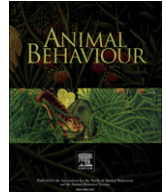




Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/yanbe

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

Robert Heinsohn*

Fenner School of Environment and Society, Australian National University

ARTICLE INFO

Article history:

Received 14 September 2007
 Initial acceptance 17 November 2007
 Final acceptance 23 January 2008
 Available online xxx
 MS. number: 9515

Keywords:

eclectus parrot
Eclectus roratus
 intrasexual competition
 mate choice
 reverse sexual dichromatism
 sex roles

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.

© 2008 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

The sexes often differ in how much they invest in searching and competing for mates, gamete production and parental care. Such 'sex roles' during reproduction are believed to be pivotal in determining the direction of sexual selection (Emlen & Oring 1977; Andersson 1994; Cunningham & Birkhead 1998; Kokko et al. 2006). Darwin (1871) was the first to note that one sex in each species is likely to invest more in competing for mates, while the other invests more in gametes and parental care. Trivers (1972) argued that this trend occurs because any investment in parental care can be made only at the expense of further reproduction, and that the sex with the highest investment thus becomes limiting for the opposite sex. The difficulty of measuring parental care led to further suggestions that the actual availability of mating partners may be a better empirical determinant of sex roles. Emlen & Oring (1977) suggested that sex roles were determined by the relative abundance of each sex, or the operational sex ratio (OSR) defined as the ratio of fertilizable females to sexually active males at any one time. Others have emphasized that the OSR, and consequent sexual selection, will be biased towards the sex with the higher rate (Sutherland 1985) or potential rate (Clutton-Brock & Vincent 1991; Clutton-Brock & Parker 1992; Parker & Simmons 1996; Ahnesjo

et al. 2001) of reproduction. However, a recent life history-based model showed that the OSR and the potential rate of reproduction do not necessarily capture the essence of Trivers's original definition of parental investment. Instead, the cost of a single breeding attempt (e.g. probability of death) was shown to be a better predictor of the direction of sexual selection, although this variable is often related to the OSR and the potential rate of reproduction (Kokko & Monaghan 2001).

Classical treatments of sex roles also predict that the sex with the highest parental investment will be the most choosy over mates, because individuals of this sex benefit the most by increasing the quality of their young (Trivers 1972; Clutton-Brock & Parker 1992). However, choosiness of mates may also relate to the extent of variation in quality in each sex (Owens & Thompson 1994; Johnstone et al. 1996). For example, males may be most choosy when females vary markedly in fecundity or quality. Owens & Thompson (1994) showed that individuals should optimize between reproductive rate and mate quality. Importantly their model showed that if mate quality varied enough, then the sex with the higher potential reproductive rate could none the less be the most choosy. Thus the classic notion that competition and mate choice are opposite roles need not necessarily hold, and rare but important departures from this norm can be explained (e.g. competitive and choosy females in Eurasian dotterels, *Charadrius morinellus*: Owens et al. 1994).

Polyandrous mating systems have been described as the 'exceptions that prove the rule' in the study of sex roles and sexual

* Correspondence: R. Heinsohn, Fenner School of Environment and Society, Australian National University, Canberra, A.C.T. 0200, Australia.
 E-mail address: robert.heinsohn@anu.edu.au

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 & Pinxten 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 compete vigorously for access to the females (Heinsohn & Legge 2003, unpublished data). Females appear to be choosy, and mate with only a subset of their suitors (Heinsohn et al. 2007). A recent analysis has shown that the bright red of females functions in intrasexual competition for scarce nesting hollows, and that the males' green, which can be similarly bright when viewed through parrot rather than human eyes, is important during competition for females at the nest hollows (Heinsohn et al. 2005).

Eclectus parrots present many logistical challenges in the quest to understand their unusual mating system and reversed sexual dichromatism. These include the difficulties of catching and observing the adults, and getting access to their nest hollows in emergent rainforest trees. None the less the unusual combination of behavioural traits in males and females provides a rare opportunity to tease apart the ecological basis of sex roles. The bright colour and sole defence of breeding resources by females, and the sharing of paternity between successive clutches (Heinsohn et al. 2007), are all typical of classical polyandry and reversed sex roles. However, the females' large share of parental care, especially incubation, and simultaneous contributions to parental care from males are more typical of cooperative polyandry and conventional sex roles. I examined the role of nest hollow quality in shaping reproductive success and competitive behaviour in both sexes. My aim was to use this unusual system in which both sexes are competitive and choosy, yet divergent in their sexually selected traits, to highlight additional processes of sexual selection that may not be apparent in species with conventional sex roles.

