

SIZE DIMORPHISM, INTRASEXUAL COMPETITION, AND SEXUAL SELECTION IN WATTLED JACANA (*JACANA JACANA*), A SEX-ROLE-REVERSED SHOREBIRD IN PANAMA

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ABSTRACT.—We studied sexual size dimorphism, intrasexual competition, and sexual selection in an individually marked population of Wattled Jacanas (*Jacana jacana*) in the Republic of Panama. Males are the sole incubators of eggs (28-day incubation) and primary providers of chick care (50–60 days). Females were 48% heavier than, and behaviorally dominant over, males. Females also showed greater development of secondary sexual characters (fleshy facial ornamentation and wing spurs) than males. Both sexes defended territories throughout the year against same-sex conspecifics. Competition for territorial space was intense, and many individuals of both sexes did not become breeders. Resident females further competed with one another to accumulate multiple mates, resulting in a mating system of simultaneous polyandry. Female and male residents (territory holders) were larger, heavier, and more ornamented than adult floaters of the same sex. Larger and heavier females also had more mates than smaller females. Body size was thus a critical predictor of success in intrasexual competition for territories (both sexes) and for mates (females). Three measures of sexual selection—(1) sex difference in the opportunity for sexual selection, (2) female-to-male ratio of potential reproductive rates, and (3) operational sex ratio—each indicated that sexual selection is currently operating more strongly on females than on males (female-to-male ratios ranged from 1.43:1 to 2.22:1). Values of 1.61:1 and 1.43:1 represent the first published quantitative estimates of the opportunity for sexual selection for any sex-role-reversed bird. Our study supports the theory that when increased parental care entails reduced opportunities for future reproduction, asymmetries in parental care behaviors of the sexes can influence the intensity of competition for mates and the direction and strength of sexual selection. Received 28 October 2002, accepted 2 December 2003.

RESUMEN.—Estudiamos el dimorfismo sexual en el tamaño, la competencia intrasexual y la selección sexual en una población de *Jacana jacana* con individuos marcados en la República de Panamá. Los machos son los únicos que incuban los huevos (la incubación toma 28 días) y son los principales encargados de cuidar a los pichones (50-60 días). Las hembras fueron un 48% más pesadas que los machos y fueron comportamentalmente dominantes sobre éstos. Las hembras también mostraron un mayor desarrollo de caracteres sexuales secundarios (ornamentaciones carnosas en la cara y espuelas en las alas) que los machos. Ambos sexos defendieron territorios contra individuos coespecíficos del mismo sexo a través del año. La competencia por el espacio territorial fue intensa, y muchos individuos de ambos sexos no se reprodujeron. Las hembras residentes además compitieron entre ellas por acumular múltiples parejas, lo que resultó en un sistema de apareamiento de poliandria simultánea. Las hembras y machos residentes (dueños de territorios) fueron más grandes, más pesados y más ornamentados que los adultos flotantes de su mismo sexo. Las hembras más grandes y pesadas también tuvieron más parejas que las hembras más pequeñas. Por lo tanto, el tamaño corporal fue un determinante crucial del éxito en la competencia intrasexual por territorios (ambos sexos) y por parejas (hembras). Cada una de tres medidas de selección sexual—(1) la diferencia entre sexos en la oportunidad de selección sexual, (2) la relación hembras-machos en las tasas reproductivas potenciales y (3) la proporción operacional de sexos—indicó que la selección sexual está operando actualmente con mayor intensidad en las hembras que en los machos (las relaciones hembras-machos variaron entre 1.43:1 y 2.22:1). Los valores de 1.61:1 y 1.43:1 representan las primeras estimaciones cuantitativas publicadas de la oportunidad de selección sexual en aves con roles sexuales revertidos. Nuestro estudio apoya la teoría que propone que cuando una mayor inversión en cuidado parental reduce las oportunidades para la reproducción futura, las asimetrías en los comportamientos de cuidado parental de los sexos pueden influenciar la intensidad de la competencia por parejas y la dirección y magnitud de la selección sexual.

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DIFFERENTIAL PARENTAL INVESTMENT lies at the heart of many evolutionary hypotheses about differences between the sexes. Parental investment was defined by Trivers (1972) as any investment by the parent in an offspring that increases the survival of that offspring while decreasing the parent's ability to produce or invest in additional offspring. It includes the cost of producing the gamete plus any additional effort expended on behalf of the offspring until the offspring becomes independent. In most organisms, females provide greater parental investment (gametic and parental care) than males. Assuming that increased parental investment involves a cost in terms of decreased availability for additional reproductive opportunities, the potential reproductive rate (PRR) of males will come to exceed that of females (Clutton-Brock and Vincent 1991), and the operational sex ratio (OSR; i.e. the ratio of reproductively available males to females) will become male-biased (Emlen 1976, Emlen and Oring 1977). Females, and the parental investment they provide, then become "limiting resources" for males, and males compete for access to females. Sexual selection then operates more strongly on males than females. It also influences processes that result in males being larger, more aggressive, and more ardent than females, and females being more choosy than males in selection of mates (Williams 1966, Trivers 1972, Andersson 1994).

When traditional sex roles become reversed, as may occur in species in which males provide a disproportionate share of postfertilization parental care, the aforementioned traits may be affected. If the reversal in parental care is strong enough, and if providing such care constrains opportunities for future reproduction enough, the direction of sexual selection may become reversed. Females rather than males will then be selected for greater competitiveness, larger body size, and increased ardor. That, in turn, may influence the mating system as well as the behavioral dynamics between the sexes.

Species that exhibit sex-role reversal and also provide intensive care for their young are rare. They are found in several groups of fishes (e.g. Vincent et al. 1992) and 35 species of birds (Jenni 1974; Oring 1982, 1985). Such species are of interest to evolutionary and behavioral biologists because they offer potential for answering questions about the evolutionary origins of sex-role reversal, male uniparental care, and

polyandrous mating systems. They also provide opportunities for studying cooperation and conflict between mated partners when females are the behaviorally dominant sex.

