

Final Report on the Project: Integrative Approach to Unravel Demographic and Behavioral Drivers of Male-Biased Sex Ratio and Sex Role Reversal in the Pheasant-Tailed Jacana (*Hydrophasianus chirurgus*)

Introduction and Objectives

This project aimed to examine the demographic and behavioral factors that contribute to male-biased adult sex ratios (ASR) and sex-role reversal in the pheasant-tailed jacana (*Hydrophasianus chirurgus*). This polyandrous species exhibits male-only parental care, making it an ideal model for studying how ecological, demographic, and evolutionary processes contribute to these unique mating dynamics. In the pheasant-tailed jacana, females display larger body sizes and greater competitive behaviors, marking a reversal of typical avian sexual selection.

Project Objectives

1. **Identify Demographic Drivers of Male-Biased ASR:** Assess the factors that produce a male-biased ASR by investigating sex ratios across age classes, sex-specific mortality rates, and age of maturity.
2. **Examine Temporal ASR Variation and Its Impact on Parental Investment:** Evaluate how seasonal changes in ASR influence reproductive behaviors and parental investment, particularly regarding incubation and brood care.
3. **Identify Behavioral Mechanisms to Offset Polyandry Costs:** Investigate male strategies, such as mate guarding, egg removal, and increased copulation, that may reduce the risk of males investing in unrelated offspring.
4. **Examine Sexual Selection Effects on Survival and Secondary Traits:** Quantify sexual dimorphism and secondary traits to understand how these traits influence reproductive success, survival, and selection pressures.

Methods and Study Sites

Study Sites

Data were collected at two primary sites:

- **Jacana Educational Park, Tainan, Taiwan:** From June to September 2019, this protected area of 0.15 km², comprising 25 ponds, provided a controlled setting for observation.
- **Kaeng Nam Ton Lake, Khon Kaen, Thailand:** Data were gathered from May to August 2021 and April to September 2022 at this larger 10 km² lake, which was divided into seven zones for systematic data collection. This area is shared by fishing, grazing, and lotus harvesting activities, adding unique disturbance variables.

Data Collection and Analytical Techniques

1. **Population Monitoring and ASR Estimation:** Weekly and biweekly censuses provided ASR estimates, with designated observation points to prevent double-counting and minimize observer bias. Sex was determined based on size, behavior, and plumage.

2. **Capture and Marking of Individuals:** Adults were captured using mist nets and floating walk-in traps, while chicks were captured via a "spot-and-catch" technique. Blood samples were collected for molecular sexing using PCR to target the CHD1 gene's intron 16 region. These data were critical for validating ASR and monitoring chick sex ratios. Adult and chicks were measured for biometrics measurement to measure sex specific size and growth differences.
3. **Advanced Statistical Modeling for ASR:** N-mixture models controlled for sex-specific observation biases, site-specific detectability, and seasonal changes, refining ASR estimates beyond traditional field counts.
4. **Behavioral Observations and Incubation Monitoring Attempts:** Observations of mate guarding, egg removal, and copulation rates were made to evaluate male strategies for paternity assurance. Attempts to monitor male incubation with floating cameras were ultimately unsuccessful due to frequent flooding and disturbance, resulting in insufficient data for reliable analysis.
5. **DNA Analysis and Kinship Testing:** Molecular analyses of parent-offspring relationships within broods are planned and will provide insights into extra-pair fertilization rates and male paternity assurance strategies.

Field Challenges and Adaptive Responses

Environmental and Logistical Challenges

1. **Delayed Breeding Seasons:** Variability in rainy season timing delayed breeding in 2021 and 2022, impacting data collection schedules and necessitating adaptive rescheduling to align with active breeding phases.
2. **Flooding and Heavy Rainfall:** Intense rainfall caused substantial flooding, destroying up to 40% of nests in some years. This required alterations to data collection protocols and necessitated repeat surveys to account for nest losses.
3. **Lake Level Fluctuations Due to Dam Construction:** Dam construction led to sudden drops in water levels, displacing jacanas and resulting in further nest losses. Census points had to be adjusted and new monitoring areas established to account for these disturbances.
4. **Vegetation Loss Due to Caterpillar Infestation:** In 2023, caterpillar infestations devastated floating vegetation, reducing breeding territory size and exposing nests to predation. Observation points were modified to cover the remaining viable habitats.
5. **Human Disturbance:** The increasing transformation of Kaeng Nam Ton Lake into a tourist destination heightened human disturbances from fishing, lotus harvesting, and construction, prompting nest abandonment.
6. **Challenges in Capturing Adults:** Jacanas were adept at evading capture. Various adjustments, including net color changes, decoys, and repositioned nets, helped but proved insufficient to reliably capture females, limiting the sample size of marked adults.
7. **Insufficient Data from Incubation Cameras:** Cameras placed near nests to capture male incubation behaviors were frequently flooded or disturbed, providing insufficient data for analysis. This approach was ultimately abandoned.
8. **Low Resighting Rates of Marked Individuals:** Low resighting rates of ringed individuals, particularly chicks, indicated high dispersal or delayed maturation. This posed challenges for long-term tracking.

Results

ASR Estimation and Demographic Findings

Over three years, a consistent male-biased ASR averaging 0.68 was confirmed in the Thailand population. Advanced N-mixture modeling provided robust ASR estimates, controlling for biases related to site and sex-detection differences. The cumulative dataset of 48 sexed chicks from 21 broods provided crucial insights into age-specific sex ratios and dispersal patterns. Low resighting rates of marked chicks suggest either high dispersal rates or delayed maturation, both of which may contribute to the male-biased ASR observed.

Temporal ASR Variation and Parental Investment

ASR fluctuated seasonally, with a gradual decrease in male presence over time. This shift corresponded with increased female brood care, supporting the hypothesis that mate availability influences reproductive behavior in this sex-role-reversed species. Although camera data on male incubation could not be obtained, observational data indicate that female investment in brood care may increase as male availability declines.

These findings underscore the role of mate availability in shaping reproductive strategies within this polyandrous system, suggesting that females may adjust their reproductive effort in response to ASR shifts.

Behavioral Mechanisms to Offset Polyandry Costs

Observed behaviors such as mate guarding and egg removal likely serve as male strategies to mitigate polyandry costs. These behaviors could reduce the likelihood of males investing in offspring sired by other males. Although molecular analysis of extra-pair fertilization rates is pending, the observed behaviors support the hypothesis that males employ adaptive strategies for paternity assurance under high polyandry pressures.

Planned kinship analyses will provide further insights into the frequency of extra-pair fertilizations and the effectiveness of these behaviors. This analysis, once completed, will reveal how behavioral and genetic factors interact to shape reproductive success in male jacanas.

Sexual Selection and Sexual Dimorphism Findings

Biometric data from adults revealed significant sexual dimorphism, with females being larger and displaying more conspicuous secondary traits. These findings align with theories of reversed sexual selection in polyandrous systems, where female competition drives selection for size and ornamental traits. While chick growth measurements are still pending, these data will provide further insights into sex-specific growth patterns, particularly in relation to early development under sexual selection pressures.

The observed dimorphism supports the concept that competitive pressures among females influence morphological and behavioral adaptations, further reinforcing sex role reversal in this species.

Scientific Publications and Dissemination

1. Peer-Reviewed Publications:

- "*Sex Role Reversal and High Frequency of Social Polyandry in the Pheasant-Tailed Jacana*" in *Frontiers in Ecology and Evolution* (2021).
- "*The Evolution of Sex Roles in Shorebirds: Importance of Mating Opportunities and Food Abundance*", published in *PNAS* (2024), contextualizing these findings within broader shorebird evolutionary patterns.

2. Conference Presentations:

- IV. ÉLVONAL Conference on Sex Roles and Breeding Ecology of Shorebirds, Debrecen, January 2021.
- University of Bath lecture on sex role reversal, February 2021 (online).
- International Ornithological Congress, Symposium on "Adult Sex Ratios, Mating Systems, and Conservation," Durban, 2022 (online).
- International Wader Study Group Annual Conference, on breeding timing and environmental impacts, Szeged, Hungary, September 2022.

3. University Lectures:

- Invited presentations at University of Khon Kaen (2022, 2023).
- Guest lectures on sexual conflict and avian sex roles at the University of Bath (2021, 2022).
- Class discussion on the PNAS paper at the University of Cincinnati (2024, online).

4. Public Outreach:

- Collaboration with BBC1 documentary crew to raise public awareness on jacana biology, with release planned for 2025.

5. Manuscripts in Preparation:

- "*Measure of Adult Sex Ratio of Unmarked Individuals: An Application of New Techniques Using the Pheasant-Tailed Jacana*", planned submission in February 2025.
- "*Brood Sex Ratio in a Sex-Role Reversed Shorebird, the Pheasant-Tailed Jacana*", pending lab results.
- "*Breeding Biology of the Pheasant-Tailed Jacana: A Three-Year Study of a Population in Thailand*", in preparation.

Conclusion

This project significantly advanced the understanding of male-biased adult sex ratio (ASR) and sex-role reversal in the pheasant-tailed jacana. Despite logistical and environmental challenges, such as seasonal delays, flooding, and human disturbance, adaptive methodologies allowed for the collection of comprehensive, multi-season data across diverse ecological contexts. Results confirmed a consistent male-biased ASR, with seasonal fluctuations influencing female parental investment and reproductive behaviors, underscoring how mate availability shapes reproductive strategies within polyandrous, role-reversed systems. Observed male behaviors, such as mate guarding and egg removal, further underscore the strategies used to ensure paternity, an adaptation to the unique pressures of polyandry. These findings provide a foundation for continued investigation into kinship and extra-pair fertilization analysis, promising to clarify the effectiveness of these adaptive male behaviors.

Notably, the project culminated in the publication of *The Evolution of Sex Roles in Shorebirds: Importance of Mating Opportunities and Food Abundance* in *PNAS* (2024), a significant scientific contribution that contextualizes these results within broader evolutionary patterns among shorebirds. This paper highlights the demographic and ecological factors that

drive mating systems across species, offering new insights into sex role evolution. Additionally, *Frontiers in Ecology and Evolution* published *Sex Role Reversal and High Frequency of Social Polyandry in the Pheasant-Tailed Jacana* (2021), further validating the role of mate competition and parental investment shifts in this unique mating system.

The project's outreach extended to the public through collaboration with the BBC1 documentary crew, highlighting the jacana's distinct biology and the ecological factors underlying sex-role reversal. Scheduled for release in 2025, this documentary will bring broader visibility to the pheasant-tailed jacana and the evolutionary significance of role-reversed systems.

This work was communicated extensively through academic channels, including presentations at the IV. ÉLVONAL Conference on shorebird ecology, the International Ornithological Congress Symposium on "Adult Sex Ratios, Mating Systems, and Conservation," and multiple invited university lectures. Engaging students and researchers at the University of Khon Kaen, the University of Bath, and the University of Cincinnati, this project has helped to inform ongoing discussions on sexual conflict, sex roles, and avian mating systems.

In summary, this project provided a robust framework for understanding the demographic and behavioral drivers of sex-role reversal and male-biased ASR. The scientific findings, peer-reviewed publications, and public outreach achieved through this work underscore the importance of integrative research on sex-role-reversed species, yielding insights with broad implications for evolutionary ecology and conservation.



The evolution of sex roles: The importance of ecology and social environment

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Males and females often have different roles in reproduction, although the origin of these differences has remained controversial. Explaining the enigmatic reversed sex roles where males sacrifice their mating potential and provide full parental care is a particularly long-standing challenge in evolutionary biology. While most studies focused on ecological factors as the drivers of sex roles, recent research highlights the significance of social factors such as the adult sex ratio. To disentangle these propositions, here, we investigate the additive and interactive effects of several ecological and social factors on sex role variation using shorebirds (sandpipers, plovers, and allies) as model organisms that provide the full spectrum of sex role variation including some of the best-known examples of sex-role reversal. Our results consistently show that social factors play a prominent role in driving sex roles. Importantly, we show that reversed sex roles are associated with both male-skewed adult sex ratios and high breeding densities. Furthermore, phylogenetic path analyses provide general support for sex ratios driving sex role variations rather than being a consequence of sex roles. Together, these important results open future research directions by showing that different mating opportunities of males and females play a major role in generating the evolutionary diversity of sex roles, mating system, and parental care.

sex-role reversal | mating system | parental care | adult sex ratio | habitat productivity

Reproduction is a key stage in all organisms' life, and thus, understanding the causes of variation in reproductive behavior across dioecious species is a main goal in behavioral and organismal biology (1–3). Sex differences in mate choice, pair-bonding, and parental care are conveniently labeled as sex roles (3–7). Although females tend to invest more in offspring care while males typically invest more in competition for access to females (8–10), there is a large variation both between and within species, and in a fair number of organisms, the opposite is true: females compete for males, and the males alone look after the offspring (3, 11–13). In addition, sex roles may be balanced so that both sexes exhibit social monogamy and provide substantial parental care (3, 5, 9, 14–18).

Differences between male and female investment in breeding start with gamete production. Male gametes are cheaper to produce and more of them can be used in reproduction. Thus, males can potentially fertilize the eggs of many females so that mating with multiple mates can increase reproductive success more in males than in females (Bateman's Principle, 5, 8, 19). Although anisogamy can explain some sex differences in reproduction and parental care (20), the high variation in sex roles—particularly why males sacrifice their mating potential and provide substantial care in a number of species—suggests that ecology, life history, demography, and social environment could tune male and female roles in reproduction (3, 6, 19, 21, 22).

Traditionally, different breeding systems have been interpreted as evolutionary responses to specific ecological conditions (9, 23–25). Consistently, comparative analyses across several taxa demonstrated links between mating systems and ecological variables (26–29). In birds, for example, food availability has been considered particularly important for sex-role reversal (30–32) since high food availability can allow females to produce clutches for several males (food abundance hypothesis henceforward) and facilitates uniparental care by lowering the effort needed to locate and defend food sources for the offspring (33, 34). On the contrary, limited or clumped food distribution may facilitate male polygyny because a subset of males can defend rich food sources that grants access to multiple females (24, 35–37).

Furthermore, in an environment where the clutch or brood loss is high, e.g., due to high predation rate, high investment would be needed by the female for providing multiple replacement clutches (nest loss hypothesis henceforward, 30, 32, 38) restricting her time and energy essential to care for the egg or young (25, 39). Thus, high maternal investment in frequent clutch production could select for females to produce several clutches rapidly,

Significance

This study tackles the evolutionary conundrum of why males and females have different roles in reproduction and especially why some species exhibit reversed sex roles whereby the males take on full parenting duties instead of fertilizing many females. Previously, it was thought that sex-role reversal is due to ecological factors (e.g., food availability); however, here, our results show that social factors, i.e., the availability of potential mating partners, are the main drivers of sex role differences. This finding based on the most comprehensive evaluation of both ecological and social factors in any taxa to date—using shorebirds that exhibit diverse sex roles in nature—highlights the importance of social environment in shaping reproductive behavior and parenting.

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and it facilitates the evolution of male-only care (33). In addition, high clutch failure rate can increase the pool of mates that are free from parental care and available for females and thus favor polyandrous mating (see below, 9, 25, 32).

Besides the aforementioned ecological hypotheses, recent studies are emphasizing the social environment in shaping sex roles (32, 40–42). Uniparental care by a particular sex should evolve only if the benefit of desertion (e.g., the chance of remating) for one sex is low, and thus, caring for the current clutch would be more beneficial than looking for another mate (9, 41). Adult sex ratio (ASR, the proportion of males in the adult population) is a likely factor affecting mating opportunities: for example, male-skewed ASRs can provide high remating opportunity for females but less for males (sex ratio hypothesis henceforward). This will decrease the benefit of male desertion, so instead will facilitate males' investment in their current reproduction by providing paternal care. ASR and a subset of ASR, the ratio of available males and females for mating (operational sex ratio, OSR), have been highlighted as crucial drivers of sex role evolution by theoretical models (41, 43–46) as well as an increasing number of empirical studies (22, 47–53).

