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Rufous Hornero”**

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Running head: Coordinated parental care in the Rufous Hornero

“High coordination and equitable parental effort in the Rufous Hornero”

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Abstract. Avian parental care is understudied in temperate southern hemispheric regions, in particular for the Neotropical Furnariidae family. We measured rates of nest building, mud-carrying visits, incubation, brooding, feeding and nest-sanitation behaviors provided by molecularly sexed Rufous Horneros (*Furnarius rufus*) nesting at the humid pampas of Argentina. We also evaluated the coordination of all these behaviors between the partners, and compared the frequency of uncoordinated behaviors of each sex. Males and females worked highly equitably throughout the entire nestling cycle with few exceptions: a) both sexes built the nest but males supplied somewhat less mud at the beginning of nest construction, b) though highly involved in incubating the eggs males did so slightly less often than females during early incubation, c) even if males also brooded the nestlings, they brooded less often and for a little shorter periods of time than females, and d) young nestlings were fed less often by males than by females. We found no differences in nest sanitation rates. The proportion of coordinated behaviors between partners performing different parental tasks was very high during the entire nesting cycle. Analysis of the frequency of uncoordinated behaviors revealed females were more prone than males to skip turns only during the onset of nest building and the beginning of the nestling period. The highly similar and coordinated effort is probably essential to build their remarkable nest and reach the high nesting success that characterizes the species.

Key words: biparental effort, coordinated behavior, *Furnarius rufus*, nesting success, *Rufous Hornero*

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4 *Resumen.* El cuidado parental ha sido poco estudiado en aves del Hemisferio Sur templado,
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6 en particular dentro de la familia Neotropical Furneriidae. Medimos las tasas de construcción
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8 del nido, acarreo de barro, incubación, empolle, alimentación y limpieza que realizaron
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10 machos y hembras molecularmente sexados del Hornero Común (*Furnarius rufus*)
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12 nidificantes en la pampa húmeda de Argentina. Además, evaluamos la coordinación de todos
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14 estos comportamientos entre los miembros de la pareja, y comparamos la proporción de
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16 comportamientos no coordinados de cada sexo. Machos y hembras trabajaron con alta
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18 equitatividad a lo largo de todo el ciclo de nidificación, con escasas excepciones: a) machos y
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20 hembras construyeron el nido a la par, pero los machos acarrearon ligeramente menos barro
21
22 al nido al inicio de la construcción, b) si bien ambos sexos participaron activamente de la
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24 incubación los machos incubaron por periodos ligeramente más cortos, c) aunque los machos
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26 también empollaron pichones, lo hicieron con menor frecuencia y por períodos más cortos, y
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28 d) los pichones pequeños recibieron menos visitas de alimentación de sus padres que de sus
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30 madres. No encontramos diferencias en las tasas de limpieza del nido. La proporción de
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32 comportamientos coordinados con la pareja fue muy alta durante todo el ciclo de nidificación.
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34 La alta similitud y coordinación del esfuerzo parental probablemente es esencial para
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36 construir su extraordinario nido y alcanzar el alto éxito reproductivo que caracteriza a esta
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38 especie.
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INTRODUCTION

1 Parental care is closely related to the social mating system (Emlen and Oring 1977) and,
2 though 90 % of avian taxa are socially monogamous (Lack 1968), true genetic monogamy
3 occurs in only 14 % of passerine species (Griffith et al. 2002). The resulting lack of genetic
4 relatedness between fathers and offspring might strengthen the conflict of interests between
5 the sexes on the optimal investment in parental care (Trivers 1972). Females in bird species
6 with biparental care are typically involved in all or most parental care duties, generally
7 including nest building, incubating eggs and rearing offspring (Lack 1968, Clutton- Brock
8 1991). Males, in contrast, are commonly involved in feeding young but are less frequently
9 involved in incubating the eggs and brooding the chicks (Silver et al. 1985, Ketterson and
10 Nolan 1994). Thus, most research on paternal care in biparental passerines has focused on
11 chick food-provisioning rates, in spite that incubation has been acknowledged as an
12 energetically costly component of parental care (Williams 1996, Reid et al. 2002a), and
13 brooding, as an extension of incubation, is costly too (Pearson 1994). Male involvement in
14 nest building, incubation and brooding remains poorly understood (Whittingham and Dunn
15 2001, but see Reid et al. 2002a, Van Roo et al. 2003, Auer et al. 2007).

