Differences in rates of nest-visitation and removal of faecal sacs by male and female White-rumped Swallows

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Abstract. Despite being a common and widespread species, the White-rumped Swallow (Tachycineta leucorrhoa) is one of the least-studied members of its genus. We examined the rates of nest-visitation and nest-sanitation of male and female White-rumped Swallows during the nestling period, in 23 nests, and compared them with those of the extensively studied Tree Swallow (Tachycineta bicolor). White-rumped Swallow pairs increased the rate of nest-visitation as nestlings grew older, as was found in Tree Swallows. Females made significantly more visits to the nest than males, and the asymmetry was maintained irrespectively of the age of nestlings. These results are similar to those reported from Tree Swallows in the eastern United States, but differ from the equality of roles found in Ontario, Canada. Female and male White-rumped Swallows removed faecal sacs at the same rate when nestlings were young (Day 4) but by Day 12 females had quadrupled their effort whereas the rate of sanitation by males remained constant. Overall, female White-rumped Swallows made a significantly larger parental investment than males (as measured by number of visits to nests and, thus, presumably rates of feeding, and in contribution to nest-sanitation) and, in this respect, the asymmetry in parental investment is greater than that reported for Tree Swallows.

Introduction

Provisioning young usually requires great energy expenditure by parents (Walsberg 1983) and the rate at which parents feed their nestlings is related to several life-history traits. Males and females, however, may not contribute equally to parental duties and previous studies have shown intraspecific differences in food provisioning investment by the sexes. In Tree Swallows (Tachycineta bicolor) in New York state, USA, researchers found that females made a larger contribution to feeding rates than males (Lombardo 1991; McCarty 2002), whereas studies in Ontario, Canada, found the rates of feeding by males and females was equal (Dunn and Robertson 1992; Leonard and Horn 1996; Kempenaers et al. 1998; but see Whittingham et al. 2003). McCarty (2002) indicated the difference between these populations was related to the quality of the foraging habitat available, with males decreasing their care when food becomes more abundant (Lombardo 1991; Dunn and Robertson 1992). Unlike the Tree Swallow, the White-rumped Swallow (Tachycineta leucorrhoa) has been little studied but, given the similarities in ecology and life history of Tree Swallows and White-rumped Swallows (Bulit and Massoni 2004; Massoni et al. 2007), the present study was designed to provide information on parental investment to feeding and nest-sanitation by male and female White-rumped Swallows, and to relate it to the available foraging habitat and compare the results with the behaviour of Tree Swallows.

Compared with northern hemisphere species, many southern hemisphere species remain relatively little studied and information on the parental care, in particular, is scant. White-rumped Swallows are secondary cavity nesters and socially monogamous. Their distribution, mostly temperate, ranges from southern Brazil, Paraguay, Uruguay and northern Argentina, south to La Pampa and Buenos Aires provinces (Ridgely and Tudor 1989). Only females incubate eggs, and both sexes contribute to feeding of nestlings and nest-sanitation (F. Bulit and V. Massoni, pers. obs.). Our objectives were: (1) to describe the frequency of visits to the nest and nest-sanitation effort of male and female White-rumped Swallows during the nestling period; (2) to compare the investment made by each sex as the nestlings grew older; and (3) to contrast these results with those obtained for their more extensively studied northern temperate congener, the Tree Swallow.

Methods

From October 2004 to January 2005, we studied White-rumped Swallows breeding in nest-boxes in a flat (~10 m above sea level) farming landscape in depressed pampas habitat (Soriano 1991) at the Instituto Tecnológico de Chascomús, CONICET, in Buenos Aires Province, Argentina (35°34′S, 58°01′W). We erected 96 nest-boxes, 1.3–1.7 m above ground, on fence posts or buildings, and ~30 m apart from each other.

Four days after the clutch was complete, females were captured inside nest-boxes and identified by the presence of a brood-patch. They were dyed with a unique pattern of indelible markers on the breast, abdomen, and rump to allow recognition...
in the field and on videotapes. Nest-boxes were then checked daily around the estimated date of hatching (14–15 days from the onset of incubation; Massoni et al. 2007). The day when most of the young hatched (more than 60%) was considered Day 0 of the nestling’s development.

We used video-cameras to record male and female visits and faecal sac removal events when nestlings were 4, 12, and 15 days old (hatching date = Day 0) at 23 nests. No data were collected on Days 8–9 as it would likely be affected by a short experiment performed in neighbouring nest-boxes on those days. Recordings were made for two consecutive hours between 0700 and 1400 hours using a Sony Hi 8 CCD-TRV 128 video-cassette recorder (Sony, Tokyo, Japan) placed 20–30 m away from the entrance to the nest-box. We found no relationship between the variables analysed (number of nest-visits per nestling hour and number of faecal sacs removed per nestling hour) and time of day, or time of the breeding season, so those data were pooled for each nestling age-class for the analyses. No recordings were made when it was raining. Owing to inclement weather some of the recording sessions were missed, so complete nest recording was attained for just 16 nests.