The influence of adult sex ratios on breeding systems has been recently demonstrated across a broad range of taxa that include fish, reptiles, birds, mammals, and humans (51, 54, 55). However, the direction of the association has been questioned by arguing that sex ratio skews—rather than influencing breeding systems—are generated by mortality implications of mate choice, pair-bonding, and parenting (48, 51, 55, 56). Although experimental manipulations of sex ratios generated behavioral responses in specific taxa (e.g., refs. 51, 55, and 57), the general directionality of the association between ASR and breeding system has not been tested across a broad range of taxa.

The density of breeding individuals is a further key social characteristic of populations that influences mate encounter rate (breeding density hypothesis henceforward). Low population densities are associated with monogamy in mammals and fish (58–60), and changes in population density induce changes in mating system in several fish (61). In a phylogenetic study of birds, Owens (62) showed that species with male-only care breed at lower densities than species exhibiting female-only care. The latter result suggests that low breeding densities reduce the rate of mate encounters and make it difficult to find opportunity to remate for males, favoring the evolution of male-only care.

Ecological and social factors, however, may also have interactive effects on breeding systems and sex roles. First, ASR and breeding density are likely to exert a joint influence on mating opportunities (63, 64). Consistently, both of these variables and their interactive effects may impact on sexual selection (65), female fertilization (66), and sex-specific mate search (67). Second, local food availability may depend on breeding density because high density tends to increase resource competition which ultimately increases the need for biparental care (68). However, the impacts of these interactions on breeding systems have not been tested in a general comparative framework.

Shorebirds (sandpipers, plovers, and allies) are some of the best taxa to investigate the origin and maintenance of sex roles because they exhibit unusually high diversity of mating systems and parental care that include textbook examples of sex-role reversal (3, 11, 16, 30, 69–72). They are well studied in the wild; hence, data on behavior, life history, and demography of many species are readily available (73–76). Comparative studies of shorebirds provided some of the first demonstrations that mating opportunities and ASR are associated with mating system variation and parental care (47, 48, 73). However, these seminal studies focused on a single

predictor (i.e., ASR) and were limited by a small number of taxa and crude resolution of sex role variables [e.g., 3 species (73), 6 populations (47), or 18 species (48)].

Here, we advance studies of sex roles and breeding systems by 1) evaluating the significance of both ecological (i.e., food abundance and nest loss) and social environment (i.e., sex ratio and breeding density) hypotheses (using habitat productivity, hatching success, ASR, and breeding density as explanatory variables, respectively) for sex role evolution using shorebirds as model organism. 2) We carry out a comprehensive evaluation of both ecological and social factors driving mating system variation and evaluate the interactions between ecological and social factors in a multipredictor framework using a substantially augmented dataset that includes 80 populations of 41 shorebird species. 3) Importantly, we use phylogenetic confirmatory path analyses to compare scenarios representing different relationships between sex role components and their putative predictors. Specifically, we test whether skewed ASR is a driver (as proposed by the sex ratio hypothesis) or an outcome of sex role variation as was recently argued (56). Taken together, these analyses represent the most comprehensive broad-scale evaluation of ecological and social predictors of breeding system variations including sex-role reversal in any animal taxa. These results together will advance the evolutionary understanding of reproductive behavior, sex roles, and parenting by linking breeding systems to demography and population dynamics.

Results

Diversity of Sex Roles. Sex roles show extensive variation across the shorebird phylogeny from male polygamy (i.e., polygyny) with female-only care to female polygamy (i.e., polyandry) with male-only care via monogamy and biparental care (3). The full spectra of mating systems and parenting are represented by our dataset (Fig. 1A) that includes male-biased polygamy (15.4% of 41 species, e.g., northern lapwing, *Vanellus vanellus*), female-biased polygamy (33.3%, e.g., Eurasian dotterel, *Charadrius morinellus*), and monogamy (51.3%, e.g., black-tailed godwit, *Limosa limosa*). Our dataset also represents all major types of avian care: male-biased care (39.1% of 41 species, e.g., greater painted snipe, *Rostratula benghalensis*), female-biased care (14.6%, e.g., American woodcock, *Scolopax minor*), and biparental care with similar participation by males and females (46.3%, e.g., white-fronted plover, *Charadrius marginatus*). Note that throughout this study, we focus on social mating systems since in shorebirds, social mating systems are identical (or very similar) to genetic mating systems due to low frequencies of extra-pair copulations (74).

The Effect of Food Abundance on Sex Roles. Habitat productivity, as measured by the NDVI (Normalized Difference Vegetation Index), which is typically associated with food abundance (78, 79), showed a high variation across species (Fig. 1B), and it was not associated with social mating systems and parental care in bivariate models (all $P \geq 0.1$, all $R^2 \leq 0.05$; *SI Appendix, Table S1*). However, when habitat productivity was included in multipredictor models, three out of four responses were predicted by habitat productivity (Table 1 and Fig. 2). The latter results imply that polyandry and male-only care are associated with a lower habitat productivity than polygyny and female-only care (Table 1 and Fig. 2).

The Effect of Hatching Success on Sex Roles. Hatching success was highly variable across species, ranging from 12.5% in comb-crested jacana (*Irediparra gallinacea*) to 88.5% in Eurasian dotterel

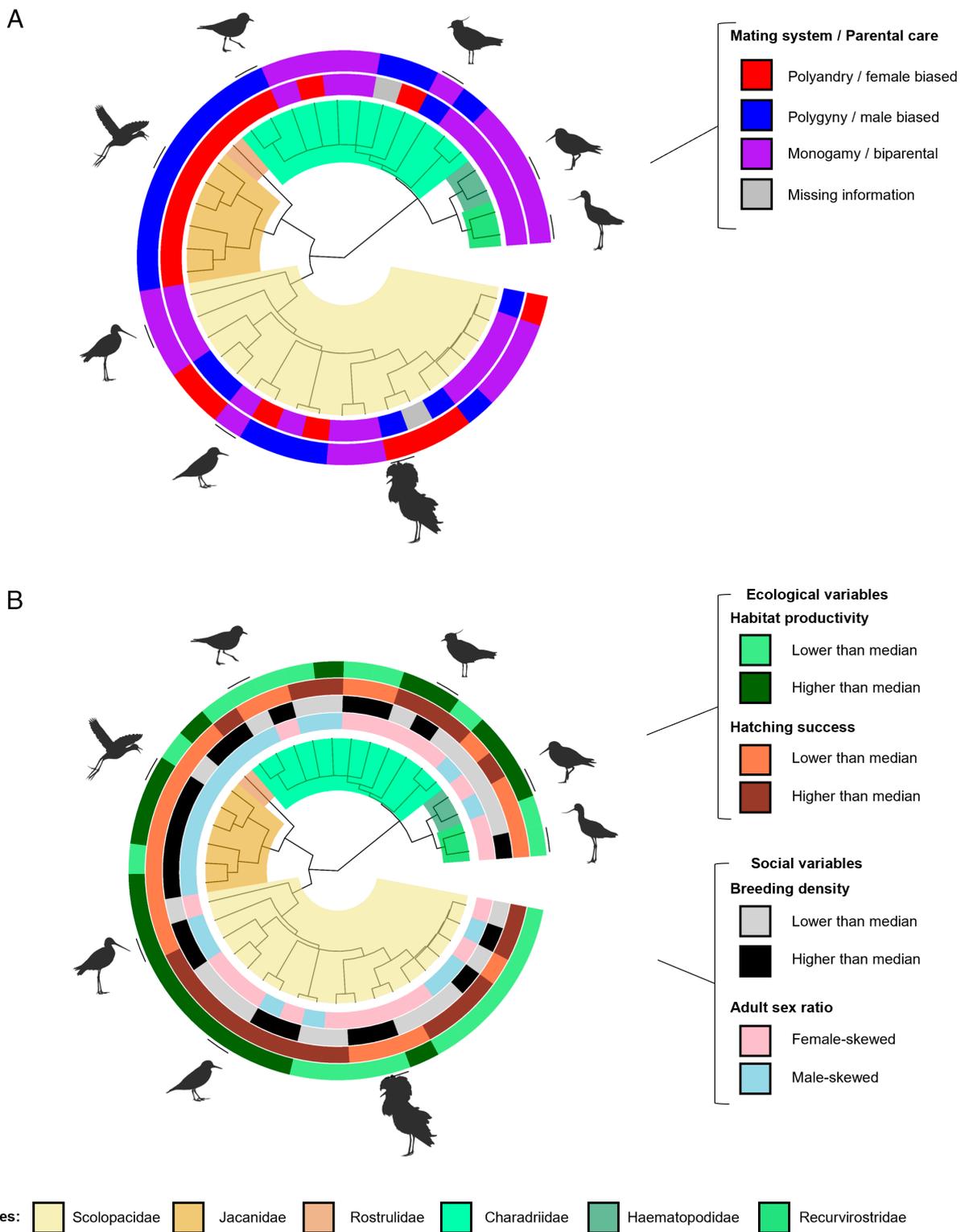


Fig. 1. Distribution of (A) mating systems and parental care and (B) ecological and social variables in 41 shorebird species included in the study. In panel (A), the colored circles show 1) parental care score bias (outer circle) and 2) polygamy bias (inner circle). The latter variable is represented either by polygamy frequency bias (most species) or by polygamy score bias (three species without polygamy frequency data, see *SI Appendix, Table S5*). In panel (B), the colored circles show 1) habitat productivity (outer circle, light and dark green), 2) hatching success (second circle, light and dark brown), 3) breeding density (third circle, gray and black), and 4) adult sex ratio (inner circle, pink and blue). Light and dark colors represent an average value for the species lower or higher, respectively, than the median in habitat productivity, hatching success, and breeding density. For adult sex ratio, pink and blue colors represent an average value for the species lower or higher, respectively, than 0.5 (i.e., even sex ratio). The phylogenetic relationships are shown according to a supertree of shorebirds (77). Silhouette images represent from bottom following clockwise direction: *Calidris pugnax*^a, *Actitis hypoleucos*, *L. limosa*^a, *Jacana spinosa*, *Charadrius alexandrinus*, *V. vanellus*^b, *Haematopus ostralegus*, *Recurvirostra americana*^a (source: <http://www.phylopic.org/>). ^{ab} reproduced here under a Creative Commons Attribution 3.0 Unported license (<https://creativecommons.org/licenses/by/3.0/>) and were generated by ^aAlexandre Vong and ^bNina Skinner. The remaining figures are public domain.

Table 1. Sex differences in social mating system and parental care in relation to ecology and social environment in shorebirds

	(a) Polygamy frequency bias	(b) Polygamy score bias	(c) Parental care score bias	(d) Parental care duration bias
	$\lambda = 0.91$ $R^2 = 0.52$	$\lambda = 1.00$ $R^2 = 0.44$	$\lambda = 1.00$ $R^2 = 0.39$	$\lambda = 1.00$ $R^2 = 0.38$
	Estimate \pm SE (<i>P</i>)	Estimate \pm SE (<i>P</i>)	Estimate \pm SE (<i>P</i>)	Estimate \pm SE (<i>P</i>)
Habitat productivity	0.44 \pm 0.19 (0.025)	0.79 \pm 0.35 (0.029)	-0.36 \pm 0.15 (0.018)	-1.15 \pm 0.59 (0.058)
Hatching success	-0.03 \pm 0.02 (0.126)	-0.02 \pm 0.04 (0.569)	0.01 \pm 0.01 (0.506)	0.02 \pm 0.05 (0.708)
Adult sex ratio	-10.55 \pm 1.95 (<0.001)	-16.88 \pm 3.48 (<0.001)	7.11 \pm 1.49 (<0.001)	28.61 \pm 5.97 (<0.001)
Breeding density	-0.29 \pm 0.09 (0.004)	-0.24 \pm 0.13 (0.082)	0.13 \pm 0.06 (0.025)	0.53 \pm 0.23 (0.024)

The table shows results of multipredictor PGLS models for (a) polygamy frequency bias (% male polygamy – % female polygamy), (b) polygamy score bias (male score – female score), (c) parental care score bias (average score of relative male participation in five types of parental care), and (d) parental care duration bias (male care duration – female care duration) as response variables. The estimates indicate the effects of four predictor variables: habitat productivity (measured by NDVI, Normalized Difference Vegetation Index, a proxy for food availability, squared and zero-centered), hatching success (the percentage of nests in a population that hatched at least one egg, species estimate), adult sex ratio (the proportion of males in the adult population, species estimate), and breeding density (pair per km², species estimate; see *Materials and Methods* in the main text for explanation of how species estimates were calculated from the raw data). Pagel's lambda (λ) and variance explained (R^2) are given for the full model, model estimates and their SE, and associated *P* values are given for each predictor. Significant effects (*P* < 0.05) are highlighted in bold. *N* = 36, 39, 41, and 41 species for models a–d, respectively.

(Fig. 1*B*). Nevertheless, none of the sex role variables was associated with hatching success either in bivariate or in multipredictor models (Table 1, *SI Appendix*, Table S1, and Fig. 2).

The Effect of Adult Sex Ratio on Sex Roles. Sex roles were strongly associated with ASR both in bivariate and multipredictor models because polyandry and male-only care were typically associated with male-skewed sex ratios. In contrast, polygyny and female-only care were typically associated with female-skewed adult sex ratios (Table 1 and *SI Appendix*, Table S1 and Fig. 2). ASR explained a high percentage of the variance in mating system (39 to 43% as indicated by R^2 in bivariate models) and 31 to 32% of variance in parental care (*SI Appendix*, Table S1).

The Effect of Breeding Density on Sex Roles. One of the two social mating system variables was negatively associated with breeding density, suggesting that polyandrous species have higher breeding densities than polygynous species (the relationship was significant both in bivariate and multipredictor models, Table 1 and Fig. 2 and *SI Appendix*, Table S1). We also found positive associations between breeding density and parental care in multipredictor models since male-biased care was associated with high breeding density whereas female-biased care was associated with low breeding density (Table 1 and Fig. 2).

The Interactive Effects of Sex Role Predictors. Breeding density and ASR tended to have an interactive effect on mating system (*P* = 0.052, Table 2), suggesting that high breeding density amplifies the effects of ASR skew on polygamy frequency bias (Fig. 3*A*). Furthermore, breeding density and habitat productivity predicted social mating system in a nonadditive way since species that breed in rich habitats responded more strongly to breeding density than species that breed in resource-poor habitat (Fig. 3*B* and Table 2). We found no interactive effect of habitat productivity, breeding density, or ASR on parental care, suggesting that their effects were independent from each other.

Phylogenetic Confirmatory Path Analyses. We used phylogenetic path analyses to fit four sets of 24 models that represent different a priori pathways linking sex roles and the putative predictors (i.e., habitat productivity, hatching success, ASR, and breeding density, *SI Appendix*, Fig. S2). Path analyses corroborated the relationships between sex roles and ecological and social predictors (*SI Appendix*, Table S2). Model comparisons supported two best models: i) a model in which ASR and breeding density influenced parental care bias, which in turn influenced mating system bias

(*SI Appendix*, Fig. S2, Model 1a), and ii) a model in which habitat productivity, ASR, and breeding density influenced mating system bias, which in turn fed into parental care bias (*SI Appendix*, Fig. S2, Model 2a). Both models include ASR as a predictor of (and not a response to) sex roles (Fig. 4 and *SI Appendix*, Table S3).

The best-supported model depended on the specific proxy variables included in the path models (Model 2a was supported in model sets 1, 2, and 3, whereas Model 1a was supported in model sets 2 and 4, *SI Appendix*, Table S3). Both supported models fitted to the data well as indicated by the modest Δ AICc between these models and their comparable fit indices (*SI Appendix*, Table S4). Importantly, the scenarios with ASR as response to sex role variation (i.e., Models 4–6) were consistently inferior in model comparisons (Δ AICc > 10 in all cases; *SI Appendix*, Table S3).

Discussion

Our study produced three key results. First, we confirmed that both ecological and social environments are associated with sex role variations, although their relative predictive powers are different. Second, our analyses uncovered interactive effects between variables that to our knowledge were not exposed previously. Third, using phylogenetic path analyses, we provide general support for that ASR variations induce changes in sex roles—rather than ASR variations are the consequences of sex-specific effects of life histories and reproductive efforts. We discuss the implications of these results below.