16 The quality of an individual as a mate may depend not only on its individual traits, but
17 also on how its traits mesh with those of its mate (Ens et al. 1993, Zeh and Zeh 2001,
18 Dingemanse et al. 2004). Indeed, the compatibility of the members of the pair during the
19 nestling period has been shown to affect the reproductive success of some species (Spoon et
20 al. 2006). Behavioral complementarity and coordination may be regarded as specific cases of
21 compatibility. Complementarity occurs when mates specialize in different contributions to
22 reproduction, while coordination comprises those cases in which mates trade-off carrying out
23 the same type of tasks (Spoon et al. 2006).

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3 24 Furnariidae is a large Neotropical family of birds that includes 236 species in 56
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5 25 genera (Remsen 2003). In spite of their ubiquitous distribution in South America and their
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8 26 relative abundance, their reduced sexual size and color dimorphism has historically delayed
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10 27 the study of how each sex contributes to parental duties (Remsen 2003). It is generally
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12 28 accepted that the contribution of males in parental duties is high (Remsen 2003). However,
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14 29 the involvement of both sexes in incubation and chick feeding has been confirmed in only
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16 30 eight species (Fraga 1980, Nores and Nores 1994, Remsen 2003, Moreno et al. 2007) and is
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18 31 suspected for other five species (Remsen 2003, Hann et al. 2004).
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22 32 The Rufous Hornero (*Furnarius rufus*) is an ideal species with which to study the
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24 33 extent of parental care provided by males and females and the existence of behavioral
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26 34 complementarity and coordination in parental duties. They are socially monogamous (Fraga
27
28 35 1980) and build a conspicuously exposed large 'oven' nest consisting of mud mixed with
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30 36 grass or dung. The wall of the nest is between 3 and 5 cm thick and the nest may weigh up to
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32 37 5 kg (Remsen 2003). Building this structure represents a large effort, as the body mass of
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34 38 Rufous Horneros is only around 60 g (Fraga 1980, Aldatz 2006) and the weight of the nest
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36 39 they build is up to 80 times their own weight. Rufous Horneros build a new nest each year
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38 40 (Fraga 1980) and nest building takes within 2-3 months, although in some cases it can take
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40 41 only 15 days (Fraga 1980). Remsen (2003) proposed that this extraordinary nest, and its
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42 42 ability to mediate the impact of extreme temperatures, is responsible for the extended
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44 43 geographic distribution of the species and its high nesting success (72 %, Fraga 1980; 71 %,
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46 44 Mason 1985; 62 %, Aldatz 2006), as well as the enhancement of nesting success of other
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48 45 species that use their nests (i.e. Saffron Finches, *Sicalis flaveola*, had higher nesting success
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50 46 when using Rufous Hornero nests than when using other cavities, Mason 1985).
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57 47 The information available on the extent of parental care provided by males and
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59 48 females is scant. In the most detailed work on the breeding biology and behavior of the
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3 49 species Fraga (1980) reported that the male is “helped” by the female during the nest
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5 50 construction, but provided no information on the relative contribution of each sex to nest
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7 51 building. Both sexes incubate eggs, but the length and frequency of the incubation bouts
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9 52 made by each sex is unknown. Finally, although both sexes deliver food at similar rates
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11 53 (Fraga 1980), quantitative data on feeding across the nestling period is lacking. Therefore,
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13 54 available information on parental care does not accurately represent the contribution of each
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15 55 sex to parental duties or the extent of coordination of those behaviors across the nesting
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17 56 cycle.