The family Jacanidae comprises eight species of shorebirds that have adapted to living on aquatic vegetation in freshwater wetlands throughout the Tropics. Seven of the eight species exhibit sex-role reversal, in which males are the sole incubators of eggs and provide the majority of care for the dependent young. Each of the seven species exhibits reversed sexual size dimorphism, whereby females are much larger than males.

We conducted a six-year study on an individually marked population of Wattled Jacanas (*Jacana jacana*) in Panama. Here, we (1) quantify the reversal in sexual size dimorphism between females and males; (2) examine body size as a predictor of territorial occupancy for females and males, and of subsequent mating success for females; and (3) estimate the direction and strength of sexual selection operating on the species.

METHODS

Study site.—We studied Wattled Jacanas on the Chagres River, 2.5 km northwest of the town of Gamboa, in the Republic of Panama. The river was ~0.9 km wide at that location, and it supported mats of floating aquatic vegetation on which hundreds of jacanas resided. We studied a 13-ha area (approximately 325 × 400 m) located near the center of the river. No part of the study area was closer than 0.20 km to the nearest shore, and water depth varied mainly between 4 and 9 m. The Chagres River is a permanent body of water and jacanas bred on it during all months of the year (S. T. Emlen and P. H. Wrege unpubl. data). Data were obtained during six field seasons (1990: March–June; 1991 and 1993: January–June; 1992: February–July; 1994 and 1995: January–December). Investigators varied from one to six persons, depending on time of year, with effort concentrated between February and June.

Study population.—On a monthly basis, an average of 18 resident females (range 4–29), 30 resident males (range 9–40), and a variably sized population of nonresident "floaters" occupied the 13-ha site. We attempted to capture all resident jacanas and a large number of floaters on the study area through a variety of techniques, including mist nets and walk-in traps. By the end of each field season, an average of 78% of all resident females and 90% of all resident males had been individually color-banded. All bands were placed above the tarsal-metatarsal joint to increase

visibility. Overall, 150 females, 311 males, and 172 juveniles were captured, banded, and measured.

Morphology.—Wattled Jacanas in Panama are sexually monomorphic in plumage and ornamentation. They are black birds with bright yellow bills and wing spurs, pale yellow wing patches, and reddish frontal shields and wattles. The frontal shield and wattles are fleshy protuberances. The shield extends from the upper mandible over the forehead, whereas the two wattles hang down on each side of the bill. The wing spurs are keratinous structures that grow anteriorly from the carpal-metacarpal joints. They are exposed whenever the wing is opened, as it is during agonistic displays (Jenni and Collier 1972).

At the time of capture, we measured: (1) mass (to nearest 1 g using a Pesola balance), (2) right tarsus (to 0.5 mm, measured on an angle block from back of heel to point between inner and middle toe), (3) right wing length (to 0.5 mm, as unflattened chord using a stopped ruler; measured only in 1990 and 1991), (4) bill length (to 0.1 mm, from proximal opening of the nares to tip, using calipers), and (5) right wing spur (to 0.1 mm, from proximal lip of the base to the tip, using calipers). Changes in morphology with age were examined by comparing values measured from 42 individuals recaptured and remeasured after intervals ranging from one to three years.

Because body size and mass are confounded, we regressed mass on tarsus length for each sex and used the residuals as a measure of weight that is independent of skeletal size. That "residual mass" (sometimes referred to as "condition") reflects how heavy an individual bird is for its body size. Values are distributed around a mean of zero; positive values denote birds that are heavy for their skeletal size, negative values indicate birds that are light for their skeletal size. To test whether characters were dimorphic after correcting for the allometric effects of body size, we performed multivariate analyses of variance with the trait of interest as the dependent variable and skeletal size (tarsus) and sex as predictor variables (Type I GLM in SAS).

We also quantified size and color of the fleshy facial shield and wattles. Size measures included (1) right shield height (from distal opening of the nares to the highest point on the right lobe of the frontal shield), (2) shield width (maximum left-to-right dimension), (3) shield area (right height \times width), (4) right wattle height (flattened length, from the point of connection on the facial shield to its tip), (5) right wattle width (measured at point where the wattle bends forward, with calipers held parallel to the axis of the bill), and (6) right wattle area (height \times width). All measures were taken to 0.1 mm, using calipers.

We scored shield color by reference to the Munsell color scale (Munsell 1976, Burley and Coopersmith 1987) that breaks color into three orthogonal measures of hue, value, and intensity. Hue scores increased

from purple-red to red to red-orange (0 to 7.5). Value scores measure luminosity and increased from dark to light (1 to 6). Chroma scores measure saturation and increased from low to high (6 to 14). Because the axes of the color measures are orthogonal, the three scores can be summed to yield a total composite color score (Munsell 1976, Wyszecski and Stiles 1982). Higher composite color scores indicated brighter, more intense, red-orange coloration of the frontal shield. Color of the frontal shield was highly variable across different individuals. In juvenile birds and birds molting into adult plumage for the first time, the shield was typically a deep purple. In adults, color ranged from purple-red to red-orange.

Behavioral observations of the territorial system.—A grid of reference poles was erected on the study site to aid in mapping. Observers plotted locations of all identified individuals on large-scale (1 inch = 30 m) maps of the grid. Summary maps of territorial boundaries of each resident bird were compiled monthly.

The adult population consisted of two status categories, residents and floaters. We defined residents as individuals that restricted their activities to a specific location and defended that location against same-sex conspecifics. Residents were always paired. Occupied areas served as all-purpose territories and were used for foraging, roosting, and nesting. Once an individual became a resident it was site-faithful, and the likelihood was high (>95%) that it would remain in that location throughout its lifetime (S. T. Emlen and P. H. Wrege unpubl. data). The resident population at our study site was sedentary and, if suitable habitat was present, some residents bred in each month of the year (P. H. Wrege and S. T. Emlen unpubl. data).