Mating Opportunities, Adult Sex Ratios, and Sex Roles. A major conclusion of our study is that the more abundant sex in a population is more likely to take up parenting than the less abundant sex, whereas the less abundant sex in the population tends to acquire multiple mates. Thus, the opportunity for finding a mate is associated with the reproductive roles of males and females. The associations between adult sex ratios, mating systems, and parental care are consistent in both bivariate and multipredictor models, and ASR explains a high proportion of variation (31 to 43%) in all sex role components. Our study thus provides support to Liker et al. (48) seminal results that were limited to 18 shorebird species and extends its conclusions to a broader taxonomic coverage. Such associations between male-skewed sex ratios and sex-role reversal (and conversely, between female-skewed sex ratio and polygynous mating and female-biased care) have now been proposed by both theoretical and empirical studies (45, 47, 51, 72, but see ref. 7).

Importantly, phylogenetic path analyses support ASR as a predictor, rather than an outcome of sex roles, consistently with

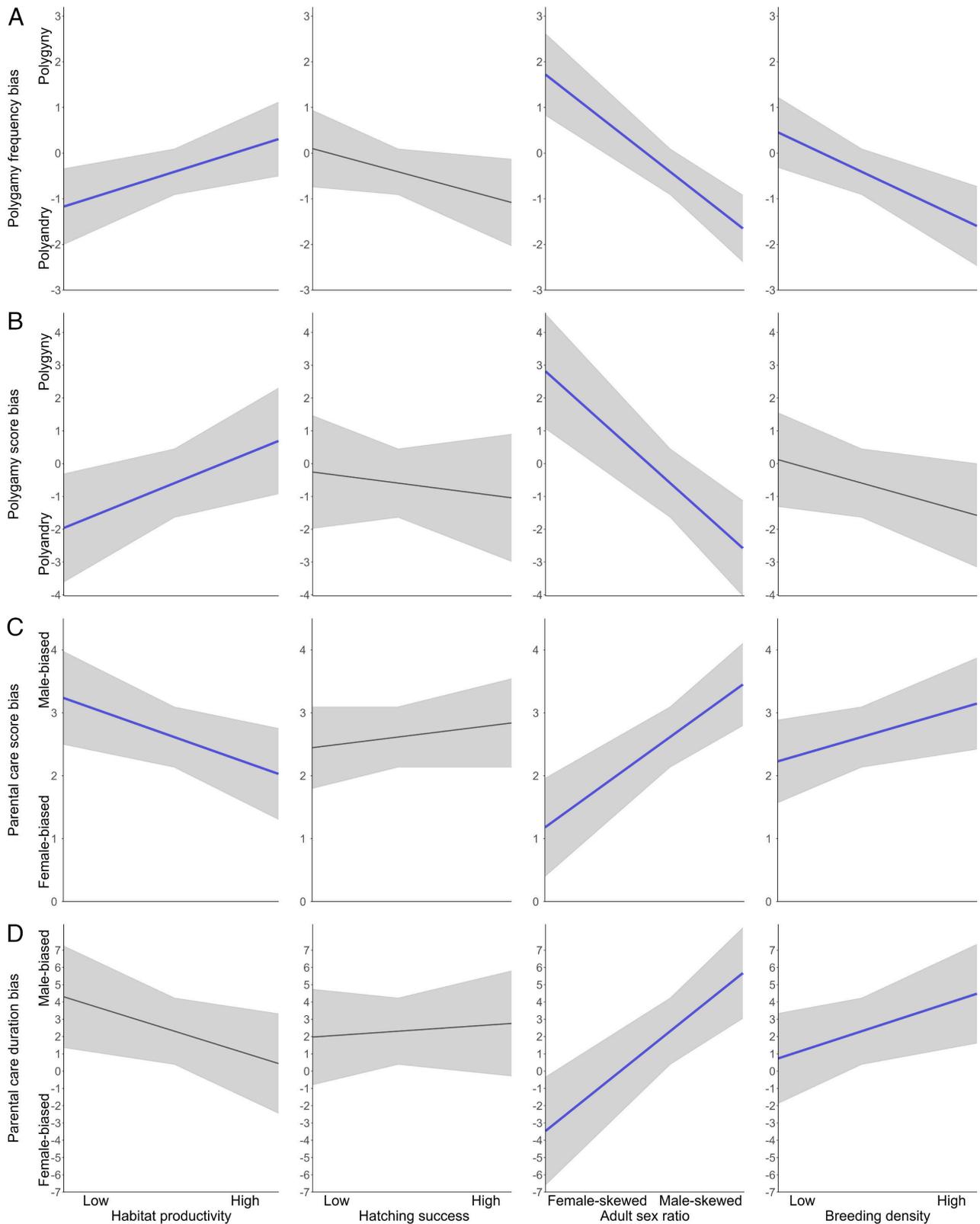


Fig. 2. Components of sex roles (response variables) in relation to ecology (habitat productivity, hatching success) and social environment (adult sex ratio and breeding density). Panels show regression lines estimated by multipredictor PGLS models (blue: significant; black: not significant) and their SE (gray shading). (A) Polygamy frequency bias, (B) polygamy score bias, (C) parental care score bias, and (D) parental care duration bias. See Table 1 legend and *Materials and Methods* in the main text for definitions of variables. See Table 1 for details of the statistical models and sample sizes.

experimental manipulations of ASR (51, 57). Although ASR variation can be generated by sex-specific mortalities linked to sexual differences in mating competition and parental care (51, 56), and ASR variation could also emerge via sex differences in maturation

(51, 56, 80) our phylogenetic path analyses support models in which ASR is a predictor of sex roles: These models provide better fit to the data and are robustly favored over models where ASR is an outcome of sex role variation ($\Delta AIC_c > 10$, *SI Appendix, Fig. S2*, Models 4–6).

Table 2. Phylogenetically corrected associations between sex role components and the interactive effects of ecology and social environment

	(a) Polygamy frequency bias	(b) Polygamy score bias	(c) Parental care score bias	(d) Parental care duration bias
	$\lambda = 1.00 R^2 = 0.61$	$\lambda = 1.00 R^2 = 0.46$	$\lambda = 1.00 R^2 = 0.37$	$\lambda = 1.00 R^2 = 0.37$
(I)	Estimate \pm SE (<i>P</i>)	Estimate \pm SE (<i>P</i>)	Estimate \pm SE (<i>P</i>)	Estimate \pm SE (<i>P</i>)
Habitat productivity	0.47 \pm 0.19 (0.019)	0.84 \pm 0.34 (0.020)	-0.37 \pm 0.15 (0.024)	-1.21 \pm 0.60 (0.051)
Hatching success	-0.03 \pm 0.02 (0.170)	-0.01 \pm 0.04 (0.758)	0.01 \pm 0.01 (0.542)	0.02 \pm 0.05 (0.750)
Adult sex ratio	-12.51 \pm 2.24 (<0.001)	-20.16 \pm 4.06 (<0.001)	7.23 \pm 1.81 (<0.001)	31.09 \pm 7.22 (<0.001)
Breeding density	-0.30 \pm 0.08 (0.001)	-0.12 \pm 0.15 (0.443)	0.13 \pm 0.07 (0.062)	0.46 \pm 0.26 (0.089)
ASR \times Breeding density	-2.54 \pm 1.26 (0.052)	-3.40 \pm 2.28 (0.146)	0.13 \pm 1.03 (0.903)	2.56 \pm 4.09 (0.536)
(II)	$\lambda = 1.00 R^2 = 0.62$	$\lambda = 1.00 R^2 = 0.42$	$\lambda = 1.00 R^2 = 0.38$	$\lambda = 1.00 R^2 = 0.36$
Habitat productivity	0.42 \pm 0.19 (0.031)	0.79 \pm 0.35 (0.032)	-0.37 \pm 0.15 (0.020)	-1.17 \pm 0.59 (0.057)
Hatching success	-0.04 \pm 0.02 (0.066)	-0.02 \pm 0.04 (0.576)	0.01 \pm 0.01 (0.600)	0.02 \pm 0.05 (0.778)
Adult sex ratio	-9.94 \pm 1.86 (<0.001)	-16.88 \pm 3.54 (<0.001)	7.19 \pm 1.50 (<0.001)	28.82 \pm 6.05 (<0.001)
Breeding density	-0.26 \pm 0.09 (0.009)	-0.23 \pm 0.17 (0.189)	0.15 \pm 0.06 (0.017)	0.59 \pm 0.25 (0.026)
Breeding density \times Habitat productivity	-0.13 \pm 0.06 (0.037)	-0.001 \pm 0.11 (0.992)	-0.03 \pm 0.04 (0.436)	-0.08 \pm 0.16 (0.612)

The table shows the results for multipredictor PGLS models with (a) polygamy frequency bias (b) polygamy score bias, (c) parental care score bias, and (d) parental care duration bias as response variables, indicating the effects of habitat productivity, hatching success, adult sex ratio, and breeding density as explanatory variables, and containing interaction between (I) ASR and breeding density and between (II) breeding density and habitat productivity. See Table 1 legend and *Materials and Methods* in the main text for variables' explanation. Pagel's lambda (λ) and variance explained (R^2) are given for the full model, model estimates and their SE, and associated *P* values are given for each predictor and interaction. Significant effects (*P* < 0.05) for the interactions are highlighted in bold. *N* = 36, 39, 41, and 41 species for models a–d, respectively.

Note that the latter conclusion was consistent for several sex role variables.

Our results are thus in line with seminal comparative analyses in that skewed ASR is a predictor (and not a consequence) of variation in reproductive traits, such as sex differences in the age of sexual maturity (80) and sexual size dimorphism (53). However, demography and social behavior may coevolve at a faster rate than phylogenetic analyses can uncover, therefore, further experimental tests and microscale phylogenetic analyses are essential to verify the potentially tangled relationships among sex roles, mortalities, and ASR (81). While a number of short-term experimental manipulations of ASR have been carried out (e.g., refs. 62 and 69), the reverse manipulations, i.e., experimentally altering breeding systems and recording the changes in ASR, have not been reported to our knowledge.

Path analyses supported two models differing in whether mating system bias influences parental care bias or vice versa, depending on which proxy of these traits were included in the models. This may reflect that mating and parental behavior are likely coevolving tightly (at least among shorebirds), meaning that evolutionary changes in one of them can induce changes in the other trait and this effect can work in both directions (3). Currently available approaches of phylogenetic path analyses cannot include bidirectional relationships, so we were unable to include both scenarios simultaneously in the models. Consistently with comparative analyses of evolutionary effects between sexual selection and parental traits, the tight coevolution precludes us to further clarify the relationships between these two behavioral traits (82–84).

The associations among skewed sex ratios and biases in care and mating systems in shorebirds may be facilitated by two characteristics of this avian group: 1) the ability of both males and females to provide care on their own which is suggested as a prerequisite for evolutionary responses of sex roles to ASR variation (25, 32, 85) and 2) the precociality of the offspring that facilitate uniparental care (9, 16, 36, 69, 82, 86). Coucals (Centropodinae) are the only

altricial bird family where true sex-role reversal occurs, as males provide extensive parental care including incubation (25, 32, 85). Similarly to shorebirds, the male-skewed ASR (2.5 males per female) is suggested as a major driver of the evolution of sex-role reversal in the black coucal (*Centropus grillii*), which contrasts with the approximately even sex ratio (1.07 males per female) of the closely related monogamous and biparental white-browed coucal (*Clinus superciliosus*) (32, 87). Many other taxa appear to lack adaptations for male-only care (e.g., to incubate eggs in many passerines), which may constrain their evolutionary response to skewed ASRs.

The importance of mating opportunity in the evolution of sex roles is further highlighted by higher breeding densities associated with male-biased care and polyandry. High breeding density can increase encounter rate with potential mates, which in turn may promote both fertilization success and the monopolization of mates (63, 66). Our study found the opposite pattern reported by Owens (62) since at least in shorebirds, high breeding density increases mating opportunities for females. We propose two factors that contribute to the sex-specific effect of density. First, females are more time- and energy-constrained than males in producing relatively large gametes for their mates; thus, breeding with multiple males may only be feasible (or profitable) when this has relatively low costs, e.g., due to an abundance of locally available males. Second, males and females may differ in their mobility during mate search. Males in some polygynous shorebirds are extremely mobile during the breeding season which probably facilitates finding new mates even when breeding densities are low (e.g., pectoral sandpiper, *Calidris melanotos*, 88). In contrast, females in many sex-role reversed species (e.g., in jacanas) have stable breeding territory through the reproductive season and attract their mate to breed there (70, 89–91). However, females in some sequentially polyandrous shorebirds can switch quickly between breeding sites which also involves traveling large distances [e.g., snowy plovers *Charadrius nivosus* (75, 76), dotterels (92), and Kentish plovers *C. alexandrinus* (93)]. Thus, evaluating the roles of sex-specific mobility for finding new mates needs further

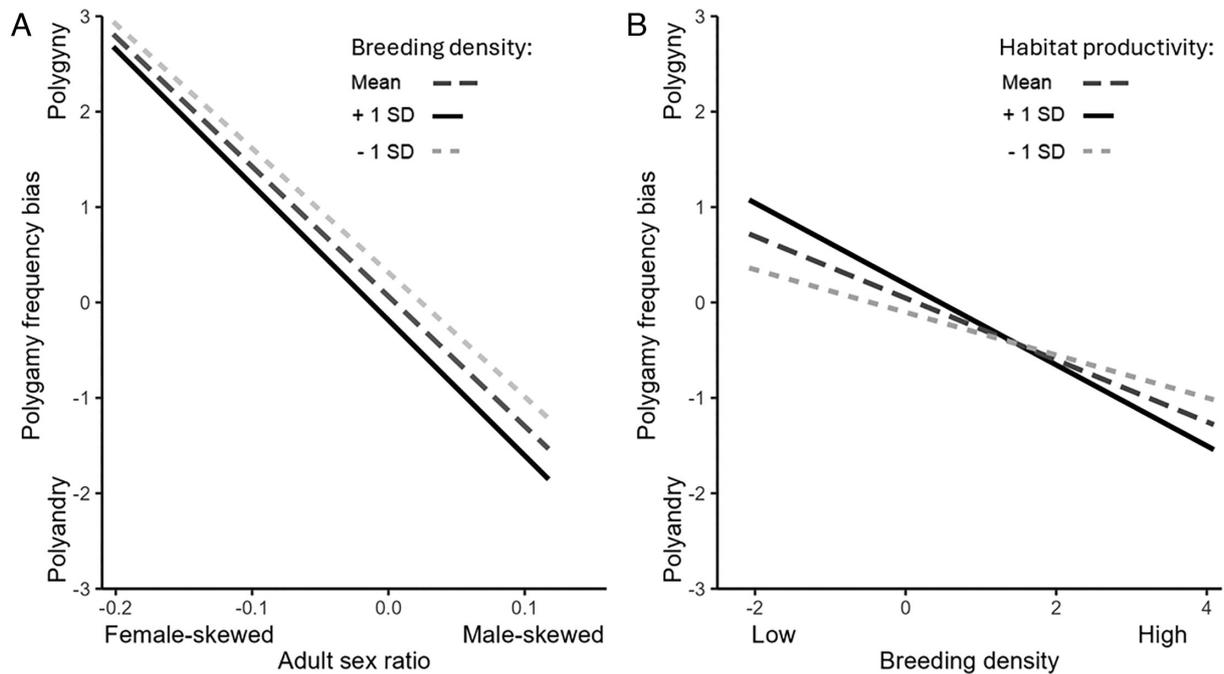


Fig. 3. Interactive effects (A) between adult sex ratio and breeding density and (B) between breeding density and habitat productivity on polygamy frequency bias (response variable). Adult sex ratio and breeding density are expressed as species estimates from raw data. See Table 1 legend and *Materials and Methods* in the main text for variables' explanation. Lines represent predictions for different values of (A) breeding density and in (B) habitat productivity (one SD higher than average: full black line, average: long dashed dark gray line, one SD lower than average: small dashed light gray line). $N = 36$ species.

studies. Finally, we note that observations in coucals parallel our results showing that the sex-role reversed black coucals tend to breed at higher densities than the monogamous and biparental white-browed coucals (87).

Importantly, ASR and breeding density had a marginally significant interactive effect on mating system, suggesting that the effects of skewed sex ratios on mating systems are modulated by densities. Theoretical models predict that mate encounter bias may increase with density (63). This has been supported by experimental studies of fruit flies (*Drosophila* spp.) since the influence of sex ratio on female fertilization is stronger at high density than at low density (66). Our result appears to be a solid evidence from wild populations confirming that breeding density can modulate the effects of ASRs on mating system.

