
Diptera	34	52.31	2.91
Coleoptera	9	13.85	2.41
Hymenoptera	7	10.77	2.51
Araneae	6	9.23	1.98
Hemiptera	5	7.69	2.65
Unidentified	4	6.15	1.74

Sánchez *et al.* 2011). Additionally, they may also function to reduce ectoparasite loads of the nestlings (Cohen 1988, Lombardo *et al.* 1995, Winkler 1993, but see Thomas & Shutler 2001). These vying explanations would predict that adjustments are made to the number of feathers in the nest throughout the nesting cycle. This hypothesis should be explored in the future to determine the role feathers perform in the nest of this tropical species.

In addition to our nest boxes, we detected ten nests in natural cavities within the site boundaries located in the trunks or branches of *Prosopis pallida* and *Capparis scabrida*. The average height from the ground to the entrance hole was 3.6 ± 0.92 m (n = 7). Nesting materials in the cavities resembled those used in the nest boxes. We observed nestlings in one natural nest five days before the first hatch occurred in the boxes, revealing that the breeding season started earlier than our nest box data alone indicates. When we began monitoring in early December we cleaned all nest boxes thus it is possible that in so doing we also removed new nests in the process of construction and thereby delayed clutch initiation for these individuals. Moreover, in early November 2006 during an El Niño season,

one of the authors observed nesting activity in a natural cavity near the vicinity of the present study site, though the stage of the nest was not determined.

One highly consistent, ubiquitous pattern of life history traits is the latitudinal trend in the fast-to-slow pace-of-life continuum. For example, bird species that breed at tropical latitudes typically have lower metabolic rates (Wiersma *et al.* 2007), lay fewer eggs per nest (Lack and Moreau 1965, Moreau 1944, Martin 1996, Martin *et al.* 2000), initiate more nests per season (Boehning-Gaese *et al.* 2000), have longer incubation periods (Ricklefs 1969, Robinson *et al.* 2008), prolonged nestling periods (e.g., Skutch 1949, Lack 1968, Ricklefs 1969), and slower nestling growth rates (Ricklefs 1976) than in closely related temperate species. The clutch size of *T. stolzmanni* is smaller than that of other *Tachycineta,* including the other tropical species (Table 4). We did not observe a seasonal decline in clutch size as is typical of *T. bicolor* (Stutchbury & Robertson 1988, Winkler & Allen 1996) and *T. leucorrhoa* (Massoni *et al.* 2007). This is expected as temperate birds are more likely to exhibit seasonal decline in clutch size than are tropical birds (Young 1994). Evidence of multiple brooding suggests that *T. stolzmanni* may double- or triple-brood more frequently than its congeners. The frequency of nest initiations indicates that post-fledgling parental care may be relatively short in comparison to other tropical species. Multiple brooding corresponds to a prolonged breeding season and, though uncommon, some other tropical species are known to lengthen their nesting season by concurrently breeding and molting (see below, Foster 1974). Similarly, we found both the incubation and the nestling periods of *T. stolzmanni* to be longer than those of other *Tachycineta* species. Long developmental periods are in agreement with low developmental rates, therefore it is anticipated that *T. stolzmanni* should exhibit the slowest nestling

TABLE 3. Adult male and female morphological measurements and statistics of Tumbes Swallows (*Tachycineta stolzmanni*) and the effect of sex on each trait from Santuario Histórico Bosque de Pomac (SHBP) in the Lambayeque Province, Peru.

	$\mu_{Female} \pm SE$	Range$_F$	$\mu_{Male} \pm SE$	Range$_M$	t	df	P
n	18	18	15	15			
Head-bill (mm)	24.78 ± 0.11	23.50–25.70	25.00 ± 0.07	24.50–25.50	1.7	29	0.10
Flatwing (mm)	93.44 ± 0.52	89.5–96.0	95.40 ± 0.85	92.0–103.0	2.0	24	0.06
Mass (g)	11.02 ± 0.16	10.00–12.25	10.72 ± 0.14	9.50–11.50	1.4	31	0.17

growth rate within the genus (Stager *et al.* unpub. data).