Floaters were defined as individuals that did not consistently defend any location. They foraged in the spaces between defended territories and on large undefended mats of *Hydrilla verticillata* that were sufficiently devoid of other vegetation so as to be unsuitable for territories. They frequently intruded onto the territories of residents and were repeatedly chased off. Floaters consisted of both juveniles and adults that foraged in close proximity to one another and roosted gregariously in dense patches of hyacinth and sedges. The floater population was fluid in composition and location. Marked floaters were sometimes observed foraging as far as 3 km from the study site, and large numbers of floaters present during the dry season left the study site with the onset of the rains in May. For analyses of mating success, the ratio of floaters to residents was estimated from censuses within the study grid conducted during the wet season only, on the assumption that floaters that disappeared were not part of the study population but rather were transient birds that migrated to breed in seasonally flooded habitat elsewhere. Sex of individual floaters was difficult to determine unless they were foraging in close proximity to an individual of the opposite sex.

We based our floater sex-ratio estimates on that subset of observations, which did not differ between the wet and dry seasons (2.02:1 vs. 1.88:1, $\chi^2 = 0.005$, $P = 0.90$; S. T. Emlen and P. H. Wrege unpubl. data).

Behavioral observations of the mating system.—Each resident female was observed at least twice weekly, for ≥ 2 h, to confirm her number of mates and to gauge reproductive activity. Females that were engaged in a laying cycle, courting new males, or contesting territory boundaries were observed more frequently, using focal sampling techniques (Altmann 1974). In addition, many *ad libitum* observations were made during the course of other research activities.

We considered a female to be paired with a male when (1) she foraged together with the male, (2) she defended most or all of the male's territory against other females, (3) she responded to the "rally" calls of the male by defending the male, and (4) she solicited the male for copulations. A female was considered to be polyandrous when she met the four criteria with two or more males simultaneously. A male was considered to be polyandrous when his mate was simultaneously paired with one or more males in addition to himself. Such extra males are called "co-mates."

Measures of mating success.—Number of males paired to each female on the 15th day of each month was used to calculate annual mean and maximum number of mates for each resident female in each year. Because number of mates varied through time, and because different females were resident for different tenure lengths, neither mean nor maximum mate number fully captures total mating success of an individual female. We therefore summed the total number of months that each female was paired with each of her male mates, annually and over her entire breeding tenure. The first sum, called "annual paired-mate months" (APMM), estimates annual mating success. The second, termed "total paired-mate months" (TPMM), provides an estimate of lifetime mating success. Individuals of both sexes were excluded from analyses of lifetime mating success if they were resident at the start or end of the study. That is because a significant portion of lifetime mating success of such individuals may have been missed. Annual and lifetime mating success values underestimate actual mating success because they are based only on data for months when observers were present on the site (average 7.5 months per year). Lifetime values are necessarily biased low because our criteria will tend to omit individuals with the longest tenures.

Tests of the effect of morphology on territorial status and mating success.—We analyzed the influence of morphological traits on territorial status by comparing the sizes of floaters and residents for each sex using unpaired *t*-tests. Assuming that large size should be important in contest competition, we predicted that territory residents would be larger than adult floaters of the same sex.

We analyzed the influence of morphological traits on mating success of females using multivariate analyses of variance. Again, assuming that size wins contests, we predicted that larger, heavier females would have higher mating success than smaller, lighter females. We used annual mean and maximum number of male mates, annual mating success, and lifetime mating success as dependent variables in multivariate analyses of variance to test the importance of various morphological measures in predicting female mating success. We used general linear models that included skeletal size (tarsus length) and residual mass as potential predictor variables and that controlled for between-year effects and repeated measurements on the same female, when applicable. We also analyzed an expanded model that included area and color of the frontal shield as well as wing spur length to determine whether their inclusion explained more of the variance in female mating success than residual mass and tarsus length alone.

Analyses of annual data employed repeated measures models (using the MIXED procedure in SAS). For analyses of lifetime mating success, mean measures of morphology were used for females with multiple sets of measurements. Data on number of male mates were available for the first half of each of the six years of the study, but for the entirety of the year only in two years (1994 and 1995). We therefore included an indicator variable (long vs. short season) in the analyses to reflect the number of years of entire-year data available for each female. The Satterthwaite method was used for determining denominator degrees of freedom in models with random effects or repeated measures (SAS Institute 1997).

Measures of sexual selection.—We estimated the direction and intensity of sexual selection in three ways: (1) as the difference in standardized variances in mating success of females and males (the sex difference in the opportunity for sexual selection; Wade 1979, Wade and Arnold 1980, Shuster and Wade 2003), (2) as the ratio of the PRR of the two sexes (Clutton-Brock and Vincent 1991), and (3) as the OSR (Emlen 1976, Emlen and Oring 1977). Mating success was estimated in two ways: (1) as annual mean number of mates for individual females and males, and (2) as lifetime mating success, estimated as TPMM. For resident males, mate number always equaled one, and TPMM was simply their total months of residency. That is because males were never resident without being paired and were never paired to more than one female at a time. Number of female and male nonbreeders (i.e. individuals with mating success = 0) was estimated from census data. Number of nonbreeders was calculated by multiplying the number of residents in the relevant data set (annual mean mate number or TPMM) by the ratio of floaters to residents present in the censuses. The sex ratio of nonbreeders was taken as the sex ratio of floaters present in the censuses. Because male

residents greatly outnumbered female residents, more territory vacancies are expected for male than for female floaters. To correct for the greater probability of territory acquisition by male floaters over their lifetimes, we adjusted our estimate of male floater number in the TPMM dataset by multiplying by the sex ratio (F:M) of the resident population.

Potential reproductive rate was calculated as the maximum number of broods that an optimally successful member of each sex could produce in a year. Operational sex ratio was calculated, following Parker and Simmons (1996), as the ratio of the amount of time that each sex was available for additional matings ("time in"). "Time in" was calculated as number of days per reproductive event that each sex was not occupied with production or care of the clutch or brood. Each of those measures is influenced by the adult sex ratio of the population (residents plus floaters), because an excess of the sex with the smaller PRR (or shorter "time in") will reduce the sexual difference in intensity of sexual selection. The ratios of female to male PRR and "time in" were corrected by multiplying by the population sex ratio, defined as the number of females divided by number of males counted during regular censuses (Clutton-Brock and Parker 1992, Parker and Simmons 1996, Ahnesjö et al. 2001).