Finally, our findings indicate that habitat productivity and population density have an interactive effect on mating system.

Specifically, at low density, habitat productivity is associated with polygyny whereas at high breeding density, habitat productivity is associated with polyandry. This outcome contrasts with our initial expectations, wherein we anticipated that high breeding density would diminish food access due to competition, thus reducing the impact of habitat productivity on polygamy. However, our result aligns with the hypothesis that higher habitat productivity (indicative of food abundance) promotes polygamy (both polygyny and polyandry, see *Discussion*, 25, 33). Nonetheless, the latter effect may be constrained by mate encounter rates, as indicated by breeding density. Future research might benefit exploring further interactive effects of these two environmental variables on avian mating systems.

Ecology and Sex Roles. Our study revealed that high habitat productivity, which is typically associated with high food abundance, is linked to polygyny and female care. This is in contrast with the

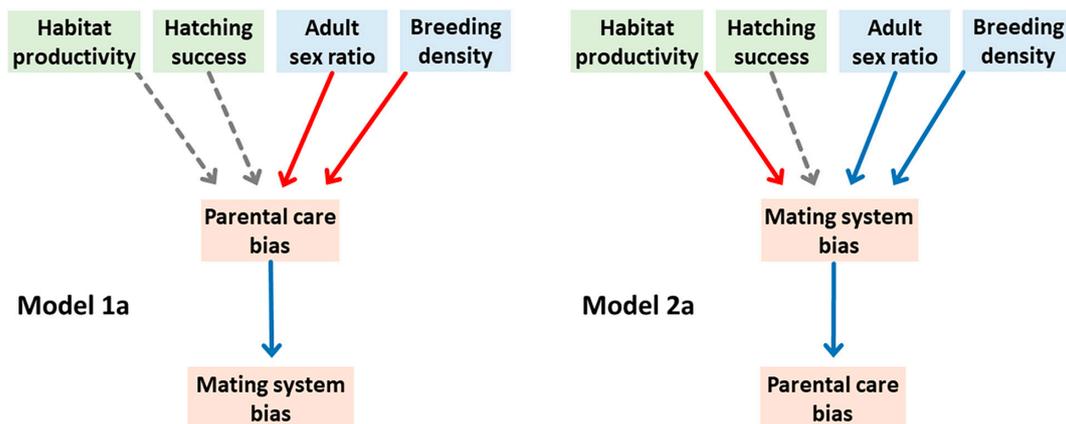


Fig. 4. Best-supported phylogenetic path models of sex role components and ecological and social predictor variables. Path analyses supported either Model 1a or Model 2a (or both) against alternative scenarios depending on which variables were used to represent parental care bias and mating system bias (see *SI Appendix, Table S3* for model comparisons and *SI Appendix, Fig. S2* for the full model set). Red and blue arrows indicate significant positive and negative relationships, respectively; dashed gray arrows show nonsignificant relationships.

predictions of the food abundance hypothesis (25, 33). Our findings are consistent, however, with seminal avian studies which also showed that increased food availability can promote polygamy in males and/or reduce it in females (24, 94–97). For example, both the Bicknell's thrush *Catharus bicknelli* and the dunnock *Prunella modularis* exhibited a decrease in polyandry frequency with increasing food availability (96, 97). The presence of both polyandrous and monogamous coucals' species, such as the black coucal and the white-browed coucal, respectively, in the same habitat also suggests that habitat productivity is not a primary driver of polyandrous mating in these species (87).

The idea that superabundant food resources would increase the involvement of males in parental care (25, 33) was refuted in experimental studies of biparental species (98–100). These studies demonstrated that supplemental food did not alter paternal behavior but increased maternal care, suggesting that food availability can affect males and females differently (15). This idea is also confirmed by the fact that some mammals show a shift from polygyny to monogamy resulting from reduced food availability, which modifies female territory size (101, 102).

Furthermore, although it is believed that low hatching rates caused by nest predation would promote polyandry (33, 38), none of our models showed a significant association between sex role variables and hatching success. Thus, our data do not support the nest loss hypothesis which is in line with other previous studies (25, 30). Hatching success tends to vary greatly both within and among populations and species (103, 104), which could potentially obscure associations with sex roles, if they might occur. Accordingly, the within-species repeatability of hatching success (*Materials and Methods*) is lower than that of other variables in our data. Besides, response to predation level in birds can be flexible and diverse; thus, birds could compensate or avoid predation by other means than changes in sex roles or life history (105).

In conclusion, using an extensive dataset from a highly diverse avian group, the shorebirds, and comprehensive phylogenetic analyses, we show that social factors (ASR and breeding density) are better predictors of sex roles than ecological factors (habitat productivity and hatching success). In addition, we also show that the effects of some of these factors on sex roles are interactive. Importantly, we advance studies of breeding systems and sex roles by identifying ASR as a predictor of—rather than a response to—mating systems and parenting. We call for follow-up phylogenetic analyses in taxa that exhibit variable mating systems and/or parenting, for instance assassin bugs, Cichlid fishes, frogs, ratites, and cuckoos and allies. Further experimental studies are also needed to understand the underlying mechanisms of such associations, including detailed behavioral and demographic analyses. Finally, we encourage fine-scale phylogenetic analyses using within-population variations of social behavior to determine the emergence and maintenance of plasticity in sex role evolution.

Materials and Methods

All data were collected from published literature or open databases. We extensively searched the primary literature reporting the behavioral, demographic, and ecological variables used in this study through Web of Knowledge and Google Scholar. We used the keywords "shorebird", "wader", or the English and Latin name of species in combination with "sex ratio", "sex role", "mating system", "polygamy", "parental care", "breeding", or "population monitoring." We also attempted to locate and screen specific publication on shorebirds not available through the above databases (e.g., annual population reports, taxon specialists' group reports). First, because ASR was usually the limiting information, we searched for data on this variable to update and extend the dataset used in ref. (48). Then, for the species with ASR estimates, we also screened the sources for other variables

(mating system, parental care, hatching success, breeding density, see below). Data collection was conducted between January 2019 and June 2020. The total number of records and populations and their references are given in [SI Appendix, Table S5](#). All data used in the study is available in Dryad (106).

Sex Role Variables.

Social mating system. We used two proxy measures of mating system, following the methods we developed in earlier comparative analyses (6, 22, 42, 48). First, we calculated mating system bias as the difference between the estimated percentages of the male's and female's polygamy (polygamy frequency bias henceforward). For each species, we recorded the percentage of individuals in a population that breed in social polygamy, separately for males (i.e., polygyny) and females (i.e., polyandry). We recorded any type of social polygamy (sequential or simultaneous) if it was observed within the same breeding season. Lekking birds (in our dataset: pectoral sandpiper, buff-breasted sandpiper *Calidris subruficollis*, ruff, American woodcock, and Eurasian woodcock *Scolopax rusticola*) do not exhibit social pair bonds, thus, to express the common assumption that male-male competition is intense in lekking species (107), we allocated 100% male polygamy for these species. For the analysis, following the recommendation of Wilson and Hardy (108), we used the logit transformation for this variable before analyses. For five species, we did not get any information for this variable (sharp-tailed sandpiper *Calidris acuminata*, mountain plover *Charadrius montanus*, snowy plover *C. nivosus*, Kittlitz's plover *C. pecuarius* and Eurasian dotterel); thus, these were omitted from the analyses of polygamy frequency bias.

Second, we calculated a polygamy score bias as the difference between male polygamy score and female polygamy score in order to include species where precise estimates of polygamy were not recorded but the occurrence of polygamy could be broadly categorized by qualitative descriptions. We scored evidence of polygamy for males and females separately on a scale of 0–4, with 0 corresponding to no (or very rare) polygamy (<0.1% of individuals when quantitative data are available), 1 to rare polygamy (0.1 to 1%), 2 to uncommon polygamy (1 to 5%), 3 to moderate polygamy (5 to 20%) and 4 to common polygamy (>20%) (following refs. 45, 48, and 109). The scoring of polygamy frequency is highly and significantly repeatable between two independent observers (intraclass correlation, ICC = 0.914, 22). We did not find accurate information for mating score in two species (sharp-tailed sandpiper and Kittlitz's plover); thus, these were omitted from all analyses of social mating systems.

Parental care. We used two different proxy measures for sex roles in parental care following our earlier work (6, 22, 42, 48). First, we scored the total male participation in parental care relative to females (parental care score bias henceforward). Scores were calculated on a scale of 0 to 4 for five forms of parental activities: nest building, incubation, nest guarding, chick brooding, and chick guarding. For each form of care, score 0 indicated no male participation (i.e., all care carried out by females), score 1 indicated substantially more female than male care (1 to 33% male care when quantitative data were available), score 2 indicated similar role of the sexes (34 to 66% male care), score 3 indicated substantially more male than female care (67 to 99% male care), and score 4 indicated 100% male care (i.e., no female care). These scores were based on quantitative data if available (e.g., % incubation provided by males) or on qualitative descriptions of care in the data sources. We calculated the average of the scores of the five investigated parental activities, with higher scores meaning more care provided by the males. The scoring is highly and significantly repeatable between observers (ICC = 0.792, 22).

Second, we estimated sex bias in parental care duration (parental care duration bias henceforward) as proposed by Székely & Reynolds (71). We divided the total length of parental care into seven periods: 1 to 3 for incubation and 4 to 7 for brood care. If one sex deserts the brood before incubation, it was given a score of 0, if one sex cares until the chicks fledge, it was given a score of 7, and intermediate scores represent desertion between these extremes and are proportional with time the parents are present during incubation and brood care. Then, sex bias was calculated as the difference between male and female scores.

Ecological and Social Factors.

Habitat productivity (NDVI). Since direct estimates of food availability during breeding are scarce in shorebirds, we used habitat productivity as a measure to evaluate the food abundance hypothesis. NDVI was used to quantify primary productivity of the breeding habitat. We used this index as a proxy for food abundance

because it has been shown that NDVI predicts the local biomass of consumers (e.g., arthropods) that are the main components in the diet of shorebirds (78, 79). NDVI data were obtained from Moderate Resolution Imaging Spectroradiometer (MODIS, NASA EOSDIS Land Processes DAAC) using Google Earth engine to access the "MOD13A2" data (110). NDVI was calculated from a sample of 1 km² resolution for all populations in our dataset using geographic information given in the studies (i.e., geographic coordinates or name of the study place). For each population, we extracted all available NDVI values from the years 2000 to 2010 during the breeding season of the targeted species. Then, we calculated the median values (to avoid biases due to extreme values) in order to have only one data point per population. When we had data from several populations for a species, we used the average NDVI values of the populations in the final species-level analyses (see below). MODIS-NDVI data are not available before 2000 so we chose the oldest available data from this database, and we used 10 y of data to avoid biased results due to years with unusual conditions (which were likely more frequent in more recent years). We log transformed the final NDVI estimate obtained per species and then squared and zero-centered to obtain a distribution in the same range as in other variables (see *Species estimates from raw data* hereafter).

Hatching success. Hatching success was estimated as the percentage of nests in a population that hatched at least one egg. We scored the quality of data as either low when the study included only a small subset of nests from the population, or only from a part of the breeding season, or if the methodology is not well detailed (31 records out of 191); or good when the study represented more than half of the total nests of the population and measured throughout the breeding season (160 records out of 191). Data for all the 41 species were obtained, and for 27 species, we obtained data for more than one population (and for many populations several estimates were available, resulting in the total of 191 records). Our hatching success data show a significant but low within-species repeatability (ICC = 0.210, $P < 0.001$). Further details are given in *SI Appendix, Table S5*.

Adult sex ratio. We calculated adult sex ratio as the proportion of males in the adult population (108, 111). We also recorded the sample size (number of individuals) and the time of sampling (breeding season: 96 records; nonbreeding season: 41 records; all year: 12 records; or during an unknown period: 8 records out of 157) for all ASR estimates. We also gave a quality score for each record on a 0–3 scale: 0 when the quality could not be estimated (6 records out of 157), 1 being a low-quality record (i.e., only a small fraction of the local population censused, and/or the method may be biased, 48 records out of 157), 2 being a medium quality (i.e., a significant part of the population was counted/captured, and the method was likely unbiased, 45 records out of 157), and 3 being a good quality (i.e., all or most individuals of the local population were counted or captured or a significant part of the population was counted or captured, with an effort to make the method unbiased; or the ASR was obtained from statistical models based on good quality data, 58 records out of 157). For 20 of the 41 species, we obtained data for more than one population, and for 25 populations (21 species), ASR was separately estimated for multiple years (resulting in the total of 157 records). Our ASR data show a significant within-species repeatability (ICC = 0.585, $P < 0.001$; see also ref. 111 for repeatability of ASR in birds). Details are given in *SI Appendix, Table S5*.

Breeding density. The raw data of breeding density were extracted as individuals or pairs per km². We considered any type of breeding density estimate due to differences in the survey methods and data availability between species. We recorded the method of the studies according to which type of breeding density was estimated (i.e., nest, pair, breeder, or total population counts). In order to readjust the density obtained by different methods to an approximately similar scale, we divided "breeder density" and "population density" by two; thus, we used breeding density as pair/km² in our statistical models. We also recorded data quality as either low-quality record (if density was calculated only on a small portion of the population or if the methods were not detailed, 42 records out of 339) or good quality record (i.e., all the population and breeding area were accounted for, 297 records). For 23 species we obtained data for more than one population with multiple estimates being available from some populations. Our breeding density data show a significant within-species repeatability (ICC = 0.611, $P < 0.001$). Details are given in *SI Appendix, Table S5*.

Statistical Analyses.

Species estimates from raw data. In order to control 1) for differences in data quality and/or methods between the different literature sources and 2) for differences in the number of populations found per species, we calculated species

estimates (i.e., one estimate per species per variable) for hatching success, adult sex ratio, and breeding density from the raw population-level data. These species-level estimates were obtained as predicted values from models containing one of these variables as response (i.e., separate model was used for each variable) and the variable(s) scoring quality (for hatching success model), season and quality (for adult sex ratio), and methods and quality (for breeding density) as fixed effect factors and species as random effect (following a quantitative genetic approach, but on species instead of individuals, 112). Predicted values were calculated using the MCMCglmm package in R (113), which implements Bayesian generalized linear mixed models with Markov chain Monte Carlo methods. MCMCglmm models were run for 1,000,000 iterations with a burn-in of 1,000 iterations and a thinning interval of 500 iterations, with a noninformative prior ($V = 1$, $\nu = 0.02$, following ref. 113). We checked whether the estimates correlate with the raw species values (expressed as the average of population values) to confirm whether the estimates still contain informative values (Pearson correlations, $P < 0.001$ for all the three estimates with $R^2 = 0.84$, $R^2 = 0.94$, and $R^2 = 0.87$ for hatching success, ASR, and breeding density, respectively). We used these modeled species-level estimates for hatching success, adult sex ratio, and breeding density as predictor variables in the later analyses (see below).

Phylogeny. Two hundred random phylogenetic trees (from <http://www.birdtree.org>) with Ericson and Hackett backbones were used for creating a consensus phylogenetic tree (*SI Appendix, Fig. S1*) using sumtree in DendroPy package in Python 3.10. (114). We also checked the sensitivity of our result to the phylogenetic hypothesis used in the analyses by repeating key comparative models with a supertree of shorebirds (77). Our results remained qualitatively and in terms of significance consistent between the models using different trees, except for one polygamy frequency bivariate model with breeding density as a predictor, where we observed a marginally nonsignificant effect instead of a significant effect when using the supertree instead of the consensus tree in the PGLS model: effect of breeding density, estimate -0.23 ± 0.11 , $P = 0.09$, $\lambda = 0.67$, $R^2 = 0.05$).