METHODS

I studied a population of the subspecies *E. r. macgillivrayi* at Iron Range National Park on Cape York Peninsula in far north Queensland, Australia (12°45'S, 143°17'E) over eight breeding seasons (approximately July–February) from August 1997 to March 2005. The national park is located in a lowland rainforest of approximately 500 km². Most (80%) nesting hollows are found in just four tree genera (*Alstonia*, *Castenospermum*, *Ficus*, *Melaleuca*), the mean height above the ground \pm SD is 22.4 \pm 4.3 m, and the mean depth \pm SD is 84.4 \pm 27.2 cm (Heinsohn & Legge 2003). Aerial and

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 each breeding season to calculate the proportion of time 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 hollow quality as the main factor of interest, while holding

individual quality constant. For all analyses I 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: $\chi_1^2 = 33.5$, $P < 0.001$), the proportion of the breeding season in which the hollow remained dry ($\chi_1^2 = 26.6$, $P < 0.001$), the depth of the hollow ($\chi_1^2 = 5.1$, $P = 0.024$) and the mean number of males observed feeding the female ($\chi_1^2 = 5.1$, $P = 0.024$). However, nest height ($\chi_1^2 = 0.34$), tree DBH ($\chi_1^2 = 2.3$) and the dimensions of the hollow's opening (horizontal dimension: $\chi_1^2 = 1.20$; vertical dimension: $\chi_1^2 = 0.72$) did not significantly affect female reproductive success. There were no significant interactions between any of the above ($\chi_1^2 = 0.3 - 0.72$). 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 unfeasible 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,

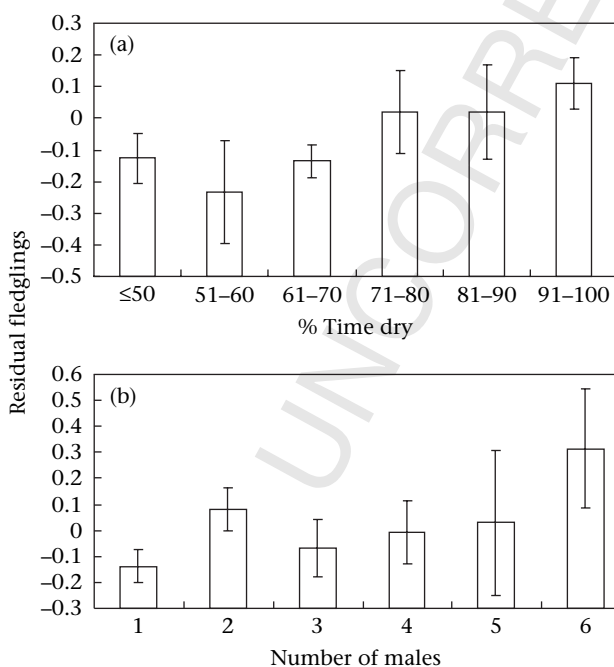


Figure 1. Mean \pm SE residual fledglings produced by females in a breeding season according to (a) the dryness of their nest hollows (% time dry during breeding season) and (b) number of males feeding them. Sample sizes for group years in each category are dryness: $\leq 50\%$ (12), 51–60% (6), 61–70% (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).

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 ($F_{1,6} = 0.74$) 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 ln rainfall was significant (ANCOVA: $F_{1,13} = 8.31$, $P = 0.014$) 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: $\chi_1^2 = 1.95$). However, the number of males was significantly affected by hollow dryness ($\chi_1^2 = 22.35$, $P < 0.001$) and tree DBH ($\chi_1^2 = 7.37$, $P = 0.007$; Fig. 3). There were no significant effects of the depth of the hollow ($\chi_1^2 = 1.1$), nest height ($\chi_1^2 = 0.43$), or dimensions of the hollow's opening (horizontal dimension: $\chi_1^2 = 0.22$; vertical dimension: $\chi_1^2 = 0.56$). Male numbers at nest hollows varied between years as indicated by a strong year effect ($\chi_7^2 = 28.40$, $P < 0.001$) and significant interactions between year and hollow dryness ($\chi_7^2 = 17.43$, $P = 0.015$), and year and tree DBH ($\chi_1^2 = 21.63$, $P = 0.003$). Figure 3 shows the effects of both hollow dryness ($F_{1,211} = 8.48$, $P = 0.004$) and tree DBH ($F_{1,211} = 4.44$, $P = 0.036$) 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).

