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## REVERSED SEXUAL DIMORPHISM AND DIFFERENTIAL PREY DELIVERY IN BARN OWLS (*TYTO ALBA*)

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**ABSTRACT.**—We studied reversed sexual dimorphism (RSD) and foraging behavior of Barn Owls (*Tyto alba*). Bill length, tarsus length, wing chord, tail length, and mass of Barn Owls showed RSD. Mass of the prey items brought by the males was significantly less than that brought by females, which may be attributed to the positive correlation between size of the owl and prey mass. However, male owls had a significantly higher frequency of visits with prey than did females. There was relatively little overlap in the species and mass of prey captured by males and females, suggesting that food-niche partitioning between the sexes may exist, possibly to reduce intersexual food competition. Further, because these differences were also observed between the male and female owls within each pair, our findings support reproductive role division as a possible explanation for RSD in Barn Owls.

**KEY WORDS:** *Barn Owl*; *Tyto alba*; diet; prey size; reproductive role division; reversed sexual size dimorphism.

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### DIMORFISMO SEXUAL REVERTIDO Y ENTREGA DIFERENCIAL DE PRESAS EN *TYTO ALBA*

**RESUMEN.**—Estudiamos el dimorfismo sexual revertido (DSR) y el comportamiento de forrajeo de *Tyto alba*. El largo del pico, el largo de los tarsos, el largo de la cuerda alar, el largo de la cola y la masa de *T. alba* evidenciaron DSR. La masa de las presas traídas por los machos fue significativamente menor que la de las presas traídas por las hembras, lo que puede ser atribuido a la correlación positiva entre el tamaño de la lechuza y la masa de la presa. Sin embargo, las lechuzas macho tuvieron una frecuencia de visitas con presa significativamente mayor que la de las hembras. Hubo relativamente poco solapamiento en la identidad específica y en la masa de las presas capturadas por los machos y las hembras, lo que sugiere que puede existir una partición en el nicho de alimento entre los sexos, posiblemente para reducir la competencia intersexual por el alimento. Debido a que estas diferencias se observaron también entre las lechuzas macho y hembra dentro de cada pareja, nuestros hallazgos apoyan la división del rol reproductivo como una posible explicación para la ocurrencia de DSR en *Tyto alba*.

[Traducción del equipo editorial]

Reversed sexual dimorphism (RSD; females larger than males) is common among raptors. A number of hypotheses have been proposed to understand its evolution; these can be broadly grouped under one or a combination of three explanations: sexual selection, reproductive role division, and intersexual food competition. Sexual selection can favor RSD if females choose males that are smaller so females can easily dominate them during the breeding season (Mueller 1986) or because the smaller males will be better at foraging (Lundberg 1986) as aerial agility increases with reduction in size (Korpi-

mäki 1986). Reproductive role division can favor RSD under conditions of limited resources, when larger females with extra body reserves will be better able to survive (Lundberg 1986, Korpimäki 1986). Intersexual food competition can enable food-niche partitioning between sexes, thus favoring RSD (Longland 1989). Studies have suggested that size of prey delivered and delivery rates differ between the sexes (Eldegard et al. 2003, Slagsvold and Sørnerud 2007); for example, larger female size enables the female to provide larger prey to the young (von Schantz and Nilsson 1981). Few studies have investigated this hypothesis in raptors (Olsen and Olsen 1987, Sunde et al. 2003).

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The Barn Owl (*Tyto alba*) is a common raptor that exhibits RSD. This species is distributed widely across the Indian subcontinent and breeds in tree hollows or in human-made cavities (Ali and Ripley 1986, Pande et al. 2003). We investigated intersexual food competition and reproductive role division, as predicted by RSD, by studying differences in mass of prey delivered, prey delivery rates, and food types delivered by paired male and female Barn Owls.

#### METHODS

We studied Barn Owls at seven nests in the urban fringe around Pune (18°11'N, 74°15'E), western Maharashtra state, India. All nests were in unused residential buildings and the nests were targeted for removal; thus, we easily obtained access that facilitated our study.