RESULTS

MORPHOLOGY AND SEXUAL SIZE DIMORPHISM

Female Wattled Jacanas were larger than males in every mensural character recorded (Table 1). Females, on average, weighed 148% as much as males and were 10% to 38% larger in

other mensural characters. Females also had relatively larger bills, wings, wing spurs, wattles, and frontal shields for their skeletal size than did males. Frontal shields of females were also more red-orange, brighter, and more saturated than those of males (Table 1).

Once an individual reached adult size, it did not show further skeletal growth or changes in the size or color of wattles or frontal shield (all paired *t*-tests, $P > 0.10$, incorporating Bonferroni-adjusted probabilities for multiple comparisons). Data were available from 42 recaptured adults, 22 with a one-year age difference, 13 with a two-year age difference, and 7 with a three-year age difference. The only consistent age-related change was in wing spur length, which increased 0.3 mm year^{-1} among both sexes but was significant only for males ($P = 0.33$ and 0.002 , for females and males, respectively).

MORPHOLOGICAL CORRELATES OF TERRITORIAL STATUS

Female residents were heavier and had larger tarsi, bills, and wing spurs than their same-sex floater counterparts (Table 2). They also had larger and more colorful fleshy facial shields and wattles. Male residents were similarly larger and had more colorful facial ornamentation than their floater counterparts but differed from females in having larger wings but not larger bills or wattles (Table 2). Residents of both sexes were also in better body condition

TABLE 1. Sexual size dimorphism in adult Wattled Jacanas in Panama, 1991–1995. Sample includes both residents and floaters. Sample sizes vary slightly depending on the character; for males, $n = 292\text{--}304$; for females, $n = 140\text{--}149$, except for wing, where males ($n = 120$) and females ($n = 66$). CV = coefficient of variation.

Character	Females		Males		Female: male ratio (%)	<i>P</i> value ^a absolute difference	<i>P</i> value ^b relative difference
	$\bar{x} \pm \text{SD}$	CV (%)	$\bar{x} \pm \text{SD}$	CV (%)			
Mass (g)	129.3 ± 13.1	10.1	87.5 ± 7.4	8.5	148	<0.01	NA
Tarsus (mm)	69.0 ± 2.4	3.5	62.9 ± 2.3	3.7	110	<0.01	NA
Bill (mm)	23.5 ± 1.1	4.6	21.2 ± 0.9	4.1	111	<0.01	<0.01
Wing (mm)	130.8 ± 3.9	2.7	116.0 ± 3.5	3.0	113	<0.01	<0.01
Wing spur (mm)	10.1 ± 1.5	14.5	7.9 ± 1.2	15.9	128	<0.01	<0.01
Shield area (mm ²)	343.4 ± 41.0	11.9	280.7 ± 37.8	13.5	122	<0.01	<0.01
Wattle area (mm ²)	85.0 ± 14.2	16.8	61.5 ± 10.3	16.7	138	<0.01	<0.01
Shield hue	4.2 ± 1.6	39.2	3.8 ± 1.6	42.3	111	<0.05	NA
Shield value	4.4 ± 0.5	12.2	4.1 ± 0.6	13.5	107	<0.01	NA
Shield chroma	11.2 ± 1.9	17.1	10.5 ± 2.0	19.4	107	<0.01	NA
Composite color ^c	19.7 ± 3.4	17.0	18.4 ± 3.3	17.7	107	<0.01	NA

^aSignificance values are Bonferroni-adjusted probabilities of independent sample *t*-tests.

^bSignificance of female–male difference after the allometric relationship between the character and skeletal size (tarsus length) has been factored out. Relative differences are not applicable to color (hue, value, chroma) scores.

^cSum of the three orthogonal components of shield color, using the Munsell color scheme.

TABLE 2. Comparison of morphological characters of resident and adult floater Wattled Jacanas in Panama, 1990–1995. Only first-capture measurements are included for individuals captured multiple times. Data for females (top) and males (bottom) are presented separately. Sample consisted of 85 resident and 54 floater females and 150 resident and 102 floater males. Numbers are mean \pm SD. The *P* values are from independent sample *t*-tests. Positive residual mass values denote birds that are heavy for their skeletal size; negative values indicate birds that are light for their skeletal size.

Measure	Residents	Floaters	Difference ratio (%)	<i>P</i> value
Females				
Mass (g)	135.6 \pm 12.3	120.7 \pm 8.9	112	<0.01
Tarsus (mm)	69.3 \pm 2.2	68.4 \pm 2.8	101	<0.05
Wing length (mm)	130.9 \pm 3.5	130.7 \pm 3.8	100	0.81
Bill (mm)	23.8 \pm 1.0	23.0 \pm 1.0	104	<0.01
Wing spur (mm)	10.5 \pm 1.5	9.7 \pm 1.3	108	<0.01
Shield area (mm ²)	353.4 \pm 40.9	323.7 \pm 35.7	109	<0.01
Wattle length (mm)	13.5 \pm 1.1	12.7 \pm 1.1	106	<0.01
Residual mass (condition)	+5.3 \pm 10.9	-7.0 \pm 8.4	NA	<0.01
Shield hue	4.7 \pm 1.4	3.7 \pm 1.6	127	<0.01
Shield value	4.4 \pm 0.5	4.3 \pm 0.5	102	0.43
Shield chroma	11.8 \pm 1.6	10.4 \pm 2.0	114	<0.01
Composite color score	20.9 \pm 2.7	18.4 \pm 3.5	114	<0.01
Males				
Mass (g)	90.8 \pm 6.3	82.3 \pm 6.0	110	<0.01
Tarsus (mm)	63.2 \pm 2.4	62.5 \pm 2.2	101	0.01
Wing length (mm)	116.6 \pm 3.5	115.3 \pm 3.3	101	<0.05
Bill (mm)	21.2 \pm 0.9	21.2 \pm 0.8	100	0.81
Wing spur (mm)	8.3 \pm 1.1	7.2 \pm 1.1	115	<0.01
Shield area (mm ²)	287.7 \pm 87.1	269.5 \pm 36.6	107	<0.01
Wattle length (mm)	11.4 \pm 1.0	11.3 \pm 1.1	101	0.60
Residual mass (condition)	+3.0 \pm 5.6	-4.74 \pm 5.7	NA	<0.01
Shield hue	4.3 \pm 1.4	3.1 \pm 1.7	139	<0.01
Shield value	4.0 \pm 0.5	4.2 \pm 0.6	95	<0.05
Shield chroma	11.0 \pm 1.8	9.6 \pm 2.1	115	<0.01
Composite color score	19.3 \pm 2.8	16.9 \pm 3.4	114	<0.01

(i.e. had higher residual mass) than floaters. Morphology and ornamentation thus predicted status, with smaller, less ornamented individuals being less able to obtain territories.

