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"Wife-sharing" in the Tasmanian Native Hen (*Gallinula mortierii*): Is it Caused by a Male-biased Sex Ratio?

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In many cooperatively breeding species of birds, adult males are thought to outnumber adult females (e.g. Red-cockaded Woodpecker [*Picoides borealis*], Gowaty and Lennartz 1985; Splendid Fairy-Wren [*Malurus splendens*], Rowley and Russell 1990; Pied Kingfisher [*Ceryle rudis*], Reyer 1990; see Emlen 1984, Brown 1987). The occurrence of male-biased sex ratios in some populations of species with helpers-at-the-nest has led to the hypothesis (the differential mortality model of Emlen et al. [1986]) that a shortage of females could explain—at least in part—delayed dispersal, helping behavior, and mate-sharing by males (Rowley 1965, Maynard Smith and Ridpath

1972, Emlen 1984, Curry and Grant 1989, Reyer 1990, Davies 1992). A shortage of females might result from a higher rate of mortality compared with males, perhaps associated with female-biased dispersal. An experimental test on Superb Fairy-Wrens (*Malurus cyaneus*) provided support for this model (Pruett-Jones and Lewis 1990).

A classic example in the debate on the link between sex ratios and cooperative breeding is the Tasmanian Native Hen (*Gallinula mortierii*). Ridpath (1972b) reported male-biased sex ratios among both adults (1.5 males per female) and chicks (2.8 males per female) in his study population, and an overall sex ratio of 1.22 males per female among 489 individuals collected near his study area and sexed by dissection. Maynard Smith and Ridpath (1972) used

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this evidence to propose that a male-biased sex ratio sets the stage for the occurrence of "wife-sharing" in this species by causing a shortage of available breeding females. This case has been cited in reviews as an example where male-biased sex ratios may lead to mate-sharing by males (e.g. Oring 1986, Emlen et al. 1986, Emlen 1991). Here, we present data on sex ratios and mating patterns from two populations of Tasmanian Native Hens to challenge the assumption that cooperative breeding in this species occurs as a result of a male-biased sex ratio.

Tasmanian Native Hens are flightless rails endemic to Tasmania that live in areas with a combination of open pasture, dense vegetative cover, and water. Tasmanian Native Hens live in groups of 2 to 17 individuals that defend territories year-round (Ridpath 1972b). Their mating system includes frequent mate-sharing by both sexes, at least in some populations (Goldizen et al. 1998). Tasmanian Native Hens exhibit monogamy (a single male mated to a single female), cooperative polyandry (two or more males mated to a single female), polygyny (two or more females mated to a single male), and polygynandry (two or more males and two or more females all breeding together). In groups with multiple breeding females, the females lay eggs in communal clutches. In groups with multiple breeding males, all such males copulate with the female(s) and then assist with all aspects of parental care (Ridpath 1972a, b, Gibbs et al. 1994). Mate-sharing in Tasmanian Native Hens is more common among males than among females and usually involves closely related males (Ridpath 1972b). Helping behavior also is exhibited by some nonbreeding one- and two-year-olds of both sexes that remain in their natal groups (Ridpath 1972a, b, Gibbs et al. 1994), but such helping behavior usually is minor relative to that provided by breeding adults (Goldizen and Goldizen unpubl. data).

We studied our first Tasmanian Native Hen population in cattle pastures near Geeveston, in southern Tasmania, Australia (43°10'S, 146°55'E), from December 1988 to December 1989 (Goldizen et al. 1993). Our second study population inhabited an area of cleared pasture surrounded by eucalypt woodland at the northern end of Maria Island off the eastern coast of Tasmania (42°35'S, 148°04'E). We studied this population through the consecutive breeding seasons of September to December, 1990 to 1996. We observed the population continuously through each of these breeding seasons.

Birds were trapped, banded with numbered metal bands and unique combinations of color bands, weighed, measured, and aged; blood samples were collected as described by Gibbs et al. (1994). A total of 83 native hens was banded in the Geeveston population. At Maria Island, 135 of 146 birds present in the population were trapped and banded between December 1989 and August 1990. After that, all

young were banded between six weeks and three months of age; immigrants were banded as soon as possible after their establishment in the study population. In total, 371 birds were banded at Maria Island. We found no evidence for a sex bias in capture probability. Of the 11 birds that we failed to catch at Maria Island in 1990, 8 that we captured subsequently included four males and four females.

The sex of Tasmanian Native Hens cannot be distinguished by external characteristics. Ridpath (1972b) determined the sex of individuals either by behavior, which is reliable only for some individuals, or by dissection. We determined the sex of 74 individuals from the Geeveston population by laparoscopy or dissection. At Maria Island, we assigned the sex of 231 of the 371 captured birds by laparoscopy, 118 by genetic means, and 12 using other criteria (e.g. copulation positions). Sex could not be determined for 10 of the banded birds.