Phylogenetic comparative analysis. We tested the relationships between sex role variables and their putative predictors using phylogenetic generalized least squares (PGLS) models with maximum likelihood to find the best fitting values of Pagel's λ , a measure of phylogenetic signal in the data (115, 116). Mating system and parental care variables (four variables in total: polygamy frequency bias, polygamy score bias, parental care score bias, and parental care duration bias) were tested separately as response variables. For each of these response variables, we first tested the relationships with all explanatory variables (habitat productivity, hatching success, ASR, and breeding density) separately in bivariate models and then altogether in a multipredictor model. In a separate set of analyses, we repeated the multipredictor models with the inclusion of interaction terms between (I) ASR and breeding density and between (II) breeding density and habitat productivity (see the previously for justification). We tested these two interactions in separate models because our sample sizes do not allow to have enough statistical power for testing several interactions at once (resulting in a total of eight models containing interactions). We also tested whether geographic position of the species measured by their latitude (using averaged latitude of the populations when having more than one population) has an effect on the results of our models by adding latitude as an explanatory variable to our models, but latitude did not influence any of the results and thus was removed from the analysis.

Phylogenetic path analysis: We used phylogenetically controlled confirmatory path analyses (117) to investigate the fit of models representing different pathways linking sex role variables and their putative ecological and social predictors (*SI Appendix, Fig. S2*). One group of path models represented the scenario in which ASR (the strongest correlate of sex roles, see Results) together with other predictors has a causal effect on sex role variables (Models 1–3). We tested variants of this basic scenario that differed in which sex role variable(s) has direct incoming path(s) from predictors (Models 1–3), and whether some of the predictors have either direct or indirect (or both) path leading to the sex role variables (model variants a–e). Then, we created a second group of models (Models 4–6) representing the idea that variation in ASR is an outcome, rather than a cause, of sex differences in reproductive behavior (for example due to their sex-specific mortality effects, see previously). These models differ in which sex role component(s) has an effect on ASR (Models 4–6) and whether some of the predictors of sex roles have a direct or indirect (or both) effect (model variants a–c). The full model set included a total of 24 models (*SI Appendix, Fig. S2*). Sex role components were included by one of the two parental care variables (either

parental care score bias or parental care duration bias) and by one of the two mating system variables (either polygamy frequency bias or mating system score bias), and we ran the analyses by using all 4 combinations of the 2 × 2 sex role component variables. Thus, we ran four sets of path analyses, each comparing the 24 models, but differing in which variables represent parental care and mating system. In these analyses, we used those species (N = 36) for which we had data for all predictors and sex role variables.

We used the approach proposed by Santos (118) to fit the path models to the data. First, we applied phylogenetic transformation on the data before the path analysis to control for the effects of phylogenetic relatedness among species. For this purpose, Pagel's λ was estimated separately for each variable by maximum likelihood, and this variable-specific λ value was used to rescale the phylogenetic tree. Then, we used this transformed tree to calculate phylogenetically independent contrasts for the variable using the "pic" function of the R package "ape" (119). We repeated this process for each variable, and the resulting phylogenetically transformed data were used for fitting the path models by the R package "piecewiseSEM" (120), which implements the d-separation method (121). This approach uses Fisher's C-statistic to test goodness of fit: A model is rejected (i.e., it does not provide a good fit to the data) if the C-statistic is significant, and conversely, a P-value higher than 0.05 means acceptable fit (120). Model fit was compared between different path models by their AICc values (Akaike Information Criterion corrected for low sample sizes). We showed that this procedure provides reliable model fitting and model comparison, especially when the model set contains non-nested path models (Appendix 3 in ref. 53). We preferred this method over an alternative approach developed by Hardenberg & Gonzalez-Voyer (122) because in the latter approach, a single value of Pagel's λ is estimated for each pair of traits using PGLS that may not satisfy the assumptions of path analysis, e.g., when λ estimated from a regression of Y on X is different from λ estimated if X is

regressed on Y (53). To corroborate the results of Fisher's C-statistic, we calculated four additional widely used indices of model fit (TLI, CFI, RMSEA, SRMR) using the "lavaan" R package (123). It has been proposed that values of TLI and CFI > 0.95, RMSEA < 0.06, and SRMR < 0.08 indicate acceptable/good model fit (124).

Data, Materials, and Software Availability. Data used for the analyses are available on Dryad (doi: [10.5061/dryad.pvmcndntb](https://doi.org/10.5061/dryad.pvmcndntb)) (106). All other data are included in the manuscript and/or *SI Appendix*.

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Sex Role Reversal and High Frequency of Social Polyandry in the Pheasant-Tailed Jacana (*Hydrophasianus chirurgus*)

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In a few species, males invest more than females in parental care while the females invest in mating competition and producing multiple broods for several mates. Species in the family Jacanidae are commonly used for studying this type of breeding system (called sex-role reversal), and previous studies found discrepancies and variation between species in the expected characteristics of reversed sex roles. Yet, a better understanding of sex role differences in breeding behavior in such species is crucial for disentangling possible evolutionary mechanisms leading to this peculiar breeding system. Sex-role reversal in the pheasant-tailed jacana *Hydrophasianus chirurgus* has been documented long time ago. Since the very early observation of this species, however, there was no attempt to provide a comprehensive and quantitative description of their breeding. This study aims to fill these knowledge gaps by investigating the sex role differences in the breeding behavior of pheasant-tailed jacanas, by observing and monitoring a breeding population in Taiwan. We focused on three main characteristics of sex-role reversal: (1) competition between females for access to males, such as agonistic and courtship behaviors, (2) polyandrous mating, and (3) male-only care. As expected, we found that females provide most of the territory defense toward conspecifics. Males also participated in agonistic behaviors, although less frequently than females. Furthermore, contrary to what was expected, we found that males spent more time than females on courtship behavior. Polyandrous females performed mating and laying sequentially with different mates but maintained the pair bonds simultaneously with multiple males. For the first time for the species, we could estimate that the average number of mates per female (i.e., degree of polyandry) was 2.4 and that at least 81.8% of the females in the population were polyandrous. Finally, our observations corroborated that brood care is

predominantly provided by males, nevertheless females were also participating to some degree in brood attendance but never in direct care (i.e., brooding). This study highlights that some aspects of polyandrous breeding might deviate from stereotyped view on sex-role reversal, and stress the importance of further within species and comparative studies in order to fully understand the mechanisms leading to sex-role reversal.

Keywords: polyandry, sex-role reversal, male-only care, Jacanidae, sexual competition

INTRODUCTION

In species providing parental care the sex difference in parental investment, as defined by Trivers (1972), varies widely. In most of the species, on average, females invest more in parental care (Clutton-Brock, 1991; Cockburn, 2006; Székely et al., 2013), which is often termed as conventional sex-roles. However, in a few species, we observe the opposite: males invest more than females in parental care while the females invest in mating competition and breeding with several mates. This is the case in species that have male-only parental care with a polyandrous type of mating system, called sex-role reversal (Trivers, 1985; Andersson, 1994). Occurring only in 1–2% of the species (Cockburn, 2006), sex-role reversal is the rarest type of breeding system in birds.

It was proposed that the sex providing care will be the one limiting the reproduction of the other sex (Emlen and Oring, 1977). In other words, the sex having higher potential reproductive rate will invest more in mating and territoriality (which is defined as a “masculine” role sometimes; Barlow, 2005). In a sex-role reversed species, thus, the females are expected to take upon territoriality and compete with other females for access to mates through aggressiveness. The dominance of females on males in sex-role reversed species is indeed confirmed by their reversed sexual size dimorphism with females being bigger than males and thus expected to be also more aggressive (Székely et al., 2007).

In term of caring for the young, precocial bird species are more flexible than altricial ones as often a single parents can take care of this task while the other parent deserts (Maynard Smith, 1977). This opportunity for uniparental care can lead to sex-role reversal in some cases, where males take most or all care of the young. It is hypothesized that males accept the care provider role because the cost of finding a new mate may be higher than the costs of investing in the current brood, for example due to the shortage of females, thus males may maximize fitness benefits by staying with their mates and provide care for existing offspring (Kokko and Jennions, 2008; Liker et al., 2013). In such populations the opposite is true for females, i.e., they have the opportunity to obtain multiple mates, thus may be selected to invest more in mating and less in care. Although classical polyandrous mating systems and sex-role reversal has been in the scope of many evolutionary studies, yet it is still uncertain from an evolutionary point of view why some lineages have adopted this breeding system (Betts and Jenni, 1991; Andersson, 2005). One reason for the lack of explanation might be the low level of knowledge and inconsistent information that we have about the ecology and behavior of species having such type of breeding.

The Jacanidea is one of the famous group of birds known for their sex-role reversal. All jacana species except the lesser jacana *Microparra capensis* seem to have indeed females breeding with several partners and males taking care of the brood. The polyandrous mating has been confirmed for 6 out of the 8 jacana species. The lesser jacana is monogamous (Tarboton and Fry, 1986; Hustler and Dean, 2002) and the level of information on the Madagascar jacana *Actophilornis albinucha* is insufficient to confirm its supposed polyandrous mating (D’Urban Jackson et al., 2019). However, within the other 6 polyandrous jacana species, the type of copulation pattern (i.e., simultaneous or sequential with different males) and degree of polyandry (i.e., average number of mates per female) vary a lot across the species (see **Table 1** for detailed review). Their territoriality has been described in several species as a super-territory defended by the female which includes several sub-territories defended by her mates. In sex role reversed species, we do expect the females to provide most territorial defense, and thus to be more aggressive than males toward conspecifics. Even though this has been verified in the African jacana *Actophilornis africanus* (Tarboton, 1995), this idea has been challenged with the wattled jacana, the northern jacana and with the bronze winged jacana as in these species males were more likely to be the first one to respond to a conspecific intruder on the territory (Butchart et al., 1999a; Emlen and Wrege, 2004a; Lipshutz, 2017).

In jacanas, male-only care has been confirmed in six species. Yet, the complete absence of females’ participation in the care has been challenged: female wattled jacanas and northern jacanas have been observed participating at low level in parental care, even doing some brooding of the chicks, when the male is busy with incubating another clutch (Jenni and Betts, 1978; Emlen and Wrege, 2004a). The authors of the latter study even defined the females as “backup providers of chick care.” Yet in other jacanas species the male is readily described as the solely care provider (Tarboton, 1992, 1993; Mace, 2000; Butchart, 2008).

The pheasant-tailed jacana *Hydrophasianus chirurgus* is a classic example of polyandry and sex-role reversal since the very early studies by Hoffmann (1949, 1950), although only a few later studies investigated the breeding biology of the species. Unfortunately, details about their pair bonding is not extensively available: some of the descriptions are anecdotal (Serrao and Shekar, 1962) or based only on the observations of a single female (Thong-aree et al., 1995; Chen et al., 2008a). The fact that this species is polyandrous is well known and observed repeatedly, but the degree of polyandry is yet unknown (**Table 1**). Details about territoriality, female mating competition and male care are also very scarce (Thong-aree et al., 1995; Chen et al., 2008a).

TABLE 1 | Mating system in six jacana species.

Species	Sample size (females)	Polyandry				% of polygynous males ^d	References
		Type (pair bond/copulation)	Degree ^a	Range ^b	% Females ^c		
<i>Metopidius indicus</i>	N = 8	Simultaneous/Simultaneous	1.6	1–4	50%	0%	Butchart, 1999
<i>Metopidius indicus</i>	N = 16	Simultaneous/Simultaneous	1.7	1–4	50%	0%	Butchart et al., 1999a
<i>Jacana spinosa</i>	N = 15	Simultaneous/Simultaneous	2.2	1–4	87%	0%	Jenni and Collier, 1972
<i>Jacana spinosa</i>	N = 4	Simultaneous/Simultaneous	2.5	1–3	80%	0%	Jenni and Betts, 1978
<i>Jacana jacana</i>	N = 12	Simultaneous/Simultaneous	1.2	1–2	18%	0%	Osborne, 1982
<i>Jacana jacana</i>	N = 160	Simultaneous/Simultaneous	1.7	1–4	60%	0%	Emlen and Wrege, 2004b
<i>Actophilornis africanus</i>	N = 7	Simultaneous/Simultaneous	3.9	2–7	100%	40%	Tarboton, 1992
<i>Actophilornis africanus</i>	N = 5	Simultaneous/Simultaneous	1.6	1–2	40%	33%	Tarboton, 1995
<i>Irediparra gallinacea</i>	N = 6	Simultaneous/Sequential	2.4	1–3	80%	33%	Mace, 2000
<i>Hydrophasianus chirurgus</i>	N = 1	Simultaneous/Sequential	–	3	–	–	Chen et al., 2008a
<i>Hydrophasianus chirurgus</i>	N = 1	–	–	4	–	–	Thong-aree et al., 1995
<i>Hydrophasianus chirurgus</i>	N = 11	Simultaneous/Sequential	2.4	1–5	82%	4%	This study

^aAs average number of male per breeding female.

^bRange of number of male per breeding female.

^c% of female having more than one male during the breeding season.

^d% of male having more than one female during the breeding season.

This study aims at a better understanding of sex role differences in the breeding behavior of pheasant-tailed jacanas, by observing and monitoring a breeding population in Taiwan. We focus on the three parts of the breeding: (1) mate acquisition: first we study the amount of sex differences in agonistic behavior, predicting that females are involved more often than males in territorial defense. Then we investigate possible sex differences in the courtship behavior (i.e., time spent on displays), where we would expect females investing more in courtship when starting a new clutch, since the benefits of producing additional offspring should be higher for the females than for the males with already existing brood. (2) Then we investigate the pair bonding patterns and dynamics in order to calculate the degree of polyandry in this species and proportion of polyandrous females in the population. (3) Finally we study brood care (direct: brooding, and indirect: brood attendance) to understand the extent of the role division between males and females, expecting males to be the solely sex taking care of the brood, whilst females are deserting the male and the brood for creating a new clutch with a new mate.

MATERIALS AND METHODS

Study Site and Population

The study was carried out from late June to early September 2019 in the Pheasant-tailed Jacana Educational Park (Guantian, Tainan City, Taiwan; 23°10'58.0"N 120°18'41.2"E; called Park henceforward). The pheasant-tailed jacana has been classified as an endangered species in Taiwan since 1989. In the last 10 years, the Tainan region has seen an increase in the population as the result of a successful conservation project (from 284 individuals in 2010 to 1024 individuals in 2019; Forestry, 2019), and ca. 80% of this population is found on water chestnut ponds in and around the Park. The Park (i.e., study site) was established in

2007 to promote and educate about this bird as well as providing breeding sites protected from farming activities. Jacanas breed in the reserve from mid-April until the end of September. However, we were able to conduct fieldwork only from mid-June until early September in 2019 due to logistic reasons, so the study period covered the second half of the breeding season. The total area of the study site was about 0.15 km², which was divided into 25 ponds (**Supplementary Figure 1**). Although the whole area was studied to monitor the breeding of the birds, due to time restriction and poor visibility of birds on some of the ponds only 7 of the ponds were used for behavioral observation and individual identification (**Supplementary Figure 1**: P-3.1, P-3.2, P-5, P-6, P-7.1, P-7.2, and P-7.3, called hereafter “focal ponds”). The majority of the observations were conducted on pond P-5 as it was the biggest pond with a good visibility to the human observers, which allowed the identification of most resident individuals. Observations in P-3.1, P-3.2, P-5, and P-6 were made from behind wooden hides installed by the Park for visitors. Birds were habituated to the presence of human visitors and observers in these hides that made observations possible, even from short distance, without sign of disturbance. Observations in P-7.1, P-7.2, and P-7.3 were conducted from a handmade mobile bamboo hide. The hide was not moved during the observation and birds were habituated to its presence before the observations.

Individual Identification

Only two males in the focal ponds were ringed so we used detailed drawings of plumage differences (in the black head patch, white wing patch, and tail length, **Supplementary Figures 2, 3**) to ensure reliable identification of the individuals (Byrkjedal et al., 1997; Liker and Székely, 1999). Within-individual consistency of these patterns were checked several times during the season by drawing detailed patterns of identification and re-drawing

them blindly again to see the consistency. The drawings were used for identification only in a single season, thus changes in plumage between years was not a problem (the birds molt after the breeding season and the consistency of breeding plumage between years has not been tested). Even if individuals were quite territorial, territory location in itself was not sufficient for identification as change in territory locations was observed through the season. For instance, two different males (M13 and M10, see **Table 2**) were observed nesting at exactly the same spot at different times of the season. The use of plumage differences allowed us to identify 12 females and 23 males. However, one female and one male left the focal ponds shortly after being identified and thus are not appearing in any of the results.