Videotapes were subsequently analysed and the total recording time was defined as the time elapsed between the return of any of the parents and two hours after the camera was placed. As this time was not constant, for each variable we calculated the rate for each sample period separately, and then averaged those rates per nestling hour. The time of day and the number and age of nestlings was known for each recording session. For each parent, we recorded the number of nest-visits per nestling hour, and the number of faecal sacs removed per nestling hour.

To analyse the parental investment of the pair during the nestling period, we pooled the information for each sex and used repeated-measures ANOVA. Variables were transformed using square root or natural logarithm when necessary to comply with Mauchly’sphericity test (Gleser 1966). To compare females and males over the nestling period, we considered the proportion of female investment relative to the total investment made by males and females. To avoid wasting data by deleting observations from incomplete date recording of nests, we substituted the missing observations with the mean value of the rates attained by the rest of the pairs at each specific nestling age (Quinn and Keough 2002). Instead of analysing only 16 nests with complete recordings, we increased the sample size to 23 nests by this method. As the proportion of the female’s investment is dependent on the investment made by males, instead of using sex as a factor in the ANOVA we compared the variables described above for males and females when nestlings were 4, 12 and 15 days old using paired t-tests. The variables were transformed with square root or natural logarithm when required to obtain normality. All tests were two-tailed, reported values are means ± s.e., and differences were considered significant at $P < 0.05$. We analysed data using STATISTICA for Windows, Version 5.0 (Statsoft 1995).

Results

Overall parental investment and nestling age

During videotaping, mean size of broods was $4.3 ± 0.18$ nestlings. Of the 23 nests, four had three nestlings, eight had four, 10 had five, and one had six. Probably owing to the reduced number of nests with three and six nestlings, we did not find a significant relationship between brood-size and rates of feeding and removal of faecal sacs by males, females or the pair combined (non-significant repeated-measures ANOVAs not shown). Therefore, data from all nests were combined after dividing the rates by the number of nestlings present in a nest.

We recorded 4825 visits to the nest by adults during 134 h of observation at 23 nests. For males and females combined, rates of visitation increased with age of nestlings (repeated-measures ANOVA, $F_{2,44} = 9.6, P < 0.001$; Fig. 1) as did the rate of removal of faecal sacs ($F_{2,44} = 19.6, P < 0.001$; Fig. 2). Results using the smaller dataset of 16 nests, were similar but the rate of nest-visitation showed a strong, but not statistically significant,

*Fig. 1.* Number of nest-visits per nestling hour made by male and female White-rumped Swallows combined, on Days 4, 12 and 15 of nestling period (day of hatching = Day 0; $n = 21, 23$, and 22 nests respectively). Letters denote statistical differences in Tukey post-hoc comparisons.

*Fig. 2.* Number of faecal sacs removed per nestling hour by male and female White-rumped Swallows combined, on Days 4, 12, and 15 of nestling period (day of hatching = Day 0; $n = 21, 23$, and 22 nests respectively). Letters denote statistical differences in Tukey post-hoc comparisons.
tendency to increase with the age of nestlings (repeated-measures ANOVA, \( n = 16, F_{2,44} = 3.2, P = 0.06 \)).

**Differences in contribution of sexes**

The relative contribution of females to the rate of visitation (female visitation-rate/female visitation-rate + male visitation-rate) was constant during the nestling period \( (F_{2,44} = 0.08, P = 0.92, n = 23 \text{ nests}) \) a result that remains essentially unchanged using only the smaller sample of 16 nests. The relative contribution of females to removal of faecal sacs, however, showed a different pattern. Using the larger sample \( (n = 23 \text{ nests}) \) the rate of removal remained constant during the nestling period \( (F_{2,44} = 2.1, P = 0.14) \), but using only the smaller sample \( (n = 16 \text{ nests}) \) the rate of removal showed an increase as the nestlings grew older \( (F_{1,15} = 4.7, P = 0.02) \), and was significantly greater on Day 12 than on Day 4 (Tukey Honestly Significant Difference test, \( P = 0.01 \)).

