The ecological basis of unusual sex roles in reverse-dichromatic eclectus parrots

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In theory, sex roles are determined by the potential reproductive rates of males and females, which are constrained by parental investment. Thus the sex that invests least in offspring typically competes most for matings and is most subject to sexual selection, whereas the caring sex is most choosy when selecting mates. Here I show that ecological variables, rather than patterns of parental investment, can be influential in determining sex roles and the direction of sexual selection. In the polyandrous eclectus parrot, Eclectus roratus, both sexes care for offspring, yet despite traditional parental care patterns, both sexes are competitive and both are subject to sexual selection. The bright red and blue females compete for scarce nest hollows and the iridescent green males for mates. Using data from an 8-year field study, I show that the major ecological variable driving this system is nest hollow quality. Females with drier hollows had higher reproductive success and more males feeding and competing to mate with them. Females with nest hollows that were prone to flooding had fewer fledglings in years with higher dry season rainfall, confirming that hollow quality was a primary determinant of reproductive success. Comparisons of females before and after they changed hollows during the study provided further evidence that these trends were due to hollow quality rather than individual female quality. Thus competition for a scarce resource can lead to high variance in female reproductive success, and promote competition for high-quality mates among males.

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selection (Andersson 1994, 2005). Classical polyandry entails sex role reversal with all or most parental care given by males, aggressive competition between females for territories and mates, and stronger sexual selection on females leading to either reversed sexual dichromatism or reversed sexual dimorphism (Eens & Pintken 2000; Andersson 2005). However, sex roles and the direction of sexual selection are not normally reversed in species with an alternative form of polyandry, referred to as ‘cooperative polyandry’. Paternity in these species may be shared within the same clutch and parental care is usually shared by the female and attending males (Davies et al. 1995; Hartley et al. 1995; Goldizen et al. 2000).

Eclectus parrots, Eclectus roratus, are a polyandrous species in which both sexes provide substantial parental care and compete aggressively for breeding resources or mates. They have puzzled evolutionary biologists because the bright red females, which have diverged remarkably from the green males, appear to be major targets of sexual selection in the absence of reversed sex roles (Amundsen & Parn 2006). Females mate polyandrously (Heinsohn et al. 2007) but have retained the role of incubating eggs and protecting young. The OSR throughout the breeding season appears to be strongly male biased owing to a male-biased adult sex ratio and the unavailability of females for further mating until their young have fledged. Females guard nest hollows in emergent rainforest trees for as long as 11 months each year. Throughout this period all of their food is provided by the males who do not defend territories or mates but congregate at the nest hollows where they are more likely to find food. A flooded hollow can delay breeding or cause the death of eggs or chicks by either drowning or hypothermia (Heinsohn & Legge 2003). Whether the hollow was flooded with free-standing water or dry enough to be used as a nest was recorded on each climb; for consistency I used one value for each month between July and February for each breeding season to calculate the proportion of months the hollow was dry enough to be used for chick rearing. One measure per month is sufficient to determine a hollow’s availability for nesting as free-standing water in a hollow usually takes weeks to dry. A ‘damp’ hollow without free-standing water was considered potentially usable for nesting. Other physical dimensions of each hollow potentially relating to its quality for nesting (height, depth, opening size, trunk diameter at breast height or DBH) were recorded at the beginning of each season.

To estimate the number of males feeding each female, nests were observed from canopy hides for 3 h on between three and seven occasions each season (Heinsohn et al. 2007), including the period when the female occupied the hollow but had not yet laid eggs (from 2 to 8 weeks), incubation (28 days), and the period of nestling care (up to 13 weeks). Individual recognition of males was possible in many cases as 22 of approximately 80 males in the study area were colour banded with one coloured (with industrial strength powder coating) stainless steel band on each leg. Males also often return to the nest simultaneously to feed the female. The mean of these group sizes provides a conservative estimate of the number of male attendants in each group (Heinsohn & Legge 2003).