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22 57 The aim of this study was to determine the extent of parental care provided by male
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24 58 and female Rufous Horneros during nest building, incubation, chick brooding and feeding
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26 59 periods. We also evaluated the equitability and coordination of these efforts between the
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28 60 sexes during the entire nestling period in a molecularly sexed population. Given that Rufous
29
30 61 Hornero pairs remain together throughout the breeding season and sometimes during multiple
31
32 62 years and are territorial year round and persuasively intolerant to conspecific intrusions
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34 63 (Fraga 1980), we expect both males and females to be highly and equitably committed to
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36 64 most or all parental chores and to find high levels of coordination between the sexes during
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38 65 the performance of many nesting behaviors.

39 40 41 42 43 44 45 67 METHODS

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48 68 The study was conducted at the Instituto Tecnológico de Chascomús, Buenos Aires Province
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50 69 (35° 34'S, 58° 01' W) in a flat farming landscape, during the breeding seasons (September to
51
52 70 December) of 2002, 2003 and 2004. The site is within the “flooding pampas” (Soriano 1991),
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54 71 with an annual rainfall of approximately 1100 mm and mean monthly temperatures during
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56 72 the breeding season varying from 12° C (September) to 20° C (December). Our study site is
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58 73 used mainly for raising cattle. The area is divided in paddocks whose borders are vegetated
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3 74 with *Celtis tala* and *Acacia bonariensis*, in which we found the majority of nests. We also
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5 75 found some nests on human built structures such as fence poles.
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10 77 STUDY SPECIES
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12 78 As in most Furnariidae, the Rufous Hornero does not show evident sexual dichromatism. In
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14 79 both males and females, the dorsal parts are rufous in color, they have a slight wing band, and
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16 80 the under parts are brownish grey or light cinnamon in color (Narosky and Yzurieta 1987).
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18 81 Because of their similarity in body size as well as morphology (Fraga 1980) they are not
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20 82 distinguishable in the field, though they may be identified at a distance by the sexual
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22 83 differences while they duet (Roper 2005). Their geographic distribution encompasses from
23
24 84 northeastern Brazil to the south of Neuquén and Río Negro Provinces in Argentina. Rufous
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26 85 Horneros are commonly associated with humans, who provide additional surfaces on which
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28 86 to build nests and the water needed to build their oven-like nest.
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36 88 DATA COLLECTION
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38 89 We conducted a systematic nest search within our study site and followed 59 nesting attempts
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40 90 (20, 16, and 23 during the 2002, 2003 and 2004 breeding seasons, respectively). Forty one
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42 91 nests were found during the building stage and 18 during the egg stage. The final stage of
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44 92 nest building is the construction of the eggs chamber: extending from either side of the
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46 93 entrance a curved wall of mud enters the nest, reducing the opening and forming a rounded
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48 94 chamber. Females may start to lay the eggs in it before the chamber is finished (Fraga 1980);
49
50 95 therefore, we started checking the nest content as soon as we detected the beginning of the
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52 96 chamber construction. We checked nests every day during laying to track clutch completion
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54 97 and every other day during incubation and chick rearing to track nest fate. Because the egg
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56 98 chamber is closed we had to open the back of each nest by cutting a circular hole 6 cm in
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3 99 diameter in the back of the egg chamber with a circular saw. The hole was carefully sealed
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6 100 with a wooden plug and mud after each visit (following Fraga 1980). We avoided opening the
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8 101 nests on windy or rainy days. No nest was abandoned in association with nest checking to our
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10 102 knowledge.