Mating System

Once an individual was identified, its pair bonding, nesting attempts and breeding success were monitored by regular

TABLE 2 | Breeding performance of pheasant-tailed jacana: details of monitored nests and couples (female – male pairs).

Pond ID	Female ID	Male ID	Nest ID	Number of eggs	No. hatchlings	No. fledglings
P-3.1	F1	M1	N088	2	0	0
P-3.2	F2	M2	N083	4	0	0
		NA	–			
P-5	F3	M3	N066	4	4	3
		M3	N119	4	2	NA
		M4	N093	4	4	2
		M5	N102	4	2	2
	F4	M6	–			
		M7	–			
		M8	–			
	F5	M9	N129	1	0	0
		M9	N132	4	0	0
		M10	N107	2	0	0
		M10	N118	2	1	NA
M11		N051	4	3	0	
P-6	F7	M12	–			
		M13	N080	4	2	0
		M14	N113	4	4	NA
		M15	N124	4	0	0
P-7.1	F9	M16	N099	2	0	0
		M17	N086	4	0	0
		NA	–			
P-7.2	F10	M18	N128	4	0	0
		M19	N111	4	1	NA
		NA	N096	3	0	0
P-7.3	F11	M20	N097	4	4	1
		M20	N136	4	0	0
		M21	N120	4	0	0
		M22	N060	4	4	NA

NAs for male identification (ID) denote unidentified male but still identified pair bonding (the male left the site before being accurately identified). NAs for number of fledging are from nests where the chicks were younger than 40 days old at the end of the study.

observations through the breeding season. Two individuals were considered to be paired when (1) they were repeatedly observed engaging in courtship behavior (i.e., various ground and aerial displays and vocalizations), copulation or nest building behavior, and (2) they were observed actively feeding next to each other without showing agonistic behavior (see below, these criteria are similar to those used in Butchart et al. (1999a)). Since the bond between the female and male usually persisted for long period (up to several weeks), we were able to infer the pair-bonds from multiple observations for most birds. Extra-pair paternity may occur in jacana (Emlen et al., 1998; Haig et al., 2003), however, in this study we use the term polyandry to describe the social mating system.

Nest and Brood Monitoring

When a nest was found, we considered the male performing egg care (incubation and shading) as the father. The female that was associated (paired) with that male was considered as the mother. Each nest found in the focal ponds was checked with a scope every day during egg laying, at least every three days during incubation and every day around the expected hatching date (about 23 days after the first egg laying). A nest was considered successful when at least one of the eggs hatched. After hatching, broods were monitored at least every three days and were considered successful when at least one chick reached the age of 40 days. The exact age of fledging has not been determined for this species (Jenni and Kirwan, 2020) but our observations suggest that after 40 days the chicks are quite independent and can fly at least for short distance. We followed a total of 23 nests and 11 broods produced by 19 couples (i.e., female – male pair) on the territories of 11 females (**Table 2**).

Behavioral Observations

We made three types of behavioral observations: agonistic interaction counting, pair bonding behavior observation and brood attendance behavior observation. All behavioral observation were made using a scope (Kowa TSN-601 with a 30x Kowa TSE-14WD eyepiece magnification), behind wooden fence hide or mobile hide (see above) and at least 30 min after arrival to the site for avoiding recording any possible disturbance consequences from the observer's arrival. Agonistic interaction counting was done only in P-5 (see below), pair bonding behavior observations were done in P-3.1, P-3.2, P-5, P-6, P-7.1, P-7.2, and P-7.3 and brood attendance behavior observation were done in P-5, P-7.1, and P-7.2 as the other focused pond did not have brood. All observations were made by one observer (NF) to avoid observer bias. Only identified individuals were targeted for behavioral observation.

During behavioral observation we divided the birds' behaviors into nine categories [some of these postures are also described for the African jacana in Tarboton (1992) and Bonkewitz (1997)]: (1) agonistic behaviors: threat displays including 'upright threat display,' 'wing spur display,' and ground and aerial attack, (2) courtship behaviors: head down posture (often accompanied by vocalizations), mounting, and copulation, (3) nest-building behaviors: pulling and throwing vegetation toward (potential

or existing) nest site and manipulating vegetation on a nest site, (4) egg care behaviors: incubation (i.e., sitting on the eggs) or egg shading (standing above the egg giving them some shade), (5) brooding behaviors: standing or sitting with chicks under the wing, (6) foraging behaviors: walking and pecking at vegetation in water, (7) maintenance behaviors: preening, scratching, stretching or bathing, (8) vigilance behaviors (i.e., alert): standing in an upright posture with the neck extended, without the tail upright and without the nape feather upright (as in agonistic behavior), (9) movement behaviors: walking, running or flying.

Agonistic interactions counting was made only in pond P-5 as it was the pond with a larger number of individuals identified allowing enough interactions with identified participants for statistical analysis. In this pond, the visibility allows to see the majority of the individuals at the same time, so individuals were observed about the same amount of time. It means that when spending time to observe some focal individuals on P-5, any agonistic behavior happening between other known individuals at the same time could also be noticed and counted (number of males on P-5: 11; number of females on P-5: 4). We counted all types of agonistic behavior as described previously. Every agonistic interaction occurrence was recorded throughout the day (even during other behavioral observation, i.e., during pair bonding and brood attendance observations) if it was between two identified individuals. We counted as one occurrence of agonistic interaction from the moment it starts until one or both individuals flew or walk to another area of the pond and the interaction stopped. We divided the agonistic interactions in four categories: Female–Female (FF), Male–Female (MF), whereas Male–Male interactions were split into between males sharing (i.e., had been paired to) the same female (MMP) and between males not sharing the same female (MMN). We did not create two categories in Male–Female interaction as all except one were observed between a female and a male that were not paired.

Pair bonding behavior observations and brood attendance behavior observations consisted of an instantaneous scan sampling of focal individual's behavior for 30 min every 20 s and for 60 min every 30 s, respectively. When an individual was hidden (e.g., behind high grasses) or not visible in the pond we gave a "NA" (i.e., no data) to that record. We calculated the proportion of time spent on each category during the observation (excluding the NA observation). We also noted at every 5 min the approximate distance between the focal individuals. The distances between individuals were estimated using reference objects with known size, e.g., the birds themselves and the surrounding floating lotus and water chestnuts leaves. Individuals were rarely more than 100 m away from the observer. Furthermore, all distance estimations were made by the same observer allowing a good consistency in these estimations. We considered the proximity distance to about 3 m, i.e., if couples were within 3 m distance of each other they were considered in proximity of each other. In the same way if an adult was within 3 m of its brood it was considered in proximity of its brood ("brood attendance" henceforward). We used this distance because, according to our

observation, it is the distance where the individuals interact between each other (i.e., vocalization or specific behavioral signal as head-down position or upright threat display) without one flying to the other.

Pair bonding behavior observations were made only on identified pairs observed in proximity of each other on the day of observation. Both male and female behavior were observed at the same time (if both were visible). A total of 44 courtship observations were made, involving 16 different males pair-bonded with 10 different females. Five couples were observed only once, the other 11 were observed at least two times with one couple observed nine times. The reason for the uneven observation time per couple was that some pairs were more often spending time together than others, furthermore, it was also dependent of the observer availability.

Brood attendance behavior observations were made only for identified individuals in the presence of their known chicks, whose number and approximate age were known from earlier observations of the family. Brood identity was assessed from proximity of the chicks to the identified parent and their corresponding age (i.e., size of the chicks). For each observation, we calculated the amount of time that the brood spent in proximity (i.e., within 3 m) of the male only, female only, or both parents, or in the absence of parents. Brood attendance behavior observations were observed for a total of 10 different broods which includes five females and eight males. One brood was observed only once at age of 39 days old (N066), while the rest of the broods were observed at least twice (see **Supplementary Table 1**). In 11 brood observations we did not have data for the female as the females did not appear in sight during the observation. We observed brood attendance (i.e., parent being within 3 m away from the chicks) in 8 out of 22 observations by the female and in 21 out of 22 observations by the male. In one of the observations, behaviors were recorded but neither the male nor the female approached the chick close enough to be considered as brood attendance.

Data Analysis

Agonistic interactions counting was analyzed using generalized linear mixed models with a Poisson distribution including individuals' identification as random factor. We first tested if there was a sex difference by constructing a model with the number of interactions as a response variable against the sex of the individual and the type of interaction (intrasexual interaction (FF and MM) or intersexual interaction MF) as well as their two-way interaction as explanatory variables. We then analyzed the males' interactions separately with the number of interactions as response variable against the type of interaction (intersexual interaction: MF, Male–Male interaction sharing same female: MMP and Male–Male interaction not sharing the same female MMN) as explanatory variable.

In order to measure sex difference in time spent on various behavioral categories in the pair bonding behavior observations, we used generalized linear mixed models using a Gaussian distribution, with the proportion of time spent in different behavioral categories (after square-root transformation) as response variable and sex, time of the day (i.e., if the

observation was made in the morning or the afternoon) and the time spent in the proximity (i.e., within 3 m) of the mate as well as the two-way interactions between the sex and the two other variables separately as explanatory variables. Couple identification nested in female identification were included as a random intercept. We did this analysis, with separate models, only for the following behavioral categories: (1) agonistic behaviors, (2) courtship behaviors, (3) nest-building behaviors, (4) foraging behaviors, (5) maintenance behaviors, (6) vigilance behaviors, (7) movement behaviors. Egg care behaviors and brooding behaviors were not analyzed as there were not enough occurrence during the pair bonding observations.

In the analyses of brood attendance behavior observations, first, we measured sex difference in time spent on brood attendance (in proximity of the chicks within the 60 min observation) using a generalized linear mixed model with a Gaussian distribution with the proportion of time spent in proximity of the chicks (i.e., brood attendance) as a response variable. We included the sex of the parent (here divides in three categories: male only, female only or both parents are present), the age of the offspring (divided in four categories: less than 10 days old, between 10 and 20 days old, between 20 and 30 days old and more than 30 days old), the time of the day (i.e., if the observation was made in the morning or the afternoon) as well as the two-way interactions between the sex and the two other variables separately as explanatory variables. Couple identification nested in female identification were included as a random intercept. Secondly, to measure sex difference in time spent on different behavior during brood attendance (i.e., only when in proximity of the chicks), we analyzed the proportion of time spent on each behavioral categories separately, as response variable, against the sex of the parents, the age of the offspring and the time of the day of observation as well as the two-way interactions between the sex of the parent and the time of the day as explanatory variables. Interaction between the sex and the age of the offspring could not be included in the models as there was not enough data in each category to be analyzed. We used couple identification nested in female identification as random effects. For this part we focused only on four behavioral categories: (1) agonistic behaviors, (2) foraging behaviors, (3) maintenance behaviors, (4) vigilance behaviors. Courtship behaviors, nest-building behaviors, egg care behaviors, and movement behaviors, were not analyzed here as their low occurrence during brood attendance could not allow it. Sex difference was not analyzed in brooding behavior as it was exclusively performed by the males. Brooding was observed rarely thus we had not enough data to analyze any time or age of the offspring effect.

In all cases we performed stepwise backward model selection procedures starting from the full model. Fixed effects in the models fitted with the maximum likelihood (ML) were tested by comparing a model with and without the fixed effect using likelihood ratio tests (LRTs) against a chi-square distribution (χ^2). Non-significant fixed effects ($P > 0.05$) were removed one by one from the model starting with the least significant. The final model was fitted with restricted maximum likelihood (REML) to obtain the estimates for the fixed effects (Zuur et al., 2009). All statistics were performed

in R version 3.5.0 (R Development Core Team, 2018), using the nlme package (Pinheiro et al., 2013) and lme4 package (Bates et al., 2015). Shapiro–Wilk tests were used to analyze normality and Bartlett tests to analyze homogeneity of variances. Tukey method was used for *post hoc* analyses, using emmeans and emtrends from the emmeans R package (Lenth, 2019).

RESULTS

Agonistic Interactions

Agonistic interactions were observed between 15 of the 17 identified individuals that were resident on pond P-5: 4 females and 11 males. Males were significantly less frequently involved in agonistic interaction compared to females [estimate \pm SE (male) = -1.84 ± 0.51 , $\chi^2 = 9.64$, $P = 0.002$, **Figure 1**]. Both males and females were involved in more intra-sexual interactions than in inter-sexual interactions [estimate \pm SE (intra-sexual) = 0.86 ± 0.17 , $\chi^2 = 27.10$, $P < 0.001$, **Figure 1**]. The interaction between sex and type of interaction (intra- or inter- sexual) was not significant ($\chi^2 = 2.94$, $P = 0.09$). When males were analyzed separately, they tended to be more aggressive toward males pair-bonded with another females (MMN) than toward males pair-bonded to the same female (MMP), and they were significantly more aggressive toward males pair-bonded with a different female (MMN) than toward females (MF) (interaction type: $\chi^2 = 10.92$, $P = 0.004$; *post hoc* test: MF-MMN: -0.78 ± 0.25 , $P = 0.006$; MF-MMP: -0.24 ± 0.28 , $P = 0.66$; MMN-MMP: 0.54 ± 0.23 , $P = 0.05$; **Figure 1**). All except one male-female interactions were between male and female involved in different couples.

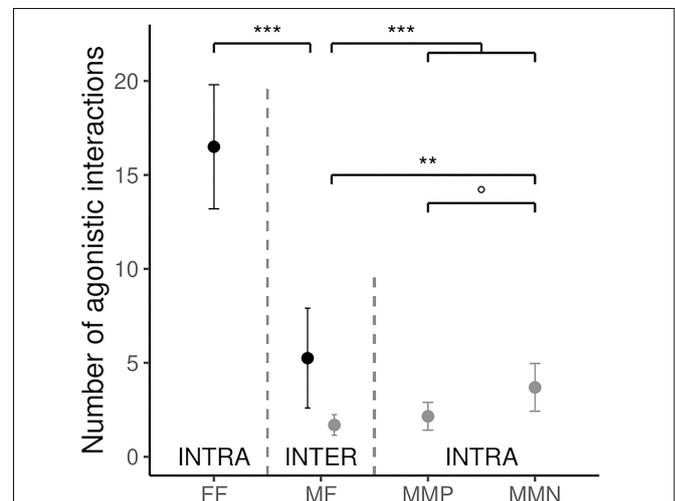


FIGURE 1 | Average number of agonistic interactions for female (in black) and male (in gray) jacanas for intra-sexual (INTRA) and inter-sexual (INTER) interactions. FF, Female–Female; MF, Male–Female; MMP, Male–Male from same Female; MMN, Male–Male from different Female. ° $P = 0.06$, ** $P < 0.01$, *** $P < 0.001$. Females: $N = 4$; Males: $N = 11$. Error bars denote standard errors.

TABLE 3 | Sex difference in amount of time spent on specific group of behaviors during pair bonding behaviors observation: courtship, agonistic behavior, vigilance, maintenance, foraging, movements, and nest building (see methods for details of these behavioral categories).