Average egg volume of *T. stolzmanni* is smaller than those of its congeners and adults of *T. stolzmanni* proved to weigh the least. Even so, the ratio of median adult mass to egg volume is the largest in the genus. The range of wing measures of *T. stolzmanni* is smaller than that of its congeners. Comparative head-bill measures exist for *T. bicolor,* whose values wholly exceed those of *T. stolzmanni* (27.6–29.3 mm; Winkler *et al.* 2011).

The nestling diet of *T. stolzmanni* contrasted markedly to that of the formerly conspecific *T. albilinea* as reported by Dyrcz (1984). *T. albilinea,* the congener most similar in mass and morphometrics, fed on prey with an average total length of 15.7 mm (n = 92), almost an order of magnitude larger than our own findings. Average prey size was instead more similar to that of *T. bicolor* (mean length = 4.5mm), a species for which odonates (mean length = 30.4 mm) are a significant part of the diet beginning on or before day 7 (McCarty & Winkler 1991). That study found prey size increased with increasing chick size and this may be true for *T. stolzmanni* as well, though it cannot be ascertained here as our sample size was small and samples were not obtained after nestlings were 12 days of age (at which point, they were similar in mass to *T. bicolor* nestlings at 5 days of age–Winkler & Adler 1996). However, during the nest excavations agrionid damselfly remains were found

in one of the nests, suggesting that larger prey items are indeed sometimes included in the nestling diet.

Because *Tachycineta* swallows are aerial insectivores, they often reside near water or in other areas characterized by high insect abundance. For instance, both of the sister taxa to *T. stolzmanni* favor wet, lowland habitats, such as mangroves, rivers, lakes, coastal beaches, and other wetlands (Turner & Rose 1989). Conversely, *T. stolzmanni* prefers to nest in the much more arid habitat of SDTFs. In spite of our work coinciding with the wet season, we witnessed unusually hot, dry weather because of a La Niña event occurring at the time. Rain fell on only two occasions during our presence, and many *Prosopis* did not produce foliage due to the drought. The Leche River, located 1.8 km from the study site, flowed for less than a week in late January and again for under 72 hours in April. In an ordinary year, the river flows intermittently throughout this January-April period, often for many days at a time (Lopresti pers. com.).

We hypothesize that this unique habitat results in both physiological and behavioral adaptations compared with the other *Tachycineta* species. For mammalian species of SDTFs, these physiological adaptations consist of changes in body temperature, torpor and hibernation, water conservation, and reproductive delay; behavioral adaptations include dietary flexibility, local movements and short distance migration, adjustments to

TABLE 4. Comparison of several aspects of morphology and breeding biology for all *Tachycineta* species. Standard errors are reported unless otherwise noted below. All data for *T. stolzmanni* are from the present study; all data from the following rows are from the study indicated with the taxon name, except for cells with separate references noted in bold. Blank cells indicate that published data does not exist for this trait. Egg volume (V) was calculated for the other species from published egg length and width data. Masses used in the ratio of adult body mass (BM) to egg volume are the middle value of the reported adult mass range for a given species. WL = wing length. Indices: [1]Dyrcz 1984, incubation period for one clutch only (determined as period from last egg to last hatch); [2]Turner & Rose 1989, wing measurements may be wing chord or flatwing; [3]Ricklefs 1976; [4]Winkler unpubl. data *in* Allen 1996, standard deviation is reported for clutch size and incubation period; [5]McCarty 2001; [6]Allen 1996, standard deviation is reported for clutch size and incubation period; [7]Townsend *et al.* 2008, standard deviation is reported for clutch size; [8]American Museum of Natural History (AMNH) specimen; [9]Massoni 2007; [10]Liljesthrom 2011; [11]Ricklefs 1968, using data from Edson 1943; [12]Edson 1943.