MORPHOLOGICAL CORRELATES OF FEMALE MATING SUCCESS

The mating system of Wattled Jacanas was one of simultaneous polyandry, with resident females being mated to an average of 1.7 males (range 1–4). However, number of mates varied among females. Tarsus length was a significant predictor of annual mean number of mates (Fig. 1, Table 3). Tarsus length and residual mass each predicted annual maximum number of mates and annual mating success (i.e. APMM; Table 3). Larger, heavier females were more successful in obtaining and holding large numbers of mates than smaller, lighter females. Examination of the interaction effect in the annual mating success

model suggested that females in good condition (i.e. those with higher residual mass) did increasingly well as their skeletal size increased (larger tarsus), but when in poor condition the larger females did more poorly than smaller females in poor condition. Body size was less important in predicting a female's lifetime mating success (i.e. TPMM). Only residual mass remained as a predictor of TPMM (Table 3). Neither size nor color of the frontal shield, nor length of the wing spur, added to any of the models once the effects of tarsus length, residual mass, or both were accounted for.

REVERSED SEXUAL SELECTION

Opportunity for sexual selection was greater for females than for males.

(1) *Annual mating success (mean number of mates per year).*—Data were available for 213 female-years and 380 male-years (Fig. 2). The

TABLE 3. Predictors of female mating success in Wattled Jacanas in Panama, 1990–1995. Results are from MANOVA models (GLM–SAS) that examined tarsus length, residual mass (condition), spur length, shield area, shield color, and year (except in model D) as predictors. Only significant predictors are listed below. Models A–C controlled for repeated measures on the same female across years. *F*-tests for those models used the Satterthwaite adjusted denominator degrees of freedom. Models A–C included 62 females; for Model D, sample size was 48 females.

Predictors	df	Coefficient	<i>F</i>	<i>P</i> value
A. Annual mean number of mates				
Year	5	–	2.43	0.04
Tarsus length	1	0.136	21.70	<0.0001
B. Annual maximum number of mates				
Tarsus length	1	0.157	22.15	<0.0001
Residual mass	1	0.019	5.72	0.02
C. Annual mating success (APMM)				
Long versus short season	1	4.061	26.51	<0.0001
Tarsus length	1	0.490	6.46	0.01
Residual mass	1	–4.626	7.29	0.01
Tarsus × residual mass	1	0.068	7.67	0.01
D. Lifetime mating success (TPMM)				
Long versus short season	1	6.559	17.15	0.0001
Residual mass	1	0.289	1.99	0.05

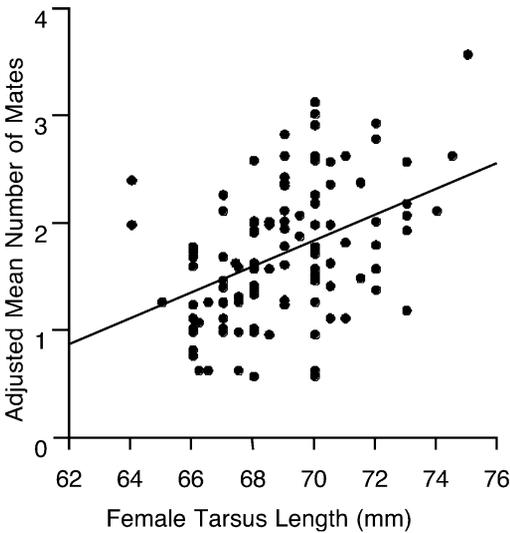


FIG. 1. Effect of female skeletal size (tarsus length) on annual mean number of male mates in Wattled Jacanas. Effect of differences between years was controlled by plotting the residuals from a model that included year as a predictor of mate number and rescaling the residuals to overall mean mate number. Larger females were more successful in obtaining multiple mates than were smaller females (see Table 3). (Line indicates best fit from general linear model; see text.)

data set meets the requirements (Shuster and Wade 2003) that the cumulative total number of mates for females equals that for males (both = 284) and the mean number of mates per year for males, adjusted for resident sex ratio, equals mean mate number for females (males = $0.747 \times [380/213] = 1.33$; females = 1.33). Mean and variance were 1.333 ± 0.969 for females, and 0.747 ± 0.189 for males. Standardized variance in annual mating success for females (variance/mean squared), I_{females} was 0.545. Standardized variance for males, I_{males} was 0.339. The sex difference in the opportunity for sexual selection (Wade and Arnold 1980) is given as $I_{\text{females}}/I_{\text{males}} = 0.545/0.339$ or 1.61:1.

(2) *Lifetime mating success (i.e. TPMM).*—Data were available for 44 females and 80 males (Fig. 3). The cumulative total mating success recorded for females (TPMM = 460) closely approximates the cumulative total for males (TPMM = 424); and mean TPMM for males, adjusted for resident sex ratio, closely approximates mean TPMM for females (males = $5.3 \times [80/44] = 9.63$; females = 10.46). Mean and variance were 10.46 ± 106.02 for females, and 5.30 ± 19.20 for males. Standardized variance in lifetime mating success for females, I_{females} was 0.97. Standardized variance for males, I_{males} was 0.68. The sex difference in the opportunity for sexual selection is given as $I_{\text{females}}/I_{\text{males}} = 0.97/0.68$ or 1.43:1.