In addition, we described and compared the effort made by males and females for each age-class of nestlings using paired \( t \)-tests (Table 1). Females made significantly more visits per nestling hour than males during the three periods (between 58% and 62%; Table 1). The rate of visits by females on Day 4 and Day 15 was \( 3.4 \pm 0.2 \text{ visits/nestling hour and 5.2} \pm 0.51, \text{ respectively. For males, the rate of visits to the nest was } 2.5 \pm 0.31 \text{ visits/nestling hour on Day 4 and } 3.3 \pm 0.32 \text{ on Day 15. The rate of nest visits by females on Day 4 was higher than the maximum visiting rate of males on Day 15; during that period males only increased their rate of visits by less than one visit per nestling hour, whereas females increased it by almost two visits per nestling hour. Males removed faecal sacs at a constant rate throughout the nestling period, whereas females removed significantly more faecal sacs than males on Days 12 and 15 than on Day 4 (Table 1).}

**Discussion**

**Overall parental investment and nestling age**

The number of visits per nestling hour by pairs of White-rumped Swallows increased with the age of nestlings, as reported for Tree Swallows (Leonard and Horn 1996; Kempenaers et al. 1998). Assuming that increased visits result in increased provisioning of food, this result indicates that adults respond to the increasing demands of nestlings by adjusting the frequency of delivery of food.

Pairs of White-rumped Swallows visited their nestlings 5.9 \pm 0.3 times per nestling hour on Day 4 after hatching, increasing to 8.5 \pm 0.5 times per nestling hour on Day 15. Adult Tree Swallows feed nestlings on 95–98% of visits to the nest (McCarty 2002; Whittingham et al. 2003), males and females provide similar amounts and types of food (Quinney 1986; McCarty and Winkler 1999; McCarty 2002), and brood-size does not influence size of food loads (McCarty 2002). If we assume this is also the case for White-rumped Swallows, the total feeding rates (as indicated by visitation-rates) are much higher than those reported for Tree Swallows (~2.5 visits/nestling hour on Day 4, and 4.0–4.8 visits/nestling hour on Day 14; Kempenaers et al. 1998; Whittingham et al. 2003), a species whose feeding rates and load sizes are similar across their breeding range (Lefèbvre and Robertson 1986; Quinney 1986; Williams 1988; Lombardo 1991; Winkler 1991; Leonard and Horn 1996; Whittingham et al. 2003; but see Dunn and Hannan 1992). There are a number of possible explanations, acting singly or in combination, for the observed differences between White-rumped and Tree Swallows: (1) it may be that a smaller proportion of visits by White-rumped Swallows are feeding visits; (2) there may be differences in the type and availability of prey, which may force adult White-rumped Swallows to feed smaller but more frequent loads to their nestlings than adult Tree Swallows; or (3) the available food may be of poorer nutritional quality so that parents need to increase their feeding effort to ensure growth of their progeny. Further, differences in feeding rates associated with climatic differences between the study sites of the two species may also have an impact on the differences observed between the two. Average temperature during the breeding season reported for the site of McCarty’s (2002) study \( (17 \pm 2^\circ\text{C}; \text{NRCC 2004}) \) is very similar to the average temperature during the breeding season at Chascomús \( (18 \pm 3^\circ\text{C}; \text{SMN 2004}) \). However, mean accumulated precipitation per month differ between the sites during the breeding season: 135.4 \pm 31.9 mm at McCarty’s (2002) site (NRCC 2004) and only 58.2 \pm 12.0 mm at Chascomús (SMN 2004).

Assuming that the great majority of nest visits are feeding visits and that the amount of food provided in each visit is the same, the higher feeding rates observed in White-rumped Swallows could also be associated with a higher adult mass or a shorter period of nestling development. White-rumped Swallows, however, are only 6.5% heavier than Tree Swallows \( (22.4 \pm 0.1 \text{ g v. } 21.1 \pm 0.3 \text{ g respectively}; \text{Peer et al. 2000; F. Bulit and V. Massoni, unpubl. data}) \) but parents make twice as many visits as Tree Swallows, and the nesting period for White-rumped Swallows is two days longer than for Tree Swallows. Thus, we cannot attribute the differences in nest visitation rates between the two species to these morphological and life-history traits.

Overall, the rate of faecal sac removal in our study increased from 0.6/nestling hour on Day 4 to 1.6/nestling hour (73% of

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**Table 1. Rates of nest-visitation and nest-sanitation by male and female White-rumped Swallows**

<table>
<thead>
<tr>
<th></th>
<th>Day 4 (n = 21 nests)</th>
<th>Day 12 (n = 23 nests)</th>
<th>Day 15 (n = 22 nests)</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Females</td>
<td>Males</td>
<td>( t )</td>
</tr>
<tr>
<td>Number of nest-visits/nestling hour</td>
<td>3.4 ± 0.21</td>
<td>2.5 ± 0.31</td>
<td>2.32</td>
</tr>
<tr>
<td>Faecal sacs removed/nestling hour</td>
<td>0.3 ± 0.08</td>
<td>0.3 ± 0.07</td>
<td>0.39</td>
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increment) on Days 12 and 15. These rates are higher than those reported for Tree Swallows (~0.4/nestling hour on Day 4, and 0.8/nestling hour on Day 15; Weatherhead 1984; Lombardo 1991). The higher rates of faecal sac removal found for White-rumped Swallows suggest that they deliver more food than do adult Tree Swallows. The growth rate of White-rumped Swallow nestlings is, however, 10% lower than that of Tree Swallow nestlings (Massoni et al. 2007), suggesting either that the nutritional quality of the food at our study site is lower than in the north, or that there are intrinsic differences in the metabolism of these species.