We conducted our study during two owl breeding seasons. Four nests were monitored during October 2005 and three nests were monitored during October 2006. At each nest, we captured both members of the breeding pair. Females were identified by the prominent brood patch, which was absent in males. To further identify sex differences, we recorded several morphometric measurements for each owl, including flattened wing chord length (distance between carpo-metacarpal joint and the tip of the longest primary feather), tail length (distance from the base of tail to the tip of longest feather), bill length (from distal edge of the cere to the tip of the bill), total tarsus length (tibiotarsus to the tarso-metatarsus) and body mass. We ringed only the female of each pair to facilitate identification of individual owls during nest observations.

To investigate prey deliveries made by male and female owls, we monitored each nest for 36 hr total (12 hr on each of three consecutive nights; for seven nests together, observations totaled 252 hr) from hides located between 3 to 4 m from the nests. At the time of these observations, nestlings in all nests were 6–12 d old. The average number of nestlings per nest was 3 (range 2–4).

The mass of all prey items brought by both parents to the nest was estimated using an electronic weighing balance (accurate to 0.1 g) that was placed at the entrance of the nest in such a manner that the parent owls, when delivering prey, perched on the balance every time before entering the nest. The digital indicator was placed in the hide where the total mass of owl with prey was recorded. Mass of the prey was determined by subtracting the known mass of the parent owl from the total mass. Owls perched

on the balance for 1–2 min during each prey delivery, which gave us adequate time to photograph and identify the prey species. Prey species were identified using Menon (2003) and Prater (1971) and with assistance from the Zoological Survey of India, Pune. We recorded the number of prey deliveries made by both male and female owls, separately, for each of the seven pairs.

To assess the degree of dimorphism, we calculated the Dimorphic Index for each morphological character (Storer 1966, Ansara-Ross et al. 2008), for both members of each owl pair using the formula:

Dimorphic Index =

$$\frac{100 (\text{Parameter of female} - \text{Parameter of male})}{0.5 (\text{Parameter of female} + \text{Parameter of male})}$$

Each parameter was the mean value of a given character, except in the case of mass, where mean value of the cube root of mass was used. We used an unpaired *t*-test to further examine differences between each morphological character for males and females. We report mean and standard deviation for all measured variables.

Principal component analysis (PCA) was used to evaluate differences between male and female morphology and to identify variables that were most important in depicting the difference between the males and females. To account for the unit and scale differences between different morphological characters, we used PCA on the correlation matrix of the variables. We performed Bartlett's sphericity test with the null hypothesis that there was no correlation between variables (Harris 2001). A correlation biplot was used to visualize PCA results (Legendre and Legendre 1984). PCA was performed in SYSTAT 12 (SYSTAT 2011).

We used a Mann-Whitney *U*-test to investigate whether the number of prey deliveries made during the three consecutive observation periods and the mass of prey per delivery differed between males and females, for all nests combined. We used Wilcoxon's signed-rank test to investigate whether the number of prey deliveries made during the three consecutive nights of observation and the mass of prey per delivery differed between the male and female of each pair.

Canonical Correlation Analysis (CCorA) was used to evaluate associations between the mass of prey delivered and number of prey deliveries as dependent variables with the morphometric measurements of the Barn Owls as independent variables

Table 1. Female Barn Owls were significantly larger than males, based on all measurements taken on breeding pairs at seven nest sites in western Maharashtra, India.

CHARACTER	MEAN (SD)		<i>t</i>	<i>P</i>	MORPHOMETRIC INDEX
	MALES ( <i>n</i> = 7)	FEMALES ( <i>n</i> = 7)			
Wing (mm)	272.1 (7.1)	309.9 (17.1)	-5.396	<0.001	12.85
Bill (mm)	34.6 (0.8)	36.4 (01.3)	-3.284	0.007	5.19
Tarsus (mm)	63.0 (1.0)	68.6 (01.9)	-6.859	<0.001	8.44
Tail (mm)	117.0 (2.9)	122.7 (04.4)	-2.879	0.014	4.74
Body mass (g)	451.9 (4.2)	506.9 (07.0)	-17.828	<0.001	3.83

(Legendre and Legendre 1984). The significance of canonical correlations was determined using Wilks' lambda and Bartlett's chi-square test (Akbaş and Takma 2005). CCorA was performed in freeware Biplot 1.1 (Smith and Lipkovich 2002).

#### RESULTS

Female Barn Owls were larger than males, overall, for all measured morphometric variables (Table 1). Results of PCA indicated that the first factor explained 75.2% of the total variation in the data while the second explained 15.0% (Fig. 1). Males and females were separated mainly on the first PCA axis, which had high factor loading for all measured morphometric characters. Loading values for mass were highest followed by wing, tail, bill, and tarsus in decreasing order.