103 We captured the adults using mist-nets (60 mm mesh) placed close to the nest. We
104 used play-backs calls to attract the territorial pair to the net. Individuals were leg-banded with
105 a unique combination of three color rings and a numbered aluminum ring. Because Rufous
106 Horneros are sexually monomorphic, we genetically sexed birds using DNA isolated from
107 blood samples following the procedures suggested by Quintana *et al.* (2008). At the time of
108 capture, we collected 20-40 μ l sample of blood from each bird via brachial venipuncture
109 using a heparinized capillary tube. We placed each sample on a 20 x 10 mm piece of
110 commercial filter paper. Samples were air-dried and stored separately at room temperature
111 separately in small sealed plastic bags until analysis. The highly conserved CHD1 gene
112 contains introns of different lengths in each sex. We used a forward primer (2550F), and a
113 reverse primer (2718R) to amplify the CHD1- W and CHD1-Z genes located on the avian sex
114 chromosomes (Fridolfsson and Ellegren 1999). We visualized the different sized introns to
115 determine the sex of each bird.

116 We recorded the parental behavior of male and female Rufous Horneros during nest
117 building, incubation, and nestling feeding periods by video recording nest activity during 2 hr
118 time intervals and checked the nest content after each recording session had ended. We
119 videotaped nests at random during the hours of 07:00 and 18:00 to maximize the number of
120 nests we could record at on a given day, as a pilot study did not find differences in parental
121 behaviors with time of the day. Due to inclement weather conditions and nest predation we
122 were unable to video-record all the nests at all stages of interest. Some nests were video-
123 recorded only once, other nests were video-recorded several times across the nesting cycle,

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3 124 but we video-recorded each nest only once during each period of interest. We used Sony Hi-8
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5 125 CCD-TRV 138 cameras placed greater than 20 m distant from the nest. We recorded 62 hr
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8 126 during nest building ($n = 19$ nests), 126 hr during incubation ($n = 23$ nests), and 84 hr during
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10 127 the nestling period ($n = 19$ nests), totaling 280 hr.

128 We divided nest building into an initial construction stage during which the birds were
129 constructing the main structure (floor, walls and roof) and an advanced construction stage,
130 when birds were building the inner wall to form the nest chamber. Using video observations,
131 we recorded for each sex separately the rate of mud carrying (number of visits h^{-1} at which
132 the individual was transporting building material) and the building rate (number of visits h^{-1}
133 where birds molded nest material with their beaks) because birds could have performed one
134 or both behaviors during a nest visit. We calculated the proportion of coordinated visits and
135 the frequency of uncoordinated behaviors of each sex. We defined a visit as coordinated if the
136 behavior displayed during the visit was the same as the behavior displayed during a previous
137 visit made by the opposite sex and uncoordinated if males or females repeated a particular
138 behavior before their mate did. We also determined the frequency of uncoordinated,
139 repetitive behaviors of each sex. We recorded incubation activity of each sex at three points
140 during incubation: early incubation (2 ± 1 days since the start of incubation), middle
141 incubation (9 ± 1 days) and late incubation (15 ± 1 days). For each sex we analyzed the
142 length of incubation visits (min:sec), their frequency (h^{-1}), the proportion of coordinated
143 incubation bouts, and the frequency of uncoordinated incubation visits made by each sex.
144 Activity during the nestling period was recorded during three stages corresponding to chick
145 age: early (5 ± 1 days of age with hatching day = age 0), middle (11 ± 1 days of age), and late
146 (18 ± 1 days of age). For each parent we calculated the feeding rate (number of visits
147 nestling $^{-1} \text{h}^{-1}$) and the rate of fecal sac removal (number of sac removal visits nestling $^{-1} \text{h}^{-1}$).
148 We calculated the proportion of coordinated feeding visits for all periods and the frequency