Skutch (1949) suggested that higher nest-predation pressures in the southern hemisphere might favour lower parental care and longer nesting periods, a relationship later reviewed by Martin (1996). More recently, however, Martin et al. (2000) found that the feeding rates of several species from Argentina were nearly double those found in Arizona, and proposed the alternative hypothesis that reduced adult mortality in southern hemisphere species may favour allocation of greater investment into fewer young. Clutch-size of White-rumped Swallows is less than one egg smaller than the clutch size of Tree Swallows (Murphy et al. 2000; Massoni et al. 2007). Our results show that the southern species doubles the feeding rate of the northern one, in accordance with the hypothesis of Martin et al. (2000).

**Differences between sexes in parental investment during the nestling period**

We found significant differences in parental investment of male and female White-rumped Swallows. Females made significantly more visits to the nest than did males, and the asymmetry was maintained, irrespective of the age of nestlings. Between Days 4 and 15, males increased the number of visits per nestling hour by 32%, whereas females, whose minimum feeding rate was higher than that of the males at all ages, also increased their visitation-rate by 34%. This asymmetry is similar to that reported for Tree Swallows at Long Island (Lombardo 1991) and Ithaca (McCarty 2002), where females made 56% and 62% of the feeding visits, respectively, but differs from the equality reported for Tree Swallows at Long Island (Lombardo 1991) of feeding roles found by researchers working with an Ontario population of Tree Swallows (Dunn and Robertson 1992; Leonard and Horn 1996; Kempenaers et al. 1996; and Robertson, R. J. 1992). The asymmetry is similar to that of the feeding visits, respectively, but differs from the equality reported for Tree Swallows at Long Island (Lombardo 1991) of feeding roles found by researchers working with an Ontario population of Tree Swallows (Dunn and Robertson 1992; Leonard and Horn 1996; Kempenaers et al. 1996; and Robertson, R. J. 1992). The asymmetry is similar to that of the feeding visits, respectively, but differs from the equality reported for Tree Swallows at Long Island (Lombardo 1991) of feeding roles found by researchers working with an Ontario population of Tree Swallows (Dunn and Robertson 1992; Leonard and Horn 1996; Kempenaers et al. 1996; and Robertson, R. J. 1992).

The relative contribution of females to nest-sanitation increased significantly during the nestling period, considering the more conservative value of the reduced sample size. Although males removed faecal sacs at a constant rate from Day 4 to Day 15, females quadrupled their effort from Day 4 to the other periods analysed. In contrast, patterns of removal of faecal sacs (per nestling) by male and female Tree Swallows during the nestling period were similar, and, although females removed more faecal sacs per hour each day of that period, the difference was not significant (Lombardo 1991).

Finally, lower parental investment by males in rates of nest-visits, and potentially feeding, might be accompanied by higher relative efforts in other aspects of care, such as nest-defence (Ardia 2007). In the case of Tree Swallows, males defend the nests with higher intensity than females (Winkler 1992) but there are no data on this for White-rumped Swallows.

In summary, White-rumped Swallow females made a significantly larger effort than males in terms of visits to the nest, and presumably feeding of young, and removal of faecal sacs from the nests. Female contributions to nestling welfare increased during the nestling period at a higher rate than did those of males, and the asymmetry in parental investment was greater than that reported for Tree Swallows. Future studies on White-rumped Swallows in different foraging habitats, and the determination of extra-pair-paternity rates will allow an understanding of the ecological and life-history traits that shape the asymmetries found.

**Acknowledgements**

We thank J. C. Reboreda for providing video cameras to conduct this study and to G. Somoza and L. Miranda for logistical support at the InTeCh-CONICET. We are grateful for the suggestions made by two anonymous referees and the Managing Editor to previous versions of this manuscript. This study was supported by an Ubacyt grant X-158 to Juan Carlos Reboreda and an Ubacyt X-140 grant to V. Massoni. F. Bulit and A. G. Palmerio are doctoral candidates at CONICET, Argentina, and V. Massoni is a Research Fellow at the same institution.

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Manuscript received 8 November 2007, accepted 13 May 2008