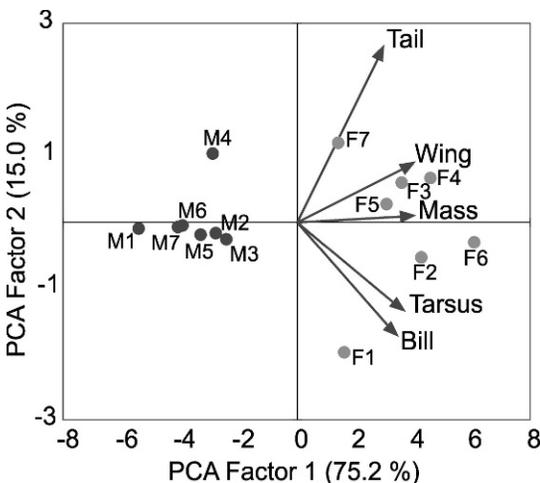


Figure 1. Female Barn Owls were larger than males for all morphometric measurements in decreasing order from body mass, wing chord, tail length, bill length, and tarsus length. Number associated with the male (M) and female (F) is the pair number.

During a total of 252 hr of observations, we observed 106 prey deliveries (representing 12 species, Table 2) combined for all seven nests (67 deliveries by the males and 39 by the females), and one prey item was brought per delivery (Table 3). All prey items were directly deposited in the nest by the delivering parent and there was no exchange of prey between male and female parents before delivery, eliminating concerns about prey delivery bias (Steen 2010). Of the 12 prey species delivered to nests, males delivered six species and females delivered nine species (three in common with the males; Table 2). Common house shrew (*Suncus murinus*) was the prey most frequently brought by males (54%) and lesser bandicoot rat (*Bandicota bengalensis*) was the prey most frequently delivered by females (50%). Both male and female owls delivered common house shrews (delivery frequency by males was 52% and females 10%), house mouse (*Mus musculus*; males, 9%; females, 3%), and Indian bush rat (*Golunda elliotii*; males, 4%; females, 3%) to the nests (Table 2).

Males (*n* = 7) made more prey deliveries ( $9.6 \pm 2.7$ ) during the 36 hr of observation at each nest, compared to females (*n* = 7;  $5.6 \pm 2.1$  deliveries, Mann-Whitney  $U = 43.50$ ,  $P = 0.01$ ; Fig. 2a). For all nests combined, the average prey delivery rate for males was  $0.27 \pm 0.07$  items per hr and for females was  $0.15 \pm 0.12$  items per hr (Table 3). However, males delivered prey at a significantly higher rate than their respective females (Wilcoxon's signed-rank test  $W = 7.5$ ,  $P = 0.057$ ) only at five nests (Table 3). For all nests combined, females brought heavier prey per delivery ( $87.1 \pm 27.8$  g) than did males ( $29.5 \pm 9.9$  g,  $U = 127.5$ ,  $P < 0.01$ ; Fig. 2b); this was also true for females compared to males, for each pair separately (Wilcoxon's signed-rank test  $W = 14$ ,  $P = 0.016$ ; Table 3). The frequency distribution of the prey masses delivered by male and female Barn Owls showed little overlap (Fig. 3).

Table 2. Frequency of delivery of different prey items brought to the nest by male and female Barn Owls during 36 hr of observation at each nest conducted in October 2005 and October 2006 at seven nests near Pune, western Maharashtra state, India. Males delivered a total of 67 items, females a total of 39 items.