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3 149 of uncoordinated feeding visits made by each sex. For the early nestling period, we calculated
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5 150 the brooding rate (number of brooding visits h^{-1}), the length of brooding events (min:sec),
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8 151 brooding coordination and frequency of uncoordinated brooding behavior made by each sex.
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10 152 Fecal sac removal events were not observed on video recordings during the early nestling
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12 153 period, and brooding events were not observed during the middle and late nestling period. We
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14 154 did not calculate the frequency of uncoordinated fecal sac removal events because of the
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16 155 small number of events detected (see Results). Because we found no year differences for any
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18 156 of the behaviors, we pooled all years for analysis. Numbers of nests at different stages vary
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20 157 because some nests were found at an advanced stage of nest construction and some nests
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22 158 failed during incubation or after hatching.
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28 29 160 STATISTICAL ANALYSIS

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31 161 We described the behaviors of each sex reporting the median value, lower and upper
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33 162 quartiles. Behavioral variables were not normally distributed and not all could be transformed
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35 163 to meet the assumption of normality for parametric tests. Because of this, we compared the
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37 164 effort made by males and females using Wilcoxon matched-pair tests. To evaluate the
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39 165 significance of results we calculated the 95 % confidence interval for the median difference
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41 166 between males and females (Daniel 1978), as suggested by Colegrave and Ruxton (2003).
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44 167 The proportion of coordinated behaviors was usually high (see Results); however, to
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46 168 determine if one sex was more prone to assume a larger involvement in a particular task by
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48 169 repeating uncoordinated behaviors, we described and compared the frequency of
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51 170 uncoordinated behaviors made by each sex during the nesting cycle using the same methods
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54 171 described above. We used STATISTICA 7.0. Statsoft Inc.
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174 RESULTS

175 We tracked 59 nests during this study. Sixty-two percent of nests (37/59) were successful and
176 fledged at least one young. Main causes of nest failure were predation (66 %, $n = 15$), nest
177 falls after extraordinary heavy rain (30%, $n = 7$), and nest abandonments after egg punctures
178 inflicted by brood parasitic Shiny Cowbirds, *Molothrus bonariensis* (4%, $n = 1$). Four nests
179 were parasitized by Shiny Cowbirds and in all cases the cowbird egg was ejected by Rufous
180 Horneros.

181

182 SEXUAL EFFORT AND COORDINATION IN PARENTAL CARE

183 Both males and females participated actively and equitably in nest building chores with some
184 exceptions. During the initial building stage, females carried material significantly more often
185 to the nest than males (Table 1). Although the proportion of coordinated visits was high (0.7
186 and 0.7 for building and mud-carrying visits, respectively) the frequency of uncoordinated
187 behaviors showed females were more prone to repeat the mud-carrying behavior before their
188 partners did (Table 2). During the advanced nest building stage there was a high proportion of
189 coordinated building behavior (0.8), while mud-carrying behavior was less so (0.4).
190 Nonetheless, neither sex was more prone to behave without coordination than the other
191 (Table 2).

192 Both sexes contributed similarly to incubation, but showed some differences at the
193 onset of incubation. Females made more early incubation visits than males and those visits
194 tended to be longer, but no differences in number and length of incubation visits occurred
195 during the middle and advanced incubation periods (Table 3). The proportion of coordinated
196 visits was very high (0.8, 0.8 and 0.9 during the initial, middle and advanced incubation). The
197 frequency of uncoordinated visits was too small to allow statistical comparison. During the
198 initial nestling period females fed chicks more often than did males. Though males brooded

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3 199 often and actively, females brooded slightly more often than males and for longer periods
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5 200 (Table 4). At this early age no adult was seen carrying fecal sacs away from the nest. During
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7 201 the middle and advanced nestling period when nestlings were 11 and 18 days of age,
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9 202 respectively, no differences in feeding and fecal sac removal rates of males and females were
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11 203 found (Table 4). During the early nestling period, although behaviors were coordinated in
12
13 204 high proportion (0.7 and 0.6 of feeding and brooding visits, respectively), we found
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15 205 differences between the sexes: uncoordinated visits to feed and brood were made more often
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17 206 by females (Table 2). The proportion of coordinated feeding visits fell to 0.5 and 0.5 during
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19 207 the middle and late nestling periods, but the frequency of uncoordinated visits was similar
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21 208 between the sexes (Table 2). The frequency of male and female sac-removal visits during the
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23 209 last two stages was similar (Table 4), and too small to detect if uncoordinated behaviors were
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25 210 made more often by one or the other sex.
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34 212 DISCUSSION