Table 1

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

Female	Drier hollow (% time dry)	Fledglings	Male attendants	Wetter hollow (% time dry)	Fledglings	Male attendants
1	100	2	4	75	0	4
2	100	2	6	63	0	2
3	88	1	3	75	0	2
4	100	2	3	63	0	2
5	88	0	3	75	1	2
6	100	2	4	50	0	2
7	88	2	3	75	1	2
8	88	1	6	75	0	4
9	100	1	3	88	0	2
10	100	1	4	75	0	4

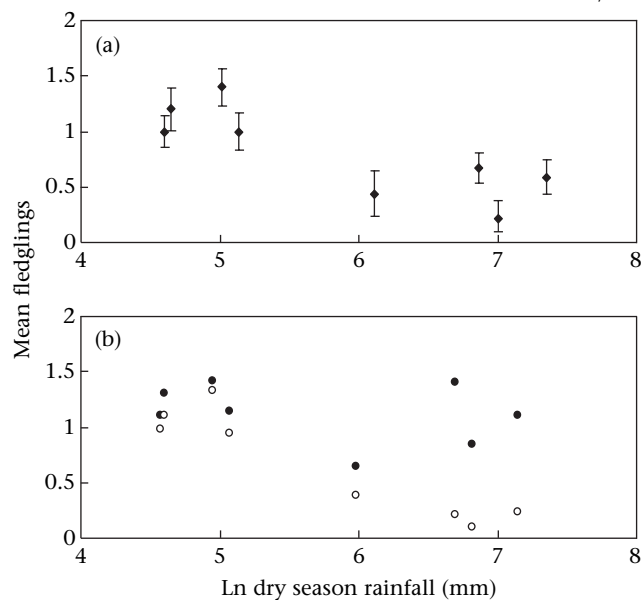


Figure 2. (a) Mean \pm SE number of fledglings produced across the population versus natural log of dry season rainfall over 8 years of study. (b) Mean number of fledglings produced over 8 years divided into hollows that never flooded (\bullet) and hollows that were prone to flooding (\circ). Sample sizes of nests for each year are 1997 (17), 1998 (33), 1999 (29), 2000 (33), 2001 (35), 2002 (24), 2003 (22), 2004 (20).

DISCUSSION

The classical view of mating system evolution emphasizes clear roles for the sexes depending on the OSR, with the precise form of the mating system determined by which sex is limiting and the degree to which the limited sex controls resources essential for breeding or monopolizing mates (Trivers 1972; Emlen & Oring 1977). However, in eclectus parrots the limiting sex (females)

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 (Bucerotiformes, Kemp 1995). My analysis suggests that such protectiveness of nest hollows may be the result of considerable variability 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

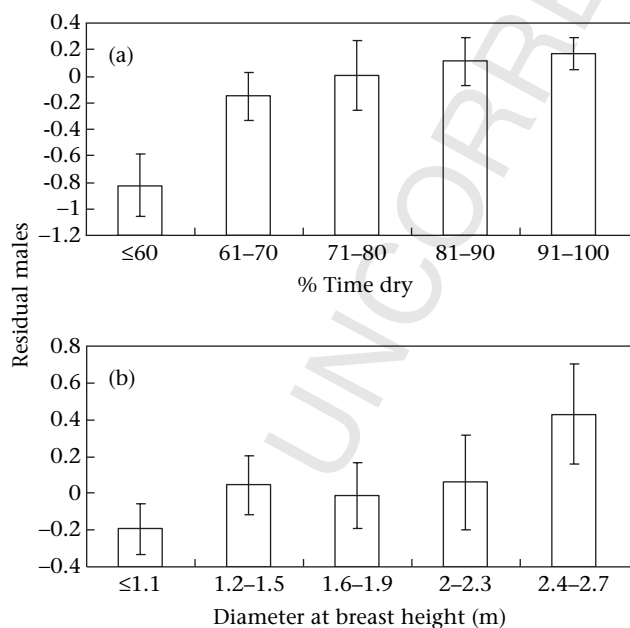


Figure 3. Mean \pm SE residual males feeding females in a breeding season according to (a) the dryness of nest hollows (% time dry during breeding season) and (b) the diameter at breast height of nest trees (DBH). Sample sizes of group years in each category are: dryness \leq 60% (15), 61–70% (48), 71–80% (16), 81–90% (51), 91–100% (83); tree DBH: \leq 1.1 m (67), 1.2–1.5 m (45), 1.6–1.9 m (57), 2.0–2.3 m (19), 2.4–2.7 m (25).