PREY ITEMS	FREQUENCY OF DELIVERY		AVERAGE MASS OF PREY IN GRAMS (SD)	
	MALE	FEMALE		
<b>Rodentia</b>				
<i>Bandicota bengalensis</i>	Lesser bandicoot rat	0.00	0.50	99.6 (14.1)
<i>Bandicota indica</i>	Large bandicoot rat	0.00	0.08	112.5 (13.6)
<i>Rattus rattus</i>	House rat	0.00	0.13	66.4 (12.4)
<i>Rattus satarensis</i>	Satara house rat	0.00	0.05	108.0 (11.3)
<i>Mus musculus</i>	House mouse	0.09	0.03	19.0 (1.9)
<i>Mus saxicola</i>	Elliot's spiny mouse	0.27	0.00	24.1 (3.7)
<i>Mus booduga</i>	Little Indian field mouse	0.07	0.00	18.0 (1.6)
<i>Gohunda elliotii</i>	Indian bush rat	0.04	0.03	64.3 (10.3)
<i>Milardia meltada</i>	Soft-furred field rat	0.00	0.05	99.0 (1.4)
<b>Insectivora</b>				
<i>Suncus murinus</i>	Common house shrew	0.52	0.10	33.1 (5.9)
<b>Chiroptera</b>				
<i>Cynopterus sphinx</i>	Greater short-nosed fruit bat	0.01	0.00	46.0 (0.0)
<i>Rousettus leschenaulti</i>	Indian fulvous fruit bat	0.00	0.03	60.0 (0.0)

Canonical Correlation Analysis revealed significant correlation between variables (Wilks' lambda =  $6.59 \times 10^{-5}$ , Bartlett's  $\chi^2 = 981.84$ ,  $P < 0.01$ ) and the first canonical axis explained 97.2% of the total variation. On the first canonical axis, the morphometric variables were positively correlated with the number of prey deliveries ( $\rho = 0.76$ ,  $P < 0.05$ ), but negatively correlated with the mass of prey delivered ( $\rho = -0.64$ ,  $P < 0.05$ ). Canonical correlations were significant for owl body mass ( $\rho = 0.92$ ,  $P < 0.05$ ), followed by tarsus length ( $\rho = 0.89$ ,  $P < 0.05$ ), wing length ( $\rho = 0.73$ ,  $P < 0.05$ ) and bill length ( $\rho = 0.71$ ,  $P < 0.05$ ; Fig. 4). We found a

negative correlation between mass of the prey delivered and the number of prey deliveries to the nest.

DISCUSSION

Prey delivery behavior of Barn Owls at our nest sites supported predictions of reversed sexual dimorphism. Unlike Sunde et al. (2003), who observed no food niche partitioning in Tawny Owls (*Strix aluco*), we observed little overlap in the prey size, prey delivery rates, and types of prey delivered by male and female Barn Owls at all nests. Of the 12 prey species, males exclusively delivered three prey

Table 3. Prey deliveries by male and female Barn Owls at seven nests during 36 hr of observation at each nest, near Pune, western Maharashtra state, India. The number of prey deliveries/hr are given in parentheses after the number of deliveries by each individual.

NEST	NUMBER OF PREY DELIVERIES		AVERAGE MASS (g) OF PREY DELIVERED (SD)	
	MALE	FEMALE	MALE	FEMALE
1	11 (0.3)	8 (0.2)	26.6 (5.4)	92.5 (24.5)
2	9 (0.3)	14 (0.4)	34.7 (15.2)	78.6 (36.2)
3	5 (0.1)	1 (0.1)	31.6 (5.0)	106.0 (0.0)
4	12 (0.3)	4 (0.1)	31.3 (8.8)	95.5 (24.6)
5	12 (0.3)	4 (0.1)	25.3 (4.5)	87.0 (33.6)
6	11 (0.3)	4 (0.1)	34.9 (12.9)	86.0 (16.3)
7	7 (0.2)	4 (0.1)	21.9 (5.1)	93.5 (5.3)