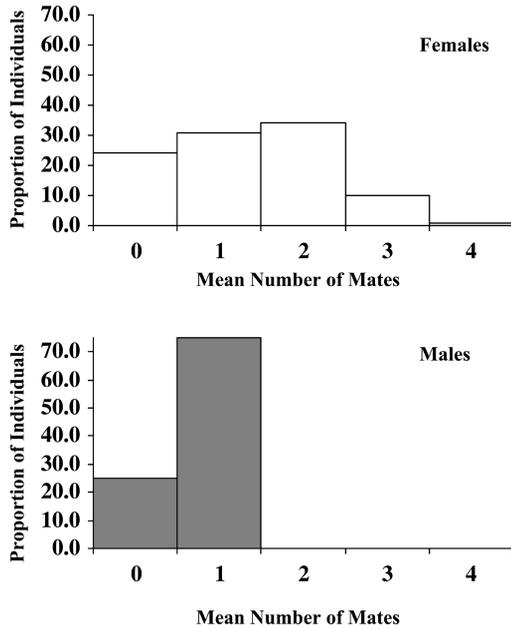


FIG. 2. Distribution of annual mating success for female and male Wattled Jacanas. Histograms show the proportion of all individuals paired with various numbers of mates, averaged across all of their months of residency in a given year. Data from each of six years (1990–1995) are included. Individuals present in multiple years are included multiple times ($n = 213$ female-years and $n = 380$ male-years).

The direction of sexual selection was reversed in Wattled Jacanas, with the intensity of sexual selection on females being 1.43 to 1.61 \times greater than that on males.

The PRR of females exceeded that of males. For males, the total time required to successfully produce a brood was 102 days (24.4 days [mean waiting time to receive a clutch of eggs] + 28 days [length of incubation period] + ~50 days [time of dependent chick care]; Emlen and Wrege 2004). Because breeding occurred in all months, maximum number of broods that a male could potentially rear in a year was 365/102, or 3.6. For females, maximum potential number of broods that could be reared in a year is the sum of all the broods that all of their mates could produce. Female PRR was 14.4 (product of the maximum number of broods that a male could produce times the maximum number of males paired simultaneously to a female, or 3.6 \times 4). The ratio of female to male PRR simplifies to the difference in maximum observed harem size between females and males, or 4:1.

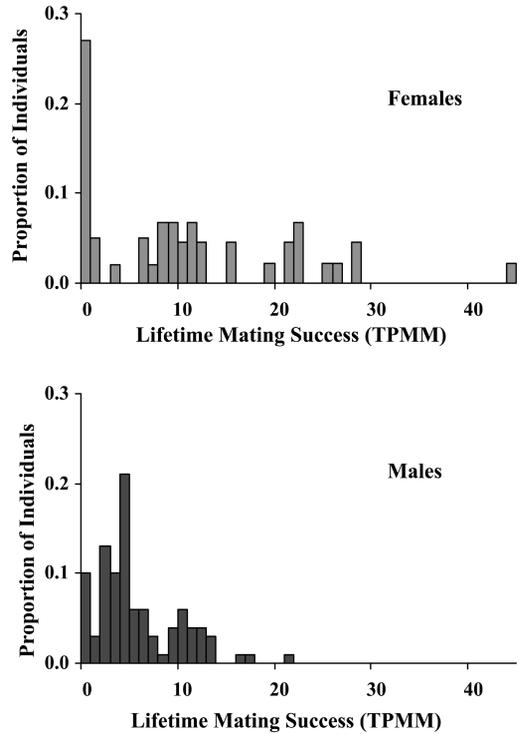


FIG. 3. Distribution of lifetime mating-success estimates for female and male Wattled Jacanas. Histograms show proportion of all individuals that were paired for particular numbers of “mate-months” (TPMM, see text; $n = 44$ females and $n = 80$ males).

The population sex ratio of Wattled Jacanas was male-biased, with 1.80 males present for every female (S. T. Emlen and P. H. Wrege unpubl. data). The effective ratio of female to male PRR is thus $4 \times (1/1.80)$, or 2.22:1.

The OSR was also female-biased. Males were occupied with intensive care-taking, and hence unavailable for additional reproductive events, during 78 days out of each 102-day reproductive event (total duration of parental care for a successful brood, which includes both incubation and dependent chick care). Females, however, because they did not provide clutch or brood care, were only unavailable during clutch production. Although females produced replacement clutches in as few as 6 days, the mean interclutch interval was 24.4 days. The ratio of female to male “time in,” which is equivalent to the operational sex ratio, was 78/24.4, or 3.20:1. When corrected for the excess of males in the general population, the effective operational sex ratio becomes $3.20 \times (1/1.80)$, or 1.78 females per

TABLE 4. Summary of estimates of reversed sexual selection in Wattled Jacanas in Panama, 1990–1995.

Measure	Females	Males	F/M ratio
Opportunity for sexual selection ^a	0.55	0.34	1.61:1
Opportunity for sexual selection ^b	0.97	0.68	1.43:1
Potential reproductive rate (broods per year)	14.4	3.6	2.22:1 ^c
Operational sex ratio ^d	78	24.4	1.78:1 ^c

^a Mating success estimated as annual mean number of mates per individual.

^b Mating success estimated as TPMM (lifetime mating success) per individual.

^c Corrected for the adult population sex ratio (1.80 males per female).

^d Defined as the ratio of female to male "time in" (time during each reproductive episode spent searching or waiting for additional reproductive opportunities; see Parker and Simmons 1996).

male. The three estimates of sexual selection in Wattled Jacanas are summarized in Table 4.

DISCUSSION

Sexual size dimorphism.—Wattled Jacanas exhibited reversed sexual size dimorphism. Females were significantly larger than males in every mensural character examined. Females weighed, on average, 1.5× as much as males (ratio of female:male mass = 1.48:1). As a result, females were physically dominant over males in all aggressive interactions. Female Wattled Jacanas also showed greater proportionate development of ornamentation (facial shield and wattle size) and weaponry (wing-spur length) relative to their body size than did males. Fleishy facial ornamentation was also more colorful in females than in males. Those findings suggest that sexual selection on secondary sexual traits is stronger among females than among males.