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36 213 This study within the Furnariidae family demonstrates that parental care is equally distributed
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38 214 and highly coordinated between male and female Rufous Horneros. Our results show that
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40 215 females build at the same or a slightly higher rate than males during the early stage of nest
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42 216 construction and that they were responsible for a relatively smaller coordination of mud-
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44 217 carrying visits during the advanced nest building stage. The paramount task of building
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46 218 Rufous Hornero's nest is a compelling example of the amount of parental effort birds may be
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48 219 willing to commit even before the eggs are laid. Because it is unlikely that the building of this
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50 220 nest could be attempted by a single or insufficiently aided partner, we suggest the
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52 221 coordination showed during nest building might serve as an indication of the general
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54 222 compatibility between the partners and the overall parental care each individual might
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56 223 provide during the rest of the reproductive effort. The idea that early effort might indicate
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3 224 later compatibility in this species, however, needs to be studied using repeated measures of
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5 225 behavior across the nesting cycle.

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8 226 Males, in turn, were more involved than females in early incubation but contributed
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10 227 the same as females during middle and late incubation. The proportion of coordinated
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12 228 behavior during early and middle incubation was high (0.8) and rose to 0.9 by late
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14 229 incubation; the uncoordinated visits were so few that their numbers preclude any statistical
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16 230 comparison. Male participation in incubation has been described to be smaller than that of
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18 231 females in some species (Reid et al. 2002b, Bartlett et al. 2005) and equal or higher in others
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20 232 (Van Roo et al. 2003, Auer et al. 2006, Hogstad 2009), but those investigations did not
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22 233 evaluate the degree of coordination of the behavior between the sexes. The elevated
23
24 234 coordination of incubation behavior might affect hatching and nesting success, eventually
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26 235 determining the duration of the pair bond between years. Delays in incubation relays are
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28 236 known to affect pair bond duration in marine birds within the reproductive season, usually
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30 237 constrained by energetic demands (Davis 1988, Dearborn 2001). A similar scenario would
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32 238 not be expected in a year round territorial species as the Rufous Hornero, but could be of
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34 239 importance in divorce rates as occurs in the territorial Lesser Spotted Woodpecker
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36 240 *Dendrocopos minor* (Wiktander et al. 2000). This aspect of Rufous Horneros behavior awaits
37
38 241 further study.

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41 242 Rufous Hornero males also participated actively in brooding, though females made
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43 243 more and longer visits than males. Although pairs showed relatively high coordination in
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45 244 brooding nestlings, females made more uncoordinated visits than males. This rather small
46
47 245 difference in brooding behavior between the sexes is surprising as males of other species are
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49 246 not often involved in this task. Finally, we found no differences in feeding rate in two out of
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51 247 three nestling stages and no differences in sac-removal rates. The majority of feeding visits
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3 248 were coordinated during the nestling period, and uncoordinated visits were similar in
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6 249 frequency for males and females.
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8 250 Significant biparental care is generally associated with monogamy and is most
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10 251 common among birds (Lack 1968). However, since the earliest applications of molecular
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12 252 paternity-assessment techniques to avian systems (Burke and Bruford 1987), this was found
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15 253 to not to be always be the case. A comparative study made by Owens and Hartley (1998)
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17 254 showed that social monogamy was related to absent or reduced sexual size dimorphism, and
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19 255 species with absent or reduced sexual size dimorphism tended to show a low rate of extra-
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22 256 pair mating and extra-pair paternity. Rufous Horneros are good candidates to show social and
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24
25 257 genetic monogamy, as suggested by Remsen (2003) because: a) they show reduced sexual
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27 258 size and color dimorphism (at least to the human eye), b) pairs remain together throughout
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29 259 the breeding season and sometimes during multiple years (Fraga 1980), c) the construction of
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32 260 an oven nest that weighs up to 80 times the weight of each bird is a monumental task, likely
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34 261 impossible to be attempted by a single individual, d) Rufous Horneros are territorial year
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36 262 round, forage together, and both sexes repel conspecifics from the territory (Fraga 1980), e)
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38 263 they sing in duets, a characteristic associated with high levels of territorial and pair defense
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41 264 from conspecifics (Hann et al. 2004), and f) both sexes have high and equitable investment in
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43 265 all stages of the reproductive effort. The equitability and high coordination of parental duties
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45 266 shown in this study suggest males have high confidence on their paternity and invest on the
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48 267 nestlings accordingly, making this species a good candidate in which to expect genetic
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51 268 monogamy. Future studies of paternity will allow this hypothesis to be tested.
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53 269