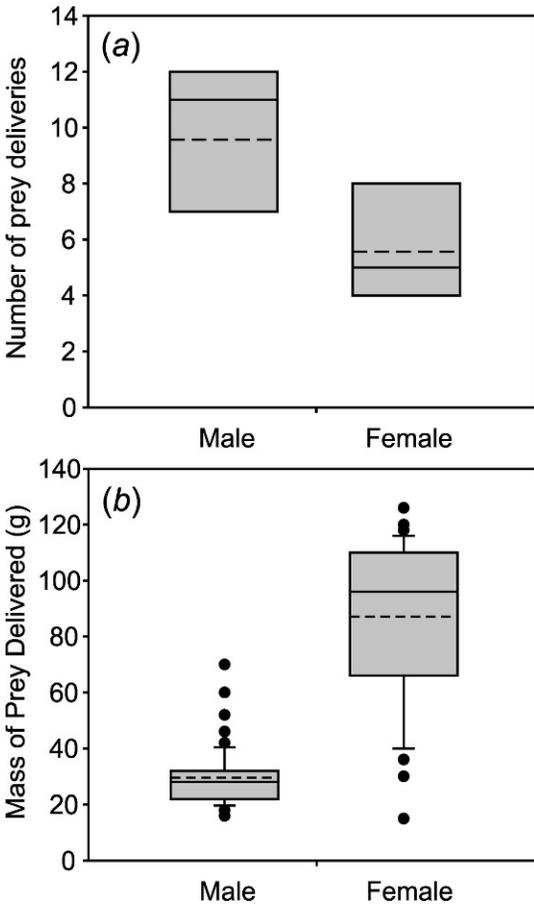


Figure 2. Sex difference in number of prey deliveries (a) and mass of prey per delivery (b) made by Barn Owls at seven nests near Pune, western Maharashtra state, India. The upper and lower edges of the box indicate the 75th and 25th percentile, respectively; the dashed line is the mean and solid line is the median; error bars are 1.5 times the inter-quartile range, while the points outside this range are outliers ( $n =$  seven male and seven female owls).

species, while females exclusively delivered six prey species. Although both males and females delivered common house shrews, house mice, and Indian bush rats, the frequency of delivery of these prey species was higher for males than females.

The smaller males brought smaller prey and had higher prey delivery rates than did the larger females, suggesting that food-niche partitioning between sexes may exist, possibly to reduce intersexual food competition (i.e., Olsen and Olsen 1987). Our findings support intersexual food competition, as is evident from the differences in the species and biomass of the prey captured by male and female owls

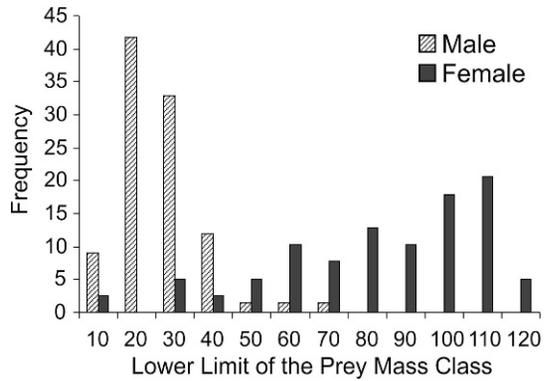


Figure 3. Little overlap was seen in the frequency of prey mass classes delivered by paired male and female Barn Owls at seven nests near Pune, western Maharashtra state, India.

(Longland 1989, Eldegard et al. 2003, Slagsvold and Sonerud 2007). Further, because these differences were also observed between the male and female owls within each pair, our findings support reproductive role division as a possible explanation for RSD in Barn Owls.

The dietary spectrum of Barn Owls in India was mentioned by Neelnarayanan (2007); however, he did not compare the prey species delivered by males and females. Although, to our knowledge, there are no reports that compare prey deliveries in male and female Barn Owls, a few studies are available for Australian Masked-Owls (*Tyto novaehollandiae*; Todd

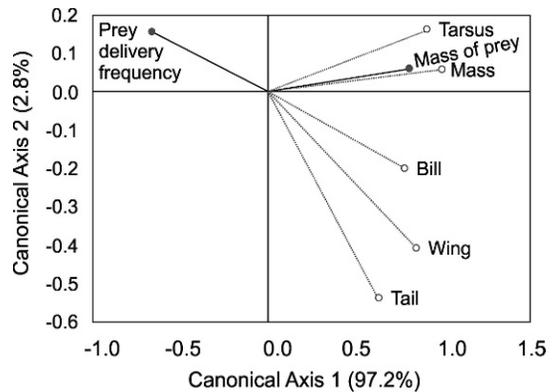


Figure 4. As depicted by Canonical Correlation Analysis, mass of prey delivered to Barn Owl nests was positively correlated with owl body mass and tarsus length. Number of deliveries made during the 36-hr observation period at each nest was negatively correlated with the mass of the prey per delivery. Percentages in parenthesis are the percent variation explained by each canonical factor.

2006), Tawny Owls *Strix aluco*; Sunde 2003), three subspecies of Eastern Screech-Owls (*Megascops asio*) and Northern Pygmy-Owl (*Glaucidium gnoma*; Earhart and Johnson 1970). Thus, our study was unique because we addressed the food-niche partitioning between sexes and reproductive role division as a cause for RSD in owls.

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