		Full model estimates ± SE		Selected model estimates ± SE	χ^2	P
Courtship behaviors						
Sex	(Male)	0.08 ± 0.06	(Male)	0.17 ± 0.03	25.41	<0.001
Time of the day	(Afternoon)	0.06 ± 0.05	(Afternoon)	0.08 ± 0.03	6.72	0.01
Time spent in proximity		− 0.02 ± 0.11		−	1.81	0.18
Sex × Time of the day	(Afternoon × male)	0.01 ± 0.07		−	0.03	0.85
Sex × Time spent in proximity	(Male × proximity)	0.25 ± 0.16		−	3.22	0.07
Agonistic behaviors						
Sex	(Male)	0.01 ± 0.06		−	0.18	0.67
Time of the day	(Afternoon)	− 0.005 ± 0.05		−	0.04	0.84
Time spent in proximity		0.23 ± 0.11		0.23 ± 0.08	8.12	0.004
Sex × Time of the day	(Afternoon × male)	− 0.01 ± 0.07		−	0.02	0.9
Sex × Time spent in proximity	(Male × proximity)	0.02 ± 0.16		−	0.01	0.91
Vigilance behaviors						
Sex	(Male)	− 0.04 ± 0.08		−	1.78	0.18
Time of the day	(Afternoon)	0.03 ± 0.06		−	0.05	0.82
Time spent in proximity		− 0.04 ± 0.15		−	<0.001	0.996
Sex × Time of the day	(Afternoon × male)	− 0.07 ± 0.08		−	0.6	0.44
Sex × Time spent in proximity	(Male × proximity)	0.08 ± 0.2		−	0.16	0.68
Maintenance behaviors						
Sex	(Male)	0.14 ± 0.08	(Male)	0.12 ± 0.07	0.12	0.72
Time of the day	(Afternoon)	0.03 ± 0.06		−	0.01	0.9
Time spent in proximity		0.13 ± 0.14		0.16 ± 0.13	0.19	0.66
Sex × Time of the day	(Afternoon × male)	− 0.05 ± 0.08		−	0.38	0.54
Sex × Time spent in proximity	(Male × proximity)	− 0.35 ± 0.19	(Male × proximity)	− 0.39 ± 0.18	4.63	0.03
Foraging behaviors						
Sex	(Male)	− 0.18 ± 0.08		−	3.45	0.06
Time of the day	(Afternoon)	− 0.09 ± 0.07		−	2.27	0.13
Time spent in proximity		− 0.17 ± 0.16		−	0.2	0.65
Sex × Time of the day	(Afternoon × male)	0.05 ± 0.09		−	0.31	0.58
Sex × Time spent in proximity	(Male × proximity)	0.22 ± 0.21		−	1.75	0.19
Movement behaviors						
Sex	(Male)	0.06 ± 0.04		0.05 ± 0.02	5.46	0.02
Time of the day	(Afternoon)	0.1 ± 0.03		0.05 ± 0.02	3.99	0.046
Time spent in proximity		− 0.11 ± 0.08		−	0.13	0.72
Sex × Time of the day	(Afternoon × male)	− 0.11 ± 0.05		−	3.58	0.06
Sex × Time spent in proximity	(Male × proximity)	0.17 ± 0.11		−	2.62	0.11
Nest building behaviors						
Sex	(Male)	0.01 ± 0.04	(Male)	0.003 ± 0.03	6.28	0.01
Time of the day	(Afternoon)	− 0.01 ± 0.03	(Afternoon)	− 0.01 ± 0.03	2.51	0.11
Time spent in proximity		− 0.004 ± 0.08		−	0.06	0.8
Sex × Time of the day	(Afternoon × male)	0.09 ± 0.05	(Afternoon × male)	0.09 ± 0.04	4.23	0.04
Sex × Time spent in proximity	(Male × proximity)	− 0.02 ± 0.11		−	0.03	0.86

Table shows the estimates and standard error for the full model and for the selected model fitted with restricted maximum likelihood (REML). Factor variables' estimates contrasts term are indicated between parentheses. Stepwise backward model selection done with models fitted with maximum likelihood (ML) are given for each variable estimates (χ^2 and associated P-value). Significant P-values are shown in bold. Proportion of time spent on each behavioral category (used as response variable) was squared root transformed. Number of observations: N = 44; Male: N = 15, Female: N = 10 (**Supplementary Figure 4A**).

Pair Bonding Behaviors

During pair bonding behavior observations, males spent significantly more time on courtship behaviors than females ($\chi^2 = 25.41$, $P < 0.001$, **Table 3** and **Supplementary Figure 4A**). They also spent more time moving around (movement behaviors) than females ($\chi^2 = 5.46$, $P = 0.02$, **Supplementary Figure 4A**). Analysis showed a significant interaction between sex and proximity on maintenance behaviors: the more time the male and female spend together during the observation the more time

the females spent on maintenance while it was the opposite for the males, i.e., the less the males spent time on maintenance (*post hoc* analysis of the interaction: slope estimation for females 0.15 ± 0.13 , slope estimation for males -0.24 ± 0.13 , $\chi^2 = 4.63$, $P = 0.03$, **Table 3**). We found a significant effect of the interaction between sex and time of the days on the time spent on nest building behaviors ($\chi^2 = 6.46$, $P = 0.01$). *Post hoc* analysis shows that males spend significantly more time on nest building than females during the afternoon only (*post hoc* analysis: female –

male difference during afternoon observations $t_{69} = -3.29$, $P = 0.01$, **Table 3** and **Supplementary Figure 4A**). There was no difference in time spent on foraging, vigilance and agonistic behavior between males and females.

Courtship behavior and movements behavior significantly happened more in the afternoon (Courtship: $\chi^2 = 6.72$, $P = 0.01$; Movement: $\chi^2 = 3.99$, $P = 0.046$ **Table 3** and **Supplementary Figure 3A**). The more time males and females spent together, the more time they both spent on agonistic behavior ($\chi^2 = 8.12$, $P = 0.004$, **Table 3**).

We observed a total of 22 copulations for seven females and nine males. On pond P-5, we observed 17 copulations for three females and five males (details are given in **Figure 2**). Copulations were observed exclusively during the afternoon. Copulations were observed from 4 to 3 days before the first egg laying and the day before each egg laying, except for one couple (F3-M3) where 2 copulations the same day were observed 7 days before the egg laying. However, we cannot exclude the possibility that the female had a nest attempt, but the nest was not found. We never observed more than 2 copulations per couple per day.

Mating System

Out of the 11 focal females, 9 females paired with more than one male (81.8%, **Table 2** and **Figure 3**). Out of the 18 males observed only one was seen changing mate by pair bonding with two different females: M6, who was seen pair bonding with F4 several times without successfully nesting but as soon as the female F4 left the breeding site permanently (i.e., was not seen anymore), the female F3 was seen actively performing displaying behavior toward M6. No nesting attempts were seen from either the couple F4-M6 or F3-M6. Females had 1–5 different males with an average of 2.4 males per females.

Brood Attendance Behaviors

On average, males performed brood guarding (i.e., stayed in proximity of the chicks) during $54.2 \pm 6.9\%$ of the observation time whereas females stayed in proximity during $5.7 \pm 2.2\%$ of the time. Mixed models analysis showed that male-only brood attendance (i.e., in proximity of the chicks without the female around) was significantly more frequent than female-only brood attendance or both parents brood attendance ($\chi^2 = 70.30$, $P < 0.001$; *post hoc* test: Male-only – Female-only: $t_{56} = -9.41$, $P < 0.001$, Male-only – Both parents: $t_{56} = -8.86$, $P < 0.001$, Female-only – Both parents: $t_{56} = 0.55$, $P = 0.84$; **Figure 4** and **Table 4**). Time spent on brood attendance was significantly higher during the first 10 days of the offspring age compared to when the offspring are more than 20 days old ($\chi^2 = 10.48$, $P = 0.01$; *post hoc* test, age 0–9 – 20–29: $t_{56} = 2.94$, $P = 0.02$; **Figure 4** and **Table 4**). There was no significant difference in time spent on brood attendance according to the time of observation (morning or afternoon) (**Table 4**). Male and female did not differ in the time spent on brood attendance according to the time of the day nor the age of the offspring (i.e., there were no significant sex \times time of the day, and sex \times age of offspring interactions, respectively; **Table 4**).

Brooding behavior was done exclusively by males (**Supplementary Figure 5**). The behaviors performed during

brood attendance were unrelated to the age of chicks, the sex of the parent nor the time of the day (i.e., morning or afternoon) for vigilance, maintenance and foraging behaviors (**Table 4**), however, males performed significantly more agonistic behaviors during brood attendance than females (**Table 4**).

Breeding Success

Out of 23 clutches produced by these couples (1–6 clutches per female and 1–2 clutches per male), 11 clutches (47.8%) hatched successfully, the other clutches failed. Out of 11 broods, we know the fate of six broods: at least four of them successfully fledged at least one chick, so that a clutch has approximately 18% chance of producing a fledged chick (four successful brood out of 18 clutches with known fate). Reason of clutch and brood failure was difficult to determine as it was not directly observed. We suspect that predation by large fishes (which are abundant in the ponds), water snakes and black shouldered kites were the main reasons, and flooding after heavy rain may also has contributed to nest losses.

DISCUSSION

This study highlights several major characteristics of the breeding behavior of the sex-role reversed pheasant-tailed jacanas: (1) We did show as expected that the females participate more than the males in territory defense, but we found that males were also substantially involved in this behavior. (2) Contrary to what is expected males were performing courtship behaviors significantly more often than females. (3) Females were involved in some brood attendance however never performed any direct brood care, for example chick brooding. Finally our study based on observations of the largest number of identified individuals to date provides new data on the frequency and dynamics of polyandrous mating of the pheasant-tailed jacana. We show that this species has a simultaneous pair bonding system with a strict sequential copulation pattern. Although some aspects of breeding behavior of the pheasant-tailed jacana have been investigated by previous studies (e.g., Hoffmann, 1950; Thong-aree et al., 1995; Chen et al., 2008a) our study provides to date the most comprehensive assessment of reproductive roles of the sexes in the species, including sex differences in agonistic behavior, courtship, and parental care. Below we discuss each of these results in detail, and explain their importance within the broader frame of the evolution of sex-role reversal.

Competition for Access to Mates: Agonistic Behaviors

Our study shows that in this species not only females are involved in agonistic behavior toward conspecifics. Even though we indeed see that females were more often involved than males in this kind of interaction, males also showed significant number of agonistic interactions against conspecifics suggesting that both sexes are actively involved in territoriality. This is an interesting finding because in sex-role reversed species it is often thought that only females are territorial (Jenni, 1974; Andersson, 2005). Interestingly, we observed only one agonistic

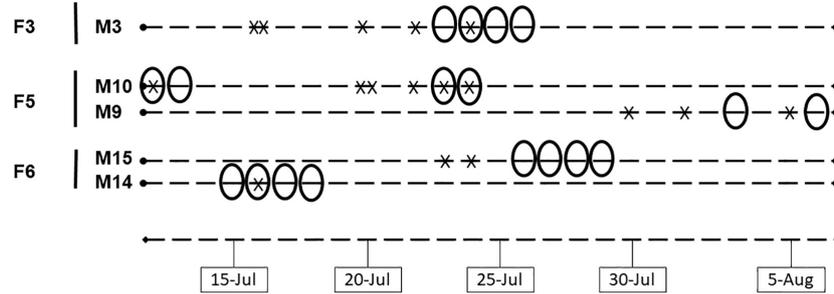


FIGURE 2 | Observed copulations (cross) in relation to egg laying (ovals) for five different couples (three females) during a 26 days period (each dash represent a day). Copulations were not monitored every day.

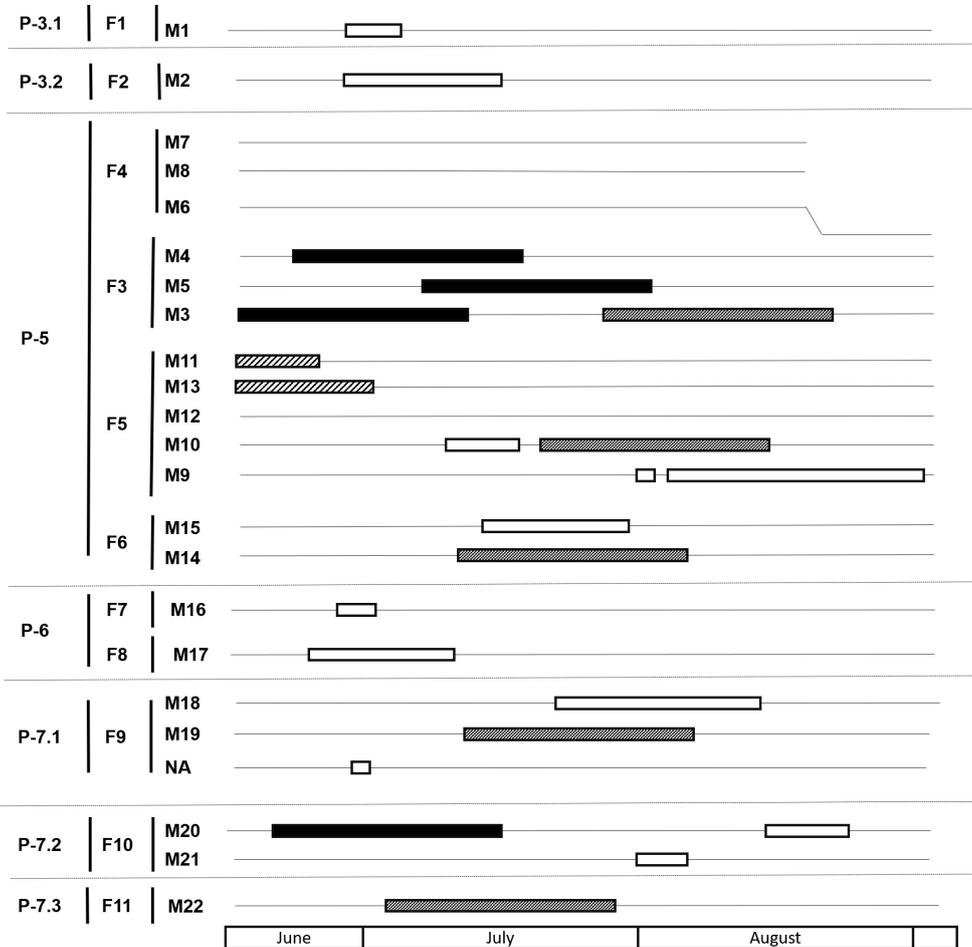
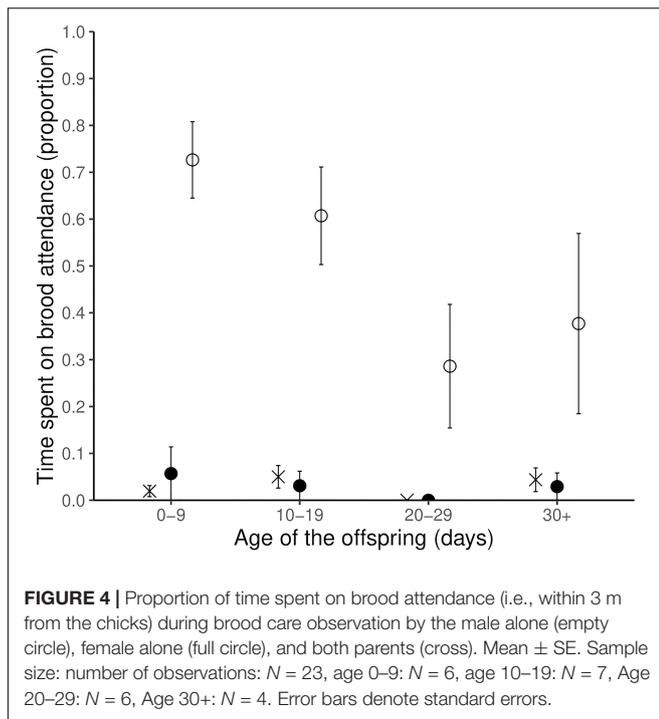


FIGURE 3 | Dynamics of pair bonding and breeding by females (F) and males (M) observed. Horizontal lines represent pair bonding. Each rectangle represents the incubation period for a clutch (performed by the male). White filled rectangles represent clutches that did not hatch. Bold striped filled rectangles represent clutches that hatched but the chicks did not survive until fledging, whereas black filled rectangles represent successful clutches (hatched and fledged at least one chick). Light striped rectangles represent clutches that hatched but chicks did not reach the age of 40 days before the end of the fieldwork, so the success of the brood is unknown. Female F4 formed pair-bonds with three different males but did not make any nest attempt during the studied period, and one of her males (M6) subsequently established a pair-bond with F3. NA denote unidentified male that left before being able to identify him. Details are also given in **Table 2**.

interaction between a female and one of its mates, otherwise all male-female agonistic interaction were between males and females involved in different pairs, which corroborates again

that males participate in territorial defense. In their paper Chen et al. (2008b) also reported that male pheasant-tailed jacanas performed some aggressive behaviors, but this study did not



differentiate between conspecific and heterospecific interactions, neither if the conspecific individual included in the interaction was female or male. Involvement of the males in the territorial and thus resources defense is thought to be yet another benefits that the female could gain by mating with multiple males (Fedorka and Mousseau, 2002; Slatyer et al., 2012), because the more mates the female would have the larger territory and more resource could be defended. In the facultative social polyandrous mammals siamang, polyandrous groups have access to larger territory with a higher food density (Lappan et al., 2017).