(Clutton-Brock et al. 2006). However, as noted by LeBas (2006), 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. Heinsohn 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 behaviours not associated with their direct choice of mate none the less set the conditions for male competition (Wiley & Poston 1996).

Owens & Thompson (1994) have shown that competition for mates and mate choice are not simply opposite sex roles, and that sex differences in variation in mate quality can influence mate choice by impacting on the OSR. This is because large variation in mate quality in one sex effectively reduces the number of individuals of that sex that are acceptable as mates. They suggested that when sex differences in mating rate and variation in quality are small, both sexes should show active choice. Monogamous species where both parents contribute large amounts of parental care fit this prediction. Alternatively, it is theoretically possible for one sex to be both more competitive and more choosy than the other sex. A rare example is provided by Eurasian dotterels where females compete for males because the OSR is female biased but are also very choosy because male quality varies greatly (Owens et al. 1994).

Male eclectus parrots provide an important example of combined competitiveness and choosiness in one sex. Males in this species gain reproductive success at multiple widely dispersed nest trees (Heinsohn et al. 2007). They are also more likely to congregate and compete for mating access with females that possess dry hollows in large nest trees (Fig. 3). Nests in larger trees may be safer from ground predators such as amethystine pythons, *Morelia amethystina*, and varanid lizards (*Varanus* sp.); however, in this study I did not detect a positive effect of nest tree size (tree height or DBH) on reproductive success. Males often try to look inside the nest hollows, possibly to assess their dryness and availability. Although competition between males appears to be driven by a shortage of females, males none the less choose whom they compete for based on the quality of the nest hollow. They appear to be most averse to very wet hollows (Fig. 3a) and the paired comparisons confirm that hollow quality is an important component of their choice, regardless of individual female quality (Table 1). Whereas male competitiveness and female choosiness are both predicted from classical notions of sex roles, the male choosiness and female competitiveness shown in this study provide important illustrations of recent extensions to sexual selection theory.

Acknowledgments

I thank Michelle Hall, Stephen Murphy, Anjeli Nathan, David Wilson and especially Clare Blackman and Sarah Legge for their essential help in the field, Peter and Emma Huybers for generous logistical support, and Michael Jennions, Naomi Langmore, Rob Magrath and three anonymous referees for helpful comments on the manuscript. This research was supported by grants from the

Australian Research Council, National Geographic Society and the Winifred Violet Scott Foundation.