Once adulthood is reached, morphology is fixed in Wattled Jacanas. The only measure that increased with age was wing-spur length, and that was significant only for males. Wing spurs of Wattled Jacanas are keratinous structures that grow continuously but are worn down by abrasion. One possible (and untested) explanation for the lack of a similar age effect in females is that females use their wing spurs more often in contest competition and thus abrade them more rapidly than males. The color of the fleshy frontal shield did not change with age in adulthood, and shield color showed no variation with stage of nesting chronology (S. T. Emlen and P. H. Wrege unpubl. data).

Reversed sexual size dimorphism has been reported for all the behavioral role-reversed species of jacanas (female:male mass ratios of 1.67:1 for the Northern Jacana [*J. spinosa*; Jenni and Collier 1972], 1.83:1 for the Pheasant-tailed Jacana [*Hydrophasianus chirurgus*; Johnsgard 1981], 1.68:1 for the African Jacana [*Actophilornis africanus*; Tarboton 1995], 1.60:1 for the Bronze-winged Jacana [*Metopidius indicus*; Butchart 2000], and 1.75:1 for the Comb-crested Jacana [*Irediparra gallinacea*; Mace 2000]). Jacanas provide the most extreme examples of reverse size dimorphism found in the class Aves. The exception is the Lesser Jacana (*Microparra capensis*) which has a female:male mass ratio of 1.04:1 (Tarboton and Fry 1986). That species shows no behavioral role reversal, and females and males share equally in incubation and chick-care activities (Tarboton and Fry 1986, Hustler 2002).

Habitat saturation and competition for territorial space.—Occupancy of a territory is a prerequisite for breeding in all species of jacanas studied. Four lines of evidence suggest that suitable breeding habitat on the Chagres River site was saturated for both female and male jacanas. (1) Adult floaters of both sexes were present in all months of all years. Floaters, as well as neighboring residents, frequently intruded on territorial spaces, requiring that a territorial occupant defend its territory on a daily basis (Emlen and Wrege 2004). Nonbreeding floaters of both sexes are also common in *J. spinosa* (Jenni and Collier 1972), *Actophilornis* (Tarboton 1995), and *Metopidius* (Butchart 2000). (2) When new vegetation grew to fill in areas formerly unsuitable for nesting (e.g. open water), those areas were immediately occupied and defended. (3) When predation on adult jacanas created vacancies, such vacancies were rapidly filled by neighbor or floater individuals ($n = 9$; S. T. Emlen and P. H. Wrege unpubl. data). (4) Finally, when territorial males were temporarily removed to experimentally create vacancies, those were filled by the following day ($n = 6$; S. T. Emlen and P. H. Wrege unpubl. data). Previous removal experiments with females yielded similar results. Replacement females filled vacancies within 24 h, after which they killed dependent chicks of the former female resident, thereby freeing the male to rapidly accept and provide parental care for their clutches of eggs (Emlen et al. 1989).

Habitat saturation increases competition for space. Many Wattled Jacanas were prevented

from breeding by their inability to obtain and defend a territory. Such competition predicts that morphology should be a strong predictor of success in obtaining a territory among both female and male jacanas.

The prediction was supported. Residents were larger and heavier, had higher residual mass (i.e. were in better body condition), had larger and more colorful ornamentation (facial shields), and had larger weaponry (wing spurs) than floaters of the same sex. Similar results—with female and male territory holders being larger than or in better body condition than floaters, or both—have been reported for *J. spinosa* (Jenni and Collier 1972) and *Metopidius* (Butchart 2000).

Polyandry and female competition for mates.—The number of independent young produced by a female Wattled Jacana is dependent on her number of mates. Males provide all the incubation care for eggs and virtually all the chick care (Emlen and Wrege 2004). Females lay clutches sequentially for their various mates and rapidly provide replacement clutches when eggs are lost to predation or other causes. Because females lay clutches rapidly, their reproductive success is limited by their access to mates that will provide parental care. Females with large numbers of mates have caretakers lined up to provide for their sequential clutches and broods.

Females competed with one another to accumulate and retain male mates. Accumulation of multiple mates required that females defend sufficient space to include the territories of more than a single male. Retention of such mates required that females actively defend their male(s) from being “taken over” by neighboring resident or floater females. Challenges by intruding females were commonplace. During 45 h of focal observation, we detected 218 instances of intrusion by foreign females (nearly 5 h⁻¹), and female residents actively confronted those intruders 74 times (1.6 times per hour; Emlen and Wrege 2004). We therefore predicted that body size would influence the outcome of agonistic contests, and that winners would accumulate and defend larger numbers of males.

The prediction was supported. Body size was a strong predictor of a female’s mating success as a resident. Larger, heavier females had higher annual polyandry levels, whether measured as mean or maximum number of mates, or as annual mating success. Residual mass was also

important in predicting lifetime mating success (i.e. TPMM). Butchart (2000) also reported a relationship between large female body size and mating success (maximum harem size) in *Metopidius*.

Surprisingly, female body size was a stronger predictor of annual than of lifetime mating success. The reason may lie in the instability of the floating vegetative substrate on which jacanas defend their territories.

To be successfully polyandrous, a female must first become resident in a location where adequate floating vegetation will accrue to permit establishment of multiple male territories. She must then have the resource-holding potential to defend an area encompassing the territories of multiple males. Finally, she must have the good fortune that existing vegetation in the area she is defending does not wash or blow away when eggs or vulnerable young are present. Substrate instability introduces an element of stochastic variation into the polyandry levels obtainable by any given female over the long term, regardless of her size and competitive ability.

Reversed sexual selection.—The standardized variance in mating success for female Wattled Jacanas, I_{females} , was greater than that for males, I_{males} . The ratio of $I_{\text{females}}/I_{\text{males}}$ is considered the best measure of the difference in opportunity for sexual selection operating on the sexes (Wade 1979, Wade and Arnold 1980, Clutton-Brock 1988, Shuster and Wade 2003). Estimates of $I_{\text{females}}/I_{\text{males}}$ based on annual mating success and lifetime mating success equaled 1.61:1 and 1.43:1, respectively, indicating that the direction of sexual selection is reversed, with the strength of sexual selection on females being roughly 1.5× that on males. Those data represent the first quantitative estimates of the opportunity for sexual selection for any species of jacana and, to our knowledge, for any sex-role-reversed species of bird.