Long-term data were used to determine the factors affecting both the reproductive success of nesting females and the number of males they attracted. To analyse Reproductive success and number of males feeding females I used generalized linear mixed models (GLMM). Data were Poisson distributed and logarithmic link functions were used in the models. To avoid pseudoreplication from repeated sampling at the same nests, ‘hollow’ was incorporated as the random term in all such models. Terms included in both models included the year of study, the proportion of the breeding season in which the hollow remained dry, the depth of the hollow, nest height (m), tree DBH (m), and the horizontal and vertical dimensions of the hollow’s opening (m). The number of males feeding the female was also included as a term in the analysis of reproductive success. All interactions between these variables were initially included, and terms that did not contribute significantly to the models were dropped sequentially. Terms were also added and dropped in varying order to confirm consistency of effects.

Trends detected in the long-term data set were further explored by using tightly controlled comparisons of the reproductive success and number of male attendants of 10 females that changed nest hollows during the study. These comparisons allowed the isolation of effects of hollow quality as the main factor of interest, while holding ground-based surveys have shown that nest trees occur at a density of approximately one per square kilometre (Legge et al. 2004). The study comprised 33 nest trees with 45 nest hollows over approximately 65 km². Most nest trees had one hollow (N = 28) but some had two (N = 4) or three hollows (N = 3). The nearest nest trees were 50 m apart, and the furthest were 10.1 km apart.

Nest trees were climbed using single-rope techniques between five and 11 times each breeding season to establish the breeding status of the female and the success of the brood. Potential disturbance to the birds was kept minimal by limiting nest visits to less than 15 min. Nests were always monitored from a distance to ensure the return of the breeding female (Heinsohn et al. 2007). The study was conducted under licence from the Australian National University Animal Ethics Committee.

A potential determinant of reproductive success is how quickly nest hollows dry out after flooding during the wet season, and how likely they are to flood if heavy rain occurs during the dry season. A flooded hollow can delay breeding or cause the death of eggs or chicks by either drowning or hypothermia (Heinsohn & Legge 2003). Whether the hollow was flooded with free-standing water or dry enough to be used as a nest was recorded on each climb; for consistency I used one value for each month between July and February for each breeding season to calculate the proportion of months the hollow was dry enough to be used for chick rearing. One measure per month is sufficient to determine a hollow’s availability for nesting as free-standing water in a hollow usually takes weeks to dry. A ‘damp’ hollow without free-standing water was considered potentially usable for nesting. Other physical dimensions of each hollow potentially relating to its quality for nesting (height, depth, opening size, trunk diameter at breast height or DBH) were recorded at the beginning of each season.

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individual quality constant. For all analyses 1 used the Genstat statistical software (Genstat Committee 2005).

RESULTS

Female Reproductive Success

Analysis of 213 female breeding years showed that the number of fledglings produced by individual females in a season was significantly related to year of study (GLMM: $\chi^2 = 33.5, P < 0.001$), the proportion of the breeding season in which the hollow remained dry ($\chi^2 = 26.6, P < 0.001$), the depth of the hollow ($\chi^2 = 5.1, P = 0.024$) and the mean number of males observed feeding the female ($\chi^2 = 5.1, P = 0.024$). However, nest height ($\chi^2 = 0.34$), tree DBH ($\chi^2 = 2.3$) and the dimensions of the hollow’s opening (horizontal dimension: $\chi^2 = 1.20$; vertical dimension: $\chi^2 = 0.72$) did not significantly affect female reproductive success. There were no significant interactions between any of the above ($\chi^2 = 0.3 – 0.72$). The within-term correlation of the random term ‘hollow’ was moderately high ($r = 0.32$) confirming the importance of its inclusion in the model. Figure 1 shows the residual number of fledglings (when other model terms have been removed) plotted against the proportion of time the hollow remained dry (Fig. 1a) and the number of males feeding the female (Fig. 1b).