References

- Ahnesjö, I., Kvarnemo, C. & Merilaita, S. 2001. Using potential rates to predict mating competition among individuals qualified to mate. *Behavioral Ecology*, **12**, 397–401.
- Amundsen, T. & Parn, H. 2006. Female coloration: a review of functional and non-functional hypotheses. In: *Avian Coloration* (Ed. by G. E. Hill & K. J. McGraw), pp. 280–348. Boston: Harvard University Press.
- Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Andersson, M. 2005. Evolution of classical polyandry: three steps to female emancipation. *Ethology*, **111**, 1–23.
- Arcece, P. 1989. Intrasexual competition and the mating system in primarily monogamous birds: the case of the song sparrow. *Animal Behaviour*, **38**, 96–111.
- Clutton-Brock, T. H. & Parker, G. A. 1992. Potential reproductive rates and the operation of sexual selection. *Quarterly Review of Biology*, **67**, 437–456.
- Clutton-Brock, T. H. & Vincent, A. C. J. 1991. Sexual selection and the potential reproductive rates of males and females. *Nature*, **351**, 58–60.
- Clutton-Brock, T. H., Hodge, S. J., Spong, G., Russell, A. F., Jordan, N. R., Bennett, N. C., Sharpe, L. L. & Manser, M. B. 2006. Intrasexual competition and sexual selection in cooperative mammals. *Nature*, **444**, 1065–1068.
- Cunningham, E. J. A. & Birkhead, T. R. 1998. Sex roles and sexual selection. *Animal Behaviour*, **56**, 1311–1321.
- Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. London: Murray.
- Davies, N. B., Hartley, I. R., Hatchwell, B. J., Desrochers, A., Skeer, J. & Nebel, D. 1995. The polygynandrous mating system of the alpine accentor, *Prunella collaris*. 1. Ecological causes and reproductive conflicts. *Animal Behaviour*, **49**, 769–788.
- Eens, M. & Pinxten, R. 2000. Sex-role reversal in vertebrates: behavioral and endocrinological accounts. *Behavioural Processes*, **51**, 135–147.
- Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**, 215–223.
- Fricke, H. & Fricke, S. 1977. Monogamy and sex change by aggressive dominance in coral fish. *Nature*, **266**, 830–832.
- Genstat Committee. 2005. *Genstat Release 8.1*. Hemel Hempstead: VSN International.
- Goldizen, A. W., Buchan, J. C., Putland, D. A., Goldizen, A. R. & Krebs, E. A. 2000. Patterns of mate-sharing in a population of Tasmanian native hens *Gallinula mortierii*. *Ibis*, **142**, 40–47.
- Hartley, I. R., Davies, N. B., Hatchwell, B. J., Desrochers, A., Nebel, D. & Burke, T. 1995. The polygynandrous mating system of the alpine accentor, *Prunella collaris*. 2. Multiple paternity and multiple effort. *Animal Behaviour*, **49**, 789–803.
- Heinsohn, R. & Legge, S. 2003. Breeding biology of the reverse-dichromatic, cooperative parrot *Eclectus roratus*. *Journal of Zoology*, **259**, 197–208.
- Heinsohn, R., Legge, S. & Endler, J. A. 2005. Extreme reversed sexual dichromatism in a bird without sex role reversal. *Science*, **309**, 617–619.
- Heinsohn, R., Ebert, D., Legge, S. & Peakall, R. 2007. Genetic evidence for cooperative polyandry in reverse dichromatic *Eclectus* parrots. *Animal Behaviour*, **74**, 1047–1054.
- Johnstone, R. A., Reynolds, J. D. & Deutsch, J. C. 1996. Mutual mate choice and sex differences in choosiness. *Evolution*, **50**, 1382–1391.
- Juniper, T. & Parr, M. 1998. *Parrots: a Guide to Parrots of the World*. Sussex: Pica Press.
- Kemp, A. 1995. *The Hornbills*. Oxford: Oxford University Press.
- Kokko, H. & Monaghan, P. 2001. Predicting the direction of sexual selection. *Ecology Letters*, **4**, 159–165.
- Kokko, H., Jennions, M. D. & Brooks, R. 2006. Unifying and testing models of sexual selection. *Annual Review of Ecology and Systematics*, **37**, 43–66.
- LeBas, N. R. 2003. Non linear and correlational sexual selection on 'honest' female ornamentation. *Proceedings of the Royal Society of London, Series B*, **270**, 2159–2165.
- LeBas, N. R. 2006. Female finery is not for males. *Trends in Ecology & Evolution*, **21**, 170–172.
- Legge, S., Heinsohn, R. G. & Garnett, S. 2004. Availability of nest hollows and breeding population size of eclectus parrots, *Eclectus roratus*, on Cape York Peninsula, Australia. *Wildlife Research*, **31**, 149–161.
- Newton, I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. *Biological Conservation*, **70**, 265–276.
- Owens, I. P. F. & Thompson, D. B. A. 1994. Sex differences, sex ratios, and sex roles. *Proceedings of the Royal Society of London, Series B*, **258**, 93–99.
- Owens, I. P. F., Burke, T. & Thompson, D. B. A. 1994. Extraordinary sex roles in the Eurasian dotterel: female mating arenas, female–female competition and female mate choice. *American Naturalist*, **144**, 76–100.
- Parker, G. A. & Simmons, L. W. 1996. Parental investment and the control of sexual selection: predicting the direction of sexual competition. *Proceedings of the Royal Society of London, Series B*, **263**, 315–321.
- Sutherland, W. J. 1985. Measures of sexual selection. *Oxford Surveys in Evolutionary Biology*, **2**, 90–101.
- Trivers, R. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 132–179. Chicago: Aldine Press.
- Wiley, R. H. & Poston, J. 1996. Indirect mate choice, competition for mates, and coevolution of the sexes. *Evolution*, **50**, 1371–1381.