Taxon	Range Adult BM (g)	Range Adult WL (mm)	Clutch size	V (cm^3)	Adult BM : V	Incubation period (d)	Growth rate (*k*)	Nestling period (d)
T. stolzmanni	9.5–11.5	89.5–103	2.68 ± 0.10	1.28	1.15	16.11 ± 0.14	0.360	26–32
T. albilinea[1]	10–16[2]	92–105[2]	4.0	1.46	0.98	17	0.406[3]	23–27
T. albiventer [2]	14–17	100–108	3–6	1.77	0.88	-	-	-
T. bicolor[4]	15.6–25.4[2]	110–125[2]	5.4 ± 0.91	1.74	0.66	14.5 ± 1.13	0.50[5]	16–29
T. cyaneoviridis[6]	16.3–19.5[2]	105–120[2]	3.0 ± 0.58	1.83	0.78	15.8 ± 1.10	0.363	22–25
T. euchrysea[7]	11.75[8]	102–113[2]	2.8 ± 0.84	1.57	1.09	-	-	21–24
T. leucorrhoa[9]	17–21[2]	111–122[2]	4.92 ± 0.05	1.90	0.74	14.8 ± 0.2	0.458	21–27
T. meyeni[10]	15–20[2]	105–117[2]	4–6[2]	1.87	0.79	16.5 ± 0.1	-	21–34
T. thalassina[2]	14–16	110–129	4–6	1.62	0.87	14–15	0.412[11]	23–26[12]

activity patterns, and seasonality of reproduction (Stoner & Timm 2011). Previous swallow observations in arid environments include timing breeding with the onset of rains and arresting molt due to seasonal changes (Earle 1988). It is likely that adaptations for arid environment not present in congeners exist for *T. stolzmanni* and future research should include further investigations into the physiology and behavior of this species.

One possible example of such an adaptation is the observed molt-breeding overlap. For individuals of both tropical and temperate species, the onset of molt usually coincides with the end of the breeding cycle (Snow 1976, Poulin *et al.* 1992, Ralph and Fancy 1994, Piratelli *et al.* 2000, Marini & Durães 2001, Rowher *et al.* 2005, Verea *et al.*

2009). Overlap of these activities can be necessitated by dependence on short-term food sources (Foster 1975) and may occur in African species of *Hirundo* (Earle 1988). High seasonality could have strong implications on resource levels for *T. stolzmanni* given that insect abundance is related to climate and weather patterns (Williams 1945, 1951, 1961). Within SDTFs, some insect species are known to go dormant or migrate to wetter forest during the dry season (Hanson 2011), indicating that food availability could be significantly lower during this period. Preliminary data suggests that there is a correlation between molting individuals and lower feeding rates. This would be expected as molting inflicts added energy demands (Lindstrom *et al.* 1983) and reduces flight efficiency (Jenni &

Winkler 1994, Chai 1997, Swaddle & Witter 1997). Although *T. bicolor* usually initiates molt after the breeding season, individuals occasionally molt while feeding fledglings (Hussell 1983, Winkler unpub. obs.). Our observations are the first documentation of a *Tachycineta* undergoing molt while simultaneously incubating. This finding is seemingly in contrast to Foster's prediction that tropical arid environment species are less likely to exhibit molt-breeding overlap than those of tropical humid environments (1974).

Within the genus *Tachycineta*, many species have large distributions spanning thousands of square kilometers (Whittingham *et al.* 2002). Only the Bahama Swallow (*T. cyaneoviridis)* and the Golden Swallow (*T. euchrysea)* have ranges of similarly limited extent to that of *T. stolzmanni*. These two species are restricted to islands in the Caribbean and are listed as endangered and vulnerable, respectively (IUCN Redlist). Currently, *T. stolzmanni* is listed as near threatened (NT) by the Peruvian government (MINAG 2004) while IUCN lists it as a species of least concern; however the population has never been quantified. This is a cause for concern, as its true distribution may in fact be much more fragmented than is presently recognized by the international community. Within *T. stolzmanni*'s small range, very few protected lands exist (Rodriguez & Young 2000, IUCN & UNEP 2010) and fewer still are those with appropriate habitat. We were unable to locate the species in many seemingly suitable habitats, including one in which it had been previously sighted in the vicinity of Olmos. Rather, individuals seem to be localized, with regular reported sightings confined to less than ten localities (eBird). We found local guides confused *T. stolzmanni* with the similar Blue-and-white Swallow (*Pygochelidon cyanoleuca*) suggesting that *T. stolzmanni* has been over-reported in the area, as many visiting birdwatchers rely on such guides for identification. At present, the Bosque de Pomac Historical Sanctuary is the only protected area where a year-round population is known.