The long-term data provided additional evidence that hollow dryness was an important determinant of female reproductive success independently of the females’ quality. Although it proved impossible to move females or manipulate their hollows experimentally, I was able to examine whether 10 known females that changed hollows in the course of the study fared as well reproductively. These females changed nest sites when their hollows collapsed from wood rot or the nest tree fell over, or because they were taken over by other species (European bees, Apis mellifera, sulphur-crested cockatoos, Cacatua galerita, rufus owls, Ninox rufa). Four females took 1 year to renest; four took 2 years, one 3 years, and one 5 years. These delays probably reflected the low availability of new hollows. Four of the 10 females moved to new hollows that flooded less frequently (females 3, 4, 6, 7, Table 1), and six changed to hollows that flooded more frequently, which effectively controlled for changes in their age or experience. Paired comparisons revealed a significant effect of hollow dryness: nine females had higher reproductive success, whereas one did worse, when their hollows were less prone to flooding (Wilcoxon signed-ranks test, two-tailed: $T = 3.50, P = 0.014$; Table 1).

The effects of year of study and hollow dryness on reproductive success appeared to be caused by variable rainfall in the dry season (June–December), which overlaps with the breeding season. The sample of 8 years showed that mean annual reproductive success of females was significantly dependent on the extent of the natural log of rainfall during the dry season (linear regression: $F_{1,6} = 11.80, P = 0.014$; Fig. 2a), but not on the natural log of ‘wet’ season rainfall ($F_{1,6} = 0.74$) or annual rainfall ($F_{1,6} = 1.32$). The role of flooding in this trend was confirmed by dividing nest hollows into those that always remained dry (18 of 45 hollows) versus those that sometimes or always flooded in wet season rain (27 hollows). The interaction between dryness and in rainfall was significant (ANCOVA: $F_{1,63} = 8.31, P = 0.014$) with nest hollows that were prone to flooding yielding fewer fledglings in years with higher dry season rainfall (Fig. 2b).

Male Attendance

There were no significant differences in the number of males feeding females prior to egg laying and during incubation and nestling feeding (GLMM: $\chi^2 = 1.95$). However, the number of males was significantly affected by hollow dryness ($\chi^2 = 22.35, P < 0.001$) and tree DBH ($\chi^2 = 7.37, P = 0.007$; Fig. 3). There were no significant effects of the depth of the hollow ($\chi^2 = 1.1$), nest height ($\chi^2 = 0.43$), or dimensions of the hollow’s opening (horizontal dimension: $\chi^2 = 0.22$; vertical dimension: $\chi^2 = 0.56$). Male numbers at nest hollows varied between years as indicated by a strong year effect ($\chi^2 = 28.40, P < 0.001$) and significant interactions between year and hollow dryness ($\chi^2 = 17.43, P = 0.015$), and year and tree DBH ($\chi^2 = 21.63, P = 0.003$). Figure 3 shows the effects of both hollow dryness ($F_{1,63} = 8.48, P = 0.004$) and tree DBH ($F_{1,63} = 4.44, P = 0.036$) on residual male number, when other significant factors were removed. The random term ‘hollow’ had a low within-term correlation ($r = 0.06$).

Paired comparisons of the females that changed hollows again confirmed that hollow quality, independently of female quality, was an important determinant of the number of male attendants feeding females. Eight of the 10 females had more male attendants when they had drier hollows, whereas two females retained the same number of attendants (Wilcoxon signed-ranks test, two-tailed: $T = 0, P = 0.008$; Table 1).

![Figure 1](https://example.com/fig1.png)

Figure 1. Mean ± SE residual fledglings produced by females in a breeding season according to (a) the dryness of their nest hollows (% time dry during breeding season) and (b) number of males feeding them. Sample sizes for group years in each category are: ≤50% (12), 51–60% (6), 61–70% (52), 71–80% (31), 81–90% (33), 91–100% (79); number of males: 1 (38), 2 (60), 3 (52), 4 (31), 5 (8), 6 (12).

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Table 1: Effect of hollow dryness on reproductive success (number of fledglings) and number of male attendants for 10 females that changed hollows.