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Table 1: Median, lower and upper quartiles of rates of nest building and mud carrying visits made by males and females during the initial and advanced stage of nest building (see Methods). The effort of each sex is compared using Wilcoxon matched-pairs test and the 95 % confidence interval for the difference between males and females median values (M diff. ♂ - ♀).

Stage	Variables	Males			Females			Wilcoxon matched-paired test					
		25%	Median	75%	25%	Median	75%	<i>T</i>	<i>df</i>	<i>P</i>	-95%	M diff. (♂ - ♀)	+95%
Initial (<i>n</i> =12 pairs)	Building visits x hr ⁻¹	2.6	6.3	9.8	3.4	7.2	11.3	22	11	0.18	-8.5	-1.5	1.5
	Mud carrying visits x hr ⁻¹	0.8	3.5	5.7	0.6	5.6	8.6	10	11	0.02	-2.75	-1.5	-0.3
Advanced (<i>n</i> =19 pairs)	Building visits x hr ⁻¹	1	1.5	6.5	1	3	7.5	25	18	0.48	-1.5	-0.5	0.5
	Mud carrying visits x hr ⁻¹	0.5	2.5	8	3.5	5.5	7.5	23	18	0.21	-3.5	-2.5	0.5

Table 2: Frequency of uncoordinated behaviors made by males and females during different stages of the nesting period (see Methods). The contribution of each sex is compared using Wilcoxon matched-pairs test and the 95 % confidence interval for the difference between male and female median values (M diff. ♂ - ♀).

Variables	Males			Females			Wilcoxon match-paired test						
	25 %	Median	75 %	25 %	Median	75 %	<i>T</i>	df	<i>P</i>	- 95 %	M diff. (♂ - ♀)	+ 95 %	
Nest building													
Initial (<i>n</i> =12 pairs)	Building visits x hr ⁻¹	2.6	6.3	9.8	3.4	7.2	11.3	22	11	0.18	-8.5	-1.5	1.5
	Mud carrying visits x hr ⁻¹	0.8	3.5	5.7	0.6	5.6	8.6	6.5	11	0.02	-2.75	-1.75	-0.75
Advanced (<i>n</i> =19 pairs)	Building visits x hr ⁻¹	0.5	0	1.25	1.5	0.5	3.5	29.5	18	0.15	-1.25	-0.5	0.15
	Mud carrying visits x hr ⁻¹	0	0	0.5	0.5	0	1	19.5	18	0.23	-1	-0.5	1
Feeding and Brooding													
Initial feeding period (<i>n</i> =23 pairs)	Feeding x hr ⁻¹	1	2	3	5	2	8	48.5	22	0.006	-1.5	-2.5	4.5
	Brooding x hr ⁻¹	0	0	1	2	1	3	25	22	0.009	-2.75	-1.75	-0.75
Middle feeding period (<i>n</i> =23 pairs)	Feeding x hr ⁻¹	0.5	0	1.25	1.5	0.5	3.5	29.5	22	0.15	-1.25	-0.5	0.15
Final feeding period (<i>n</i> =12 pairs)	Feeding x hr ⁻¹	2.75	5.25	11.5	2.75	4.75	9.5	37	11	0.87	-2	-0.25	7.5