Seasonally dry tropical forests (SDTFs) are considered a world-wide priority for biodiversity conservation owing to the great number of endemic species that they contain (Ceballos 1995, Dinerstein *et al.* 1995, Gentry 1995). The Tumbesian region of northwestern Peru and southwestern Ecuador contains the largest expanse of coastal SDTF in the Neotropics (Best & Kessler 1995, Dinerstein *et al.* 1995). Listed as an Endemic Bird Area, the Tumbesian region supports one of the highest numbers of restricted-range bird species in South America, with over 45 species' distributions wholly confined within it (ICBP 1992, Best & Kessler 1995, Stattersfield *et al.* 1998, SERNANP 2011).

In contrast, SDTFs are recognized as the most endangered major tropical ecosystem and are severely threatened by human activities around the globe, with over 97% of these forests at risk due to development, climate change, fragmentation, fire, and conversion to pastoral and agricultural lands (Janzen 1988, Maass 1995, Miles *et al.* 2006). Coupled with understory degradation, these are the largest threats to Tumbesian avifauna, with many species vulnerable to even localized deforestation due to restricted habitat preferences (Best & Kessler 1995). In western Ecuador, less than 1% of the original dry forests remain (Dodson & Gentry 1991) and it is likely that Peru faces similar levels of deforestation (Best & Kessler 1995); only 5% of the Tumbesian region remains forested (Stattersfield *et al.* 1998). Added to habitat degradation, climate change may take a significant toll on the fauna of SDTFs. Anthropogenic climate change is predicted to lead to variation in rainfall patterns (Trenberth 2011), including an increase in the occurrence of extreme events (Easterling *et al.* 2000), and may produce modifications to the El Niño-Southern Oscillation

(Timmerman *et al.* 1999, Collins 2000, Latif & Keenlyside 2009). Such changes would inevitably alter the Tumbesian region, as the principal force in arid ecosystems is unpredictable, variable precipitation events (Noy-Meir 1973).

In light of rapid habitat loss and the changing climate, it is vital that further studies of the breeding biology, physiology, behavior, and range of *T. stolzmanni* receive immediate attention, and that the quantification of its global population be made a necessary priority. It is a high priority to protect current nesting sites with adequate management plans such as the Santuario Histórico Bosque de Pomac (SHBP) in the Lambayeque Province of Peru. While *T. stolzmanni* does share in some aspects of its congener's ecology, it also differs in many life-history traits, in morphology, in habitat, and in its limited distribution. This work will prove significant in understanding the methods with which genetically similar species cope with environmental variation.

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APPENDIX 1. Analysis of the effect of nesting attempt and lay order on egg mass, width, and length.

t-Test	Mean$_1$	Mean$_2$	t	P	df
1st att. vs > 1st att.: mass (g)	1.29	1.32	1.6	0.12	77
1st att. vs > 1st att.: width (cm)	11.94	12.18	3.5	< 0.001	79
1st att. vs > 1st att.: length (cm)	16.68	16.70	0.2	0.88	73
1st egg vs 2nd egg: mass	1.27	1.31	1.7	0.09	28
1st egg vs 2nd egg: width	11.98	12.08	0.9	0.36	30
1st egg vs 2nd egg: length	16.59	16.70	0.5	0.60	28
1st egg vs 3rd egg: mass	1.27	1.32	1.6	0.13	19
1st egg vs 3rd egg: width	11.98	12.05	0.5	0.61	20
1st egg vs 3rd egg: length	16.59	16.60	0.1	0.95	26
2nd egg vs 3rd egg: mass	1.31	1.32	0.2	0.84	23
2nd egg vs 3rd egg: width	12.08	12.05	0.2	0.60	28
2nd egg vs 3rd egg: length	16.70	16.60	0.4	0.66	27