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unilaterally controls resources essential for breeding. My analysis of the long-term data, including controlled comparisons when females changed breeding sites, shows that each female’s reproductive success depended on the quality of her nest hollow. These results support two emerging principles concerning the evolution of sex roles. First, the extreme competitiveness of female eclectus parrots over resources, together with their bright coloration (Heinsohn et al. 2005), appears to have evolved independently of the OSR to secure direct fecundity benefits. Second, the variability in female fecundity caused by those resources leads to further break-down of traditional sex roles by making the competitive males choosy over whom they attempt to mate with.

Defence of the nesting site is typical of hollow-nesting birds, and many bird species are known to be limited by this resource (Newton 1994). However, the extreme guarding behaviour of female eclectus parrots, in which they remain at their hollows for most of each year, is atypical for parrots (Juniper & Parr 1998), and rivalled only by the hornbills (Bucerosfrancus, Kemp 1995). My analysis suggests that such protectiveness of nest hollows may be the result of considerable variation in their utility for reproduction.

The reproductive success of females was strongly affected by the dryness of their nest hollows, and more weakly (albeit significantly) by the number of males observed feeding them during nesting. Hollow dryness also seemed to determine the number of males feeding the females. Although cause and effect can be difficult to disentangle with correlational data, there are two reasons to favour hollow quality as a primary determinant of reproductive success. First, reproductive success was lower in nests that were prone to flooding in the years that had unusually high rainfall during the breeding season. The cause of failure of these nests was apparent throughout the study with many recorded cases of both eggs and nestlings drowning when hollows flooded after heavy rain (Heinsohn & Legge 2003). Second, comparisons of the same female at different nest hollows showed that hollow dryness affected both reproductive success and the number of males independently of the quality of each female. The constancy of group sizes over each breeding season (Heinsohn et al. 2007; this study) also suggests that there is no confounding effect of fluctuating numbers within the season (e.g. males arriving when there are more chicks to feed) and that male number had a consistent additional effect on female reproductive success.

The effects of hollow ownership on fecundity highlight important differences between sexual selection in males and females. LeBas (2006) has recently stressed that females are less likely than males to evolve costly signals of quality. Fecundity variation in females is often directly assessable by males (e.g. through body size) making further signals of quality redundant. Even when fecundity is not directly assessable, any costly signal by females is likely to come at the direct expense of reproduction. Unlike males, females usually have certainty of parentage of their offspring, leading to a direct trade-off between the signal and further reproduction. LeBas (2006) argued that female signalling is more likely to evolve in the context of resource competition, as access to resources is more likely to lead to the necessary fitness benefits. Eclectus parrots indicate the importance of this process. Whereas a previous analysis showed that female eclectus parrots use their red coloration to advertise ownership of scarce nest hollows (Heinsohn et al. 2005), this study shows that fitness may vary markedly according to the quality of each hollow as a nest site. Other examples in which competition for breeding resources has led to independent sexually selected traits in females, despite traditional sex roles, include nuptial gifts in empidid flies (LeBas 2003), competition for breeding sites in clown fish (Amphiprion sp.: Fricke & Fricke 1977), song in female song sparrows, Melospiza melodia (Arcese 1989) and competition for breeding status in cooperative mammals.
signals that have evolved in the context of resource competition may then also be used in mate choice.

Most parrots are socially monogamous and share territorial defence and parental care, although females tend to carry out all incubation of eggs and brooding of small young while the males feed them at the nest (Juniper & Parr 1998). Female eclectus parrots appear to have responded to the scarcity and the large differential in the quality of nest hollows by making a behavioural shift from short-term to long-term defence of their hollows and care of young.

Selection may have favoured this behaviour in the females rather than the males because they were already the sex that spent most time at the hollow. In addition, nests are too widely dispersed for the males to defend multiple sites. Heino et al. (2007) have instead shown that many males use the alternative reproductive tactic of competing for the females’ attention at multiple nest trees. The females’ ability to monopolize rare and highly variable resources results in intense competition among males for access to the most fecund females, and may constitute ‘indirect mate choice’, an important component of sexual selection in which female behaviour (2008), doi:10.1016/j.anbehav.2008.01.013

References


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