The accuracy of those estimates depends on how well the sample of residents reflects the true breeding population and how well our estimate of the number of floaters reflects the true number of nonbreeders in the population. Our sample of residents in the lifetime mating-success sample was biased by the exclusion of individuals still breeding at the end of the study. That insured greater accuracy of the included data, but at a cost of excluding individuals

with longer breeding tenures. The proportion of exclusions (excluded:included) did not differ between the sexes, however, so it is unlikely that that seriously affected the resulting estimate.

The number of nonbreeders was estimated from census data on the ratio of floaters to residents during the rainy season. Floaters were mobile, however, and changes in amount and location of nondefended foraging habitat caused their numbers within the study area to vary. To examine the possible effect of erroneous counts of floaters, we recalculated the opportunity for sexual selection using the lowest and highest floater-to-resident ratios recorded. The resulting $I_{\text{females}}/I_{\text{males}}$ values, which bracket the range possible because of census error, were 1.56:1 and 2.53:1 for annual mating success, and 1.21:1 and 1.48:1 for lifetime mating success.

The PRR for female Wattled Jacanas was also greater for females than for males. The PRR is defined as the maximum number of broods that an optimally successful member of each sex could rear in a year (Clutton-Brock and Vincent 1991). Because female PRR in jacanas is the sum of the PRR of each of her male mates, the ratio of female to male PRR reduces to equal the maximum number of simultaneous mates observed for females and males, or 4:1. That PRR ratio is identical to values of 4:1 reported for seasonally breeding *Actophilornis* (Tarboton 1992) and *Metopidius* (Butchart 2000). It is larger than reported values for other sex-role-reversed species of shorebirds (2.1:1 in Grey Phalaropes [*Phalaropus fulicarius*; Ridley 1980]; 2.1:1 in Red-necked Phalaropes [*P. lobatus*; Reynolds 1987]; and 1.4:1 in Spotted Sandpipers [*Actitis macularia*; Oring and Knudson 1972, Oring et al. 1983]).

When the population sex ratio differs from unity, sex-specific values of PRR must be adjusted before they accurately reflect sex differences in intensity of sexual selection. That is because the presence of an excess of the "limiting" sex (i.e. the sex with the lower PRR) has the effect of easing competition for mates among the "limited" sex. In Wattled Jacanas, the population sex ratio was strongly male-biased (1.80 males per female; S. T. Emlen and P. H. Wrege unpubl. data). Because males are the sex with the lower PRR, the sex difference in the intensities of sexual selection will be <4:1. Incorporating that correction, the effective ratio of female to male PRR was 2.22:1. Data on population sex ratios for *Actophilornis* and *Metopidius* also show male biases of 2 and

1.94 males per female, respectively (Tarboton 1992, Butchart 2000). The adjusted ratios of female to male PRR for those jacana species thus become 2.00:1 and 2.06:1, respectively. In each of those species, the PRR method confirms that the direction of sexual selection is reversed and that the intensity of sexual selection on females is roughly twice as strong as it is on males.

The time that an individual was occupied with each reproductive event, and thus unavailable for future reproductive events, was also greater for male than for female jacanas. That led to a reversal in the OSR (Emlen 1976, Emlen and Oring 1977). Males required 78 days to successfully rear a clutch to independence, whereas females averaged only 24.4 days to produce a clutch. Applying the same correction for the excess of potential male mates because of the male-biased population sex ratio, the effective OSR was 1.78 females per male.

Each of those estimates of the intensity of sexual selection would be reduced if males could seek additional mating opportunities while occupied with the production of a current brood. Such "extrapair" sirings could potentially increase variance in male mating success and decrease the female bias in OSR. Female Wattled Jacanas frequently copulate with multiple co-mates, and males fertilize young in broods for which they are not caretakers (17% of young of polyandrous females are not sired by the caretaking male; Emlen et al. 1998). However, females never copulated with males with whom they were not already paired (Emlen et al. 1998), and they showed no preference for individual partners (S. T. Emlen and P. H. Wrege unpubl. data). Cuckoldry occurred randomly with respect to male phenotype and thus should not increase variance in male mating success.

Although the merits of different measures of sexual selection are the topic of considerable discussion (see Andersson 1994), each of the measures used here yielded the same general result. Sexual selection is currently operating 1.5–2× more strongly on females than on males. Those values are similar in magnitude, but opposite in direction, to sex differences in sexual selection reported for mildly polygynous avian species such as Song Sparrows (*Melospiza melodia*; Smith 1988), House Wrens (*Troglodytes aedon*; Payne 1984), and Marsh Wrens (*Cistothorus palustris*; modified from Payne 1984). They are smaller than estimates of sexual selection acting on males

in highly polygynous (lekking) avian species (e.g. Cock-of-the-Rock [*Rupicola rupicola*], Trail 1985; Lawes' Parotia [*Parotia lawesii*], Pruett-Jones and Pruett-Jones 1990). Our data confirm Butchart's (2000:100) conclusion that "sexual selection in jacanas may be more strongly reversed than in any other bird species."

Our study provides support for the hypothesis that sex differences in postfertilization parental care can influence many aspects of a species' biology, from its morphology to its behavior and mating system. In *J. jacana*, males provide virtually all the postfertilization parental care for the eggs and young. It takes three months for a male to successfully rear a brood to independence, whereas, on average, it takes only three weeks for a female to lay a clutch of eggs for a new male. Females therefore have a higher PRR, and an OSR that is biased toward an excess of females. With more females than males being available for future reproductive events, females compete among themselves for access to males and the parental care that males provide. Such increased competition, in turn, increases the strength of sexual selection acting on females. Because large body size enhances competitive success, the stage is set for the evolution of the reversed sexual size dimorphism and the polyandrous mating system reported for this species. Wattled Jacanas provide compelling evidence that competition for mates and sexual selection are greater in the sex with the higher PPR. What is unusual about jacanas is that, because of their role-reversal, it is females that have the higher PRR. Jacanas can thus be considered the exception that proves the rule.

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