Sex determination by laparoscopy involved the direct examination of gonads using the procedures described in Gibbs et al. (1994). The surgical procedure had no observable negative effects on the birds; all 231 individuals that underwent surgery at Maria Island were alive and well at least one week after surgery. We did not resight all of the birds that underwent surgery at Geeveston, but we believe that this was due to a high level of social instability in that population (Goldizen et al. 1993). Sex determination by laparoscopy also was extremely accurate; no bird sexed by this method was observed behaving in a manner contradictory to its assigned sex. We used two different methods for the genetic determination of sex. The first employed techniques similar to those given in Millar et al. (1996), with the following modification: Because only a single female-specific DNA fragment was detected in Tasmanian Native Hens, a control gene, beta-actin, subsequently was hybridized to ensure the presence of sufficient high-quality DNA in those individuals assigned as males. The techniques used in the second method are described by Griffiths (unpubl. data). Copulation position was used to determine sex only if the bird was seen copulating more than once.

We monitored the compositions of most of the Maria Island groups daily through each breeding season. Data on the frequencies of the different mating patterns (monogamy, polyandry, polygyny, polygynandry) refer to the mating pattern of each group each year (group-year), either at the time when the group laid its first clutch of eggs or at the beginning of November (the middle of the breeding season), whichever came first. The criteria used to determine which birds were breeders are presented in Goldizen et al. (1998). We compiled data on adult sex ratios from the information on the memberships of all groups present in this population each year at the beginning of November. Adults included all individuals that hatched in the previous breeding season or earlier.

TABLE 1. Juvenile (i.e. hatched during current breeding season) and adult (i.e. hatched during a previous breeding season) sex ratios in the Maria Island population of Tasmanian Native Hens.

	1989	1990	1991	1992	1993	1994	1995	1996	All
				Juveniles					
No. of males	31	29	6	21	6	8	15	19	135
No. of females	29	19	11	20	5	8	13	18	123
No. unknown	0	0	1	6	0	0	1	0	8
Ratio M:F	1.07	1.53	0.55	1.05	1.20	1.00	1.15	1.06	1.10
G_{adj}[a]	0.066	2.077	1.450	0.024	0.087	0.000	0.140	0.027	0.557
P greater than	0.70	0.10	0.20	0.80	0.70	0.99	0.70	0.80	0.30
				Adults					
No. of males	—	72	88	86	83	75	71	75	—
No. of females	—	65	72	63	73	61	64	66	—
No. unknown	—	5	4	4	8	7	7	13	—
Ratio M:F	—	1.11	1.22	1.37	1.14	1.23	1.11	1.14	—
G_{adj}[a]	—	0.357	1.598	3.553	0.639	1.438	0.362	0.573	—
P greater than	—	0.50	0.20	0.05	0.30	0.20	0.50	0.30	—

[a] G-test with Williams' correction testing for departure from sex ratio of 1:1.

Immature sex ratios for the Maria Island population were calculated from the total of all male and female young that hatched and survived to the age of first banding (between six weeks and three months) each season. For the Geeveston population, because of smaller sample sizes and an inability to accurately determine the age of many individuals, we calculated a sex ratio based on all individuals of all ages trapped during 1988.

Results.—At Geeveston, 74 immatures and adults (an estimated three-quarters of the total population) were successfully sexed by laparoscopy or dissection; 9 others could not be sexed. The sex ratio of this sample was not significantly different from parity (35 males, 39 females; sex ratio = 0.90 males per female; G-test with Williams' correction, $G = 0.215$, df = 1, $P > 0.5$). The sex ratio of 266 immature birds that hatched at Maria Island during the 1989 through 1996 breeding seasons also was not significantly dif-
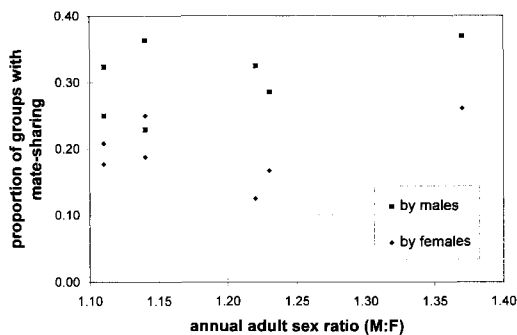

FIG. 1. Relationship between annual adult sex ratio and frequency of mate sharing by males and females in the Maria Island population of Tasmanian Native Hens.

ferent from 1:1 (1.10 males per female; Table 1). The sex ratios of the young that hatched during individual breeding seasons varied from 0.55 males per female in 1991 to 1.53 males per female in 1990. There was no significant sex-ratio bias for any year's cohort of young (Table 1). However, with such small yearly sample sizes, the chances of sex ratios being significantly biased are small (Koenig and Dickinson 1996).