Table 3: Median, lower and upper quartiles of the length (min:sec) and frequency of incubation bouts made by males and females during the initial, middle and advanced stage of incubation period (see Methods). The effort of each sex is compared using Wilcoxon matched-pairs test and the 95 % confidence interval for the difference between males and females median values (M diff. ♂ - ♀).

Stage	Variables	Males			Females			Wilcoxon matched-paired test					
		25%	Median	75%	25%	Median	75%	<i>T</i>	df	<i>P</i>	-95%	M diff. (♂ - ♀)	+95%
Initial (n=23 pairs)	Mean length of visits (min:sec)	04:50	07:40	13:40	06:40	12:30	19:22	82	22	0.09	00:00	03:50	04:30
	Visits x hr-1	0.7	1.4	2.0	1.5	1.7	2.48	48	22	0.03	-1.0	-0.7	-0.2
Middle (n=19 pairs)	Mean length of visits (min:sec)	00:00	11:20	49:30	05:40	14:50	40:30	74	22	0.15	00:00	02:20	05:20
	Visits x hr-1	0	1.9	2.8	0.5	1.9	2.8	58	22	0.60	-0.5	-0.1	0.3
Advanced (n=21 pairs)	Mean length of visits (min:sec)	09:00	12:50	17:00	14:00	15:30	17:40	47	22	0.16	00:00	02:50	06:10
	Visits x hr-1	1.0	1.6	2.1	1.4	1.6	2.2	23	22	0.37	-0.5	-0.2	0.3

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Table 4: Median, lower and upper quartiles of variables measured in the initial nestling period (feeding, brooding visits, and length of brooding visits (min:sec) made by males and females), and feeding and sac-removal visits during the middle and advanced nestling period (see Methods). The effort of each sex is compared using Wilcoxon matched-pairs tests and 95 % confidence interval for the difference between males and females median values (M diff. ♂ - ♀).

Stage	Variables	Males			Females			Wilcoxon matched-paired test					
		25%	Median	75%	25%	Median	75%	T	df	P	-95%	M diff. (♂ - ♀)	+95%
Initial (n=14 nests)	Feeding visits x nestling ⁻¹ x hr ⁻¹	1.1	1.6	2.4	1.5	1.9	2.5	68	13	0.03	-0.6	-0.3	-0.1
	Brooding visits x nestling ⁻¹ x hr ⁻¹	0.5	0.7	0.9	0.7	0.9	1.2	39	13	0.04	-0.4	-0.02	-0.05
	Average brooding (min:sec)	07:10	09:50	14:10	09:40	14:00	18:00	68	13	0.03	00:00	05:10	12:10
Middle (n=15 nests)	Feeding visits x nestling ⁻¹ x hr ⁻¹	3.2	4.1	4.8	2.1	3.6	5.6	77	13	0.30	-0.3	0.4	0.9
	Sac-removal visits x nestling ⁻¹ x hr ⁻¹	0.2	0.4	0.7	0.2	0.3	0.5	81	13	0.57	-0.1	0.10	0.12
Advanced (n=21 nests)	Feeding visits x nestling ⁻¹ x hr ⁻¹	4.7	5.7	8.9	4.2	6.3	6.9	85	13	0.45	-0.5	0.5	1.6
	Sac-removal visits x nestling ⁻¹ x hr ⁻¹	0.6	0.7	1.1	0.5	0.8	1.0	95	13	0.48	-0.1	0.0	0.4