Furthermore, we found that male-male fights were usually between males not sharing the same female's territory. This latter observation could be explained by several mechanisms. First, once the pair bonding is made with a female, the males of the same female would compete for the female's reproductive investment through other means than fighting (see below). Furthermore, since the males pair bonded with the same female live close to each other, there might be a dominance hierarchy among them based on initial interactions. This might reduce the frequency of fights within the social group and reduce the costs of competition which could ultimately lead to a decline of reproductive success (McDonald et al., 2017). In addition, it has been shown that male cooperation in reproduction could lead to several direct and indirect benefits (Díaz-Muñoz et al., 2014). Finally, the presence of an external male on the territory could not only represent an intruder but also a new potential co-mate and thus competitor for access to the female and resources of the territory, as well as a higher number of nests on the territory attracting more predators. We could then imagine that according to the quality of the habitats of the female, male could tolerate up to only a certain amount of co-mates (Lappan et al., 2017).

More studies would be needed in order to measure the frequency and temporal dynamics of such social interactions within the polyandrous groups.

Both males and females increased their aggressiveness (toward other individuals) with the time spent together, the more time they spent together the more they were aggressive. This could be a result of an increase of synchronization in territoriality when they defend together against some intruders. Indeed, we observed several cases when more than two individuals were engaging in aggressive interaction at the same place, perhaps on territory boundaries (NF and AL, personal observations), which may the results of such joint defense by the couples.

Competition for Access to Mates: Courtship Behaviors

Interestingly, males were spending more time in courtship behaviors than females which goes against what we expected for a sex-role reversed species. In polyandry, we would expect the females to invest more into producing a new clutch than the male, since females could maximize their breeding success by obtaining multiple mates whereas the males' success is determined in a large part by the successful rising of the current offspring. One potential explanation for this result is that we did not observe courtship at the beginning of the breeding season when competition between females for mates should be much intensive. Contrary to this explanation, in a previous study Chen et al. (2008b) observed that the time spent by both males and females on breeding behavior increased through the breeding season, which included courtship behavior (although they did not separate it from other activities such as parental care). Alternatively, the courtship behavior we observed may not only serve to establish new or re-establish earlier pair bonds, but may also signal the readiness of males to start a new breeding. Since both nest loss and brood loss were frequent in the study population (see section "Results"), males may compete with each other for the egg laying potential of the female, especially when there are several resident males on the female's territory (as in the case of several females in our study). This high within-male competition for female's attention was observed in the bronze-winged jacana (Butchart et al., 1999b). In such situation the male may benefit from intensively signaling his capacity for a new clutch as well as its quality (Kotiaho, 2002; Pariser et al., 2010), because otherwise he may wait for long periods until female finishes laying for other males. Male-male competition, here shown through courtship can have a strong impact on sexual selection as it has been shown in mammals (e.g., Lührs and Kappeler, 2014), insects (e.g., Russell et al., 2018), and other birds (McDonald et al., 2017). To get a better idea of the relevance of the above explanations, further data on the occurrence of courtship are needed, especially from the earlier part of the breeding season and with precise information on their timing relative to the initiation of the new clutches.

During the courtship behavior observations we found that females spent more time in maintenance behavior than males, which could show that preening might also be used as part

TABLE 4 | Brood attendance duration and behaviors.

		Full model estimates ± SE		Selected model estimates ± SE	χ^2	<i>P</i>
Proximity						
Sex of the parents attending	(Female)	0.01 ± 0.12	(Female)	−0.03 ± 0.06	70.30	<0.001
	(Male)	0.78 ± 0.12	(Male)	0.55 ± 0.06		
Time of the day	(Afternoon)	0.09 ± 0.11	–	–	0.04	0.83
Age of the offspring	(10–19)	0.02 ± 0.13	(10–19)	−0.03 ± 0.07	10.48	0.01
	(20–29)	−0.12 ± 0.13	(20–29)	−0.21 ± 0.07		
	(30+)	0.07 ± 0.14	(30+)	−0.09 ± 0.08		
Sex × Age of the offspring	(Female × age 10–19)	−0.06 ± 0.18	–	–	8.44	0.21
	(Male × age 10–19)	−0.10 ± 0.18	–	–		
	(Female × age 20–29)	0.02 ± 0.18	–	–		
	(Male × age 20–29)	−0.28 ± 0.18	–	–		
	(Female × age 30+)	−0.08 ± 0.20	–	–		
	(Male × age 30+)	−0.40 ± 0.20	–	–		
Sex × Time of the day	(Afternoon × Female)	−0.06 ± 0.15	–	–	1.5	0.47
	(Afternoon × Male)	−0.16 ± 0.15	–	–		
Agonistic behavior						
Sex	(Male)	0.14 ± 0.07	(Male)	0.13 ± 0.05	6.11	0.01
Time of the day	(Afternoon)	−0.11 ± 0.11	–	–	2.27	0.13
Age of the offspring	(10–19)	0.11 ± 0.07	–	–	4.45	0.22
	(20–29)	0.02 ± 0.08	–	–		
	(30+)	<0.001 ± 0.06	–	–		
Sex × Time of the day		−0.03 ± 0.11	–	–	0.09	0.76
Vigilance behavior						
Sex	(Male)	−0.08 ± 0.12	–	–	0.34	0.57
Time of the day	(Afternoon)	−0.12 ± 0.22	–	–	0.37	0.54
Age of the offspring	(10–19)	−0.15 ± 0.15	–	–	3.5	0.32
	(20–29)	−0.19 ± 0.17	–	–		
	(30+)	−0.24 ± 0.13	–	–		
Sex × Time of the day		0.06 ± 0.20	–	–	0.10	0.75
Maintenance behavior						
Sex	(Male)	0.13 ± 0.17	–	–	0.48	0.49
Time of the day	(Afternoon)	0.27 ± 0.29	–	–	1.61	0.20
Age of the offspring	(10–19)	−0.02 ± 0.19	–	–	2.21	0.53
	(20–29)	−0.09 ± 0.21	–	–		
	(30+)	0.18 ± 0.17	–	–		
Sex × Time of the day		−0.04 ± 0.29	–	–	0.02	0.86
Foraging behavior						
Sex	(Male)	−0.20 ± 0.15	–	–	2.25	0.13
Time of the day	(Afternoon)	−0.19 ± 0.26	–	–	0.18	0.67
Age of the offspring	(10–19)	0.14 ± 0.17	–	–	1.00	0.80
	(20–29)	0.14 ± 0.19	–	–		
	(30+)	0.09 ± 0.15	–	–		
Sex × Time of the day		0.09 ± 0.26	–	–	0.20	0.65

Table shows the results of the full linear mixed model and for the selected models. The models test the difference in time spent on brood attendance or time spent on different behavioral categories (response variables). Table shows the results of the stepwise backward model selection: χ^2 and associated *P*-value for each variables. Table shows the estimates and standard error for the full model and for the selected model fitted with restricted maximum likelihood (REML). Factor variables' estimates contrasts term are indicated between parentheses. Stepwise backward model selection done with models fitted with maximum likelihood (ML) are given for each variable estimates (χ^2 and associated *P*-value). Significant *P*-values are shown in bold. Proportion of time spent on each behavioral category (used as response variable) was squared root transformed. Number of observations: *N* = 21; Male: *N* = 8, Female (Supplementary Table 1 and Supplementary Figure 4B).

of the courtship behaviors. In the same way, we observed the males doing more nest building behaviors than the female, especially in the afternoon, when copulation happens. Nest building by the males may also be used as part of the courtship behaviors, as it has been suggested in other jacana species (e.g., Bonkewitz, 1997).

Polyandrous Mating

Our study confirmed that most female pheasant-tailed jacanas are polyandrous, although with a great variance in the number of mates (ranging from 1 to 5). The degree of polyandry (mean number of mates per females) was 2.4 and at least 81.8% of the females bred polyandrously.

This put the characteristics of the mating system of the pheasant-tailed jacana (in term of degree and proportion of polyandry) close to the northern jacana. Which, interestingly is one of the closest jacana species to the pheasant-tailed jacana on the phylogenetic tree (Whittingham et al., 2006; D'Urban Jackson et al., 2019).

Pheasant-tailed jacanas were originally classified by Oring (1986) as a classical simultaneous polyandrous species. In more recent papers, the term sequential polyandrous is sometimes used for the species (Thong-aree et al., 1995; Chen et al., 2008b). In a sense, our study inferred the sequential nature of breeding with several males by the females: females produced clutches in a sequential order for different males, having a turnover of about 7 days between the end of laying a clutch for one male and the starting of a new clutch with another male. On the other hand, several females maintained pair bonds with multiple males simultaneously. For example, female F3 had three males simultaneously incubating separate clutches on her territory (**Figure 3**). Our observation suggest that the females regularly visit the territory and nest sites of their mates after laying the clutch, both during incubation and brood care, even during periods when the female is engaged in courtship with another male (NF and AL, personal observations). This suggests that the pair bond is maintained for a longer period between the female and the males resident on her territory, which is also indicated by the laying of new clutches for the same males after clutch or brood losses (see **Figure 3** for examples). It has been observed in northern China that males become receptive to female after hatching of a clutch much sooner than in other species, with some copulation observed with males having only 2 weeks old brood (Jenni and Kirwan, 2020). This is something that we also witnessed in this population. These observations highlights the particularity of the mating system of pheasant-tailed jacanas as it is different from a strictly sequential polyandry, since in this latter system females usually desert her mate and offspring before initiate a new pair bond with another male (as in the Kentish plover or in the dotterel, Owens et al., 1994; Székely and Williams, 1995). It is nevertheless also different from classical polyandry, which refers to simultaneous pair bonding associated with simultaneous mating. In this paper, we try to clearly differentiate the terms “sequential polyandry” and “sequential polyandrous copulation” which in our opinion describe different level of mating system. We propose that the mating system of this species is closer to the system of other jacanas classified as having classical or simultaneous polyandry, as previously stated by Oring (1986), with however a sequential polyandrous copulation pattern which is different from other jacanas such as bronze-winged jacana (Butchart et al., 1999b). Maintenance of such pair bonding with the different mates through the breeding season could lower the cost of female competition for access to males. Meanwhile, the sequential polyandrous copulation could lower the probability for the male to raise unrelated chick as it was found in the comb-crested jacana (Haig et al., 2003) where pairs were genetically monogamous with only 2.8% of the chicks were unrelated to the father compared to 17% in the wattled jacana (Emlen et al., 1998).

Female birds are able to store sperms for several days, thus sperm competition between the current mate and the previous one of female jacanas is expected to be strong (Dale et al., 1999). In a strong sperm competition context, we would expect a high rate of copulation in order to ensure male's paternity. Our result shows the opposite: few copulations and mainly during egg laying. This observation goes in line with what was observed in the bronze-winged jacana (Butchart, 1999). Potential other strategies might be used by the males to reduce the chance of raising unrelated young. One strategy might be egg removal: indeed a previous paper on the pheasant-tailed jacana shows that males might remove the first egg laid in their clutch in order to reduce the possibility of cuckoldry (Chen et al., 2008a).

Male-Only Care

This study corroborated that parental care in pheasant-tailed jacanas was, as expected, essentially performed by males. This has been indeed already shown in this species (Serrao and Shekar, 1962; Chen et al., 2008b) and other polyandrous Jacanidae species (Jenni and Collier, 1972; Emlen and Wrege, 2004a; Butchart, 2008). Incubation was solely carried out by males and, contrary to what has been observed in wattled jacana (Jenni and Collier, 1972), female pheasant-tailed jacanas do not seem to perform any chick brooding, even when the males are busy with the incubation of a new clutch. Since the pheasant-tailed jacana population presents a strong male biased sex-ratio in the population, females have a more re-mating opportunity than males and are thus expected to invest more in re-mating than in parental care (Liker et al., 2013; Székely et al., 2013). This strong difference of investment could lead to the rigid sex role that we observe. The lack of flexibility by the female in her investment in parental care was observed in a mate removal experiment with polyandrous black coucal, Goymann (2019) showed that the female would not compensate the male absence in brood care.

However, we did observe some participation by the female in brood attendance, with and without the male around. Both males and females lower their time attending the brood with the age of the offspring. In the wattled jacana (Emlen and Wrege, 2004a) the female was observed attending especially young chicks (under 4 weeks). In their paper, Emlen and Wrege (2004a) described the females wattled jacana as “backup providers of chick care.” In their study they found indeed that they observed females giving care in only 3% of the observation and each case were exceptional as they occurred in only two types of context: the male was predated, or the male was attending a clutch. This is not what was observed here as we still observed some females attending the brood outside these two contexts, for example when the male was foraging elsewhere. The variance of time spent by the female attending the brood in this study is not enough to see if this investment is related to male quality, pair bonding situation or female quality. Ultimately, the occasional proximity to the broods by the female could also be related to maintaining mating opportunity as it was suggested by several studies in other polyandrous birds (Goymann et al., 2015; Zheng et al., 2021).

We found that the behaviors performed by the females when attending the brood is almost the same as the males when

attending the chicks with the exception of brooding behavior and agonistic behaviors. The latter result can be explained by longer time the males spend with the brood thus they may be present more often when the brood needs defense, for example from conspecifics or from other species.

CONCLUSION

In conclusion, our study shows a clear sex-role reversal pattern in the pheasant-tailed jacana with females being highly polyandrous and males taking most of the care of the offspring. However, we highlight some patterns that are important to take in account: (1) males also participated in territorial defense especially toward males that were not paired with the same female and males invested more in courtship behaviors than females. This led us to conclude that male pheasant-tailed jacana might undergo strong male competition for access to female through courtship, but may also cooperate with or tolerate co-mates in order to increase mate and resource defense. (2) Females also participated in brood attendance yet to a low degree confirming that female pheasant-tailed will invest more into mating than providing care, (3) polyandry in this species involves the simultaneous maintenance of bonds with several males by a female which will sequentially copulate with them. These deviations from what is expected in a sex-role reversal species suggest that the mating system shows subtle variations even among closely related species that all exhibit classical polyandry. Our study was conducted on a relatively small number of individuals and only in the second half of the breeding season, that may limit the generality of some our conclusions (e.g., for sex differences in courtship, see above). Thus, a longer study through several years would be useful for further corroboration of our findings. Ultimately, such results on sexual difference in mating and parental investment in a sex-role reversal species can help us to understand better the evolutive mechanisms leading to this unconventional sex-roles.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by the Forestry Bureau of Taiwan.

AUTHOR CONTRIBUTIONS

AL, TS, AK, and NF conceived and developed the study. W-CL and Y-FL took care of the organization and administration regarding the project and the study site in Taiwan. NF

collected the data with the help of Y-FL and W-CL. NF analyzed the data. NF and AL wrote the manuscript with input from TS, AK, and Y-FL. All authors contributed to the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.742588/full#supplementary-material>

Supplementary Figure S1 | Map of the study site surveyed: The Pheasant-tailed Jacana educational park in Guantian, Tainan, Taiwan. Dark green indicates the ponds used for behavioral observation.

Supplementary Figure S2 | Pictures of different pheasant-tailed jacana individuals from the study population. Pictures (A,B) show the sexual size dimorphism between males and females (A: male M3 on the left/front and female F3 on the right/back; B: male M20 on the left and female F10 on the right). Pictures (C-F) illustrate the variation between individuals in their plumage: note the differences in the black patch on the top of the head, in the white wing patch pattern, and in tail length (C: male M3 and one of his chicks; D: female F10 from another angle; E: male M16 and his eggs; F: male M17 and his egg).

Supplementary Figure S3 | Examples of individual variability in pheasant-tailed jacana drawn from field sketches made in the study area. (A) Male M12. (B) Male M1. (C) Female F4. (D) Female F3.

Supplementary Figure S4 | Proportion of time spent on different focused categories of behaviors by the males (in black) and females (in gray) during (A) courtship observation and (B) brood attendance (i.e., in proximity of the chicks).

Mean \pm SE. Sample size: **(A)** Number of observations: $N = 44$; Male: $N = 15$, Female: $N = 10$ and **(B)** Number of observations: $N = 21$; Male: $N = 8$, Female: $N = 5$. * $P < 0.05$; *** $P < 0.001$. Error bars denote standard errors. Details of the results are shown in **Tables 2, 3**, respectively.

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