The sex ratio of all adults in the Maria Island population ranged from a low of 1.11 males per female in 1990 and 1995, to a high of 1.37 males per female in 1992 (Table 1). We have no information on adult sex ratio for the 1989 season because we began banding in December 1989. No annual adult sex ratio was significantly different from 1:1 (Table 1). These separate annual sex ratios are not statistically independent because many individuals were present during successive years.

Of the 258 group-years for which the mating pattern was known with certainty, 56% were monogamous, 23% were polyandrous, 13% were polygynous, and 8% were polygynandrous. Thus, 31% of group-years exhibited mate-sharing by males, whereas females shared mates in 21% of group-years. The annual proportion of groups exhibiting mate-sharing by males varied from 0.23 (1996) to 0.37 (1992), whereas the proportion of groups exhibiting mate-sharing by females ranged from 0.13 (1991) to 0.26 (1992). There was no relationship between annual variation in sex ratios and mate-sharing frequencies for either males or females (rank regressions, $n = 7$; for males, $r^2 = 0.241$, $P = 0.263$; for females, $r^2 = 0.001$, $P = 0.938$; Fig. 1).

Each year there were many nonbreeding but reproductively mature birds present in their natal groups at Maria Island (Table 2). Tasmanian Native Hens are capable of breeding at one year of age; in-

TABLE 2. Number of nonbreeding adults in natal groups in the middle of each breeding season (i.e. 1 November) in the Maria Island population of Tasmanian Native Hens.

	1990	1991	1992	1993	1994	1995	1996
No. of males	22	28	14	13	13	8	9
No. of females	20	23	7	12	8	2	10

deed, most yearlings bred in Ridpath's study population (Ridpath 1972b).

Discussion.—In the two populations of Tasmanian Native Hens that we studied, sex ratios were not significantly male biased. In contrast to the small degree of male bias in our study population, Ridpath (1972b) reported sex ratios of 2.8 males per female among a sample of 68 immatures (four to six months old) and 1.5 males per female among 185 adults in his study population. Although the sex-determination procedures used by Ridpath are not totally reliable, it is unlikely that sexing errors alone accounted for the difference in the observed sex ratios between Maria Island and Ridpath's study site. It also is unlikely that Ridpath would have captured males more easily than females, because the patterns of habitat use by the sexes do not differ in any obvious way, and both sexes participate in territorial defense (Ridpath 1972a, b). It is not clear why the sex ratios of both immature and adult birds in Ridpath's population were more male biased than were the sex ratios in our populations. What is clear, however, is that not all populations of Tasmanian Native Hens are strongly male biased.

Despite differences in sex ratios between the Maria Island population and Ridpath's population at Hunting Ground in central Tasmania, the social systems exhibited by these two populations were quite similar (Ridpath 1972b, Goldizen et al. 1993, Gibbs et al. 1994, Goldizen and Goldizen unpubl. data). For instance, the percentage of group-years that displayed mate-sharing was 44% at Maria Island and 51% in Ridpath's population (Ridpath 1972b). The lack of a relationship between adult sex ratios and frequencies of mate-sharing in seven seasons at Maria Island (Fig. 1) provides further evidence that mate-sharing is not related to sex-ratio biases in this species.

Additional evidence against the hypothesized link between biased sex ratios and mate-sharing by males is provided by two other observations. First, in each year of our study at Maria Island, both males and females of reproductive age have remained in their natal groups without breeding (Table 2). This indicates that there is no shortage of available breeding birds of either sex, and this is the necessary link in Maynard Smith and Ridpath's (1972) argument. Second, mate-sharing also was commonly practiced by females, occurring in approximately 21% of all group-years at Maria Island (Fig. 1) and, in fact, was most frequent in 1992, the year with the most male-biased sex ratio. This last point makes it obvious that we need to examine alternatives to biased sex ratios to determine which factors are associated with mate-sharing in Tasmanian Native Hens.

Ridpath (1972b) also observed groups with multiple adult females in his study population at Hunting Ground, but Maynard Smith and Ridpath (1972) did not mention this in their discussion on the evolution of mate-sharing. Moreover, Ridpath (1972b) observed that most "roving" birds of both sexes (i.e. first-year birds searching for their first breeding position) eventually left the study area without settling. This suggests that potential mates were not in short supply.

In conclusion, the mate-sharing frequently exhibited by male and female Tasmanian Native Hens does not necessarily occur because of a lack of potential mates for either sex. Apparently, a slight male bias in the sex ratio existed in our Maria Island population, which may have affected the frequencies of mating patterns to some extent, but this sex bias does not explain the occurrence of mate-sharing in this species.

Our long-term study at Maria Island suggests that a shortage of high-quality breeding territories (i.e. territories with water and large amounts of edge between pasture and thick cover) is the limiting factor causing mate-sharing in this population. Multivariate models used to investigate relationships between reproductive success and a number of aspects of group compositions and territories found that breeding success was most significantly related to the amount of edge between pasture and thick cover (Goldizen et al. 1998). However, we do not understand how this link between territory quality and breeding success promotes mate-sharing.

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