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Special Report

Ecology and Evolution of the Enigmatic Eclectus Parrot (*Eclectus roratus*)

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Abstract: Eclectus parrots (*Eclectus roratus*) exhibit a form of reversed sexual dichromatism (plumage coloration) not found in other birds. The females are a striking vermilion and blue, whereas the males are shiny green. Here, I summarize the major findings of a 10-year research program conducted on a wild population of eclectus parrots on Cape York Peninsula, Australia, aimed primarily at understanding the ecologic and evolutionary forces behind their unique coloration. Unlike most other parrots, eclectus parrots breed polyandrously (where multiple males mate with 1 female) and polygynandrously (where both sexes have multiple sexual partners). Their mating system appears to be driven by a shortage of nest hollows. Females with good nest sites are rare, and this forces males to share females. The red plumage of females acts as a signal of nest hollow ownership, whereas the green of males allows them to be camouflaged while foraging to feed the females and chicks. Eclectus parrots can also control the sex of their offspring, although the reasons for this are not yet clear.

Key words: dichromatism, mating system, nest hollow, plumage color, sex allocation, avian, eclectus parrot, *Eclectus roratus*

Introduction

Few birds have puzzled scientists more than the eclectus parrot (*Eclectus roratus*). One of the 20th century's great evolutionary biologists, the late Professor Bill Hamilton of Oxford University, used to show a slide in his lecture series of a male and female parrot sitting side by side. The male was a vibrant green and the female a stunning vermilion. Whereas evolutionary theory had plenty to say about sexual selection producing greater size or gorgeous coloration in one sex, it stumbled somewhat in establishing what had happened in this species. No other bird has sexes so "beautified," but in such different ways. Hamilton ended his talk by declaring that when he understood why one sex is red and the other green, he would be "ready to die."

Male and female eclectus parrots are so different they were long thought to be different species.[1] Males from the Moluccan Islands of western Indonesia were first described in 1776 by P. L. S. Muller. Females were not described until 1837, and even the best naturalists of the 19th century such as John Gould were fooled for a long time. It was not until 1874 that cocks and hens of this species were finally united under the same name.[2] Despite the long-standing popularity of eclectus parrots among aviculturalists, no field studies of this species had been done until my research at Iron Range National Park (Cape York Peninsula, Australia) commenced in 1997.[3] This was understandable, as few birds present the field worker with such logistical difficulties. Eclectus parrots live in the canopy of forests in New Guinea, west to the Moluccas, east to the Bismarck Archipelago and Solomon Islands, and south to the tip of Cape York Peninsula in northern Australia. Apart from living in such remote locations, their nest hollows can be 20–30 m (65–100 feet) above the ground, and they are notoriously shy birds that fly away over the treetops when disturbed.[1]

The eclectus parrot study began by investigating 3 unusual but interrelated aspects of their biology that, if understood, promised unique insights into the evolutionary processes shaping this species in nature. These were their reversed

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plumage coloration (also called reversed sexual dichromatism), a system of shared, cooperative breeding not normally seen in parrots, and their apparent ability to manipulate the sex of their young. All of these traits appear to relate to the scarcity of nest hollows in the rainforest landscape, which leads to high competition among both sexes for both nesting sites and mates.

Reversed Sexual Dichromatism

Brilliant plumage is typical of male birds and reflects the differential enhancement of male sexual traits used in competition for females.[3,4] Traits that help individuals of just one sex compete for mates are favored by the process of sexual selection and can be divided into 2 general categories. Bulkier size or weaponry can allow males to fight for access to females, whereas ornaments are used to attract female attention. Long tails and bright colors in birds normally fit the second category. Males are usually the most colorful sex because females are likely to be in short supply because of the extra work and dangers involved during chick rearing. Males thus compete for the chance to mate with females.[3] In an interesting twist, a handful of species are known to have reversed sex roles in which males incubate eggs, and females defend territories and fight among themselves for access to males.[5] These species provide the exceptions that prove the rule because they demonstrate that the competitive sex is the one most likely to have bright colors. Phalaropes (*Phalaropus* species), sandpipers (family Scolopacidae), and buttonquail (*Turnix* species) are good examples of species with more colorful females.[6]

Eclectus parrots break this apparent rule because their extreme reversed coloration is not associated with reversed sex roles but instead with stiff competition for rare nest hollows. Behavioral research and analysis using spectroradiometry of plumage colors showed that the males and females look dissimilar because they have very different selective pressures acting on them.[7] The males face higher predation pressure because they are the ones that travel widely to find food, whereas the females must compete especially hard for nesting space. Good nest hollows in large rainforest trees are in short supply and only occur at about 1 site/km^2.[8] Unlike most parrots, the females do not join the males in foraging for themselves and their chicks; instead, they remain at the nest hollow and defend it for up to 11 months each year. They literally do not leave the nest tree during this period and have been observed to fight to the death in protracted battles over this scarce resource.[7,9] In contrast to most parrots, which are monogamous, each female eclectus parrot mates with up to 5 males and relies on them to bring all the food required by her and her chicks.[10] Females with more males feeding them generally have higher reproductive success.

Understanding the functions of the different colors of males and females requires an ability to ''look through'' their eyes rather than our own. This is important because birds have a broader range of color vision than humans and, in particular, can see ultraviolet (UV) coloration, which is beyond our capabilities. The colors of eclectus parrots were measured objectively with a spectroradiometer and then the data were processed through a computer model that captured the color-sensing abilities of the parrots.

Hollow-owning females sit out among the leafy branches before commencing breeding and are viewed by competing females against a background of green leaves. This provides the highest possible contrast to her red and blue coloration and acts as a powerful visual signal that the hollow in that tree is occupied.[7] For a male, the green color usually has the opposite effect, although with an interesting twist. The green provides important camouflage against predators such as peregrine falcons (*Falco peregrinus*) and rufus owls (*Ninox rufa*) when the male is out foraging among fruiting trees. However, it also has a second purpose by making them very conspicuous against the wood of the tree trunks near the nest hollows where they compete with other males for access to the females. The males' green is also laced with UV coloration, which the parrots' eyes can detect much better than their predators such as hawks. Thus, the males' colors are a clever compromise between camouflage from their enemies when they need it and showiness to their own kind at the nest trees.[7] A fundamental difference between the plumage types of male and female eclectus parrots is that males can ''switch'' their signal on and off depending on the background they choose. In contrast, females are always bright no matter which background they are against, but they can escape unwanted attention from predators by retreating inside their hollows, if they are fortunate enough to own one.

Social and Mating System

The second key aspect of the study was to use molecular techniques to unravel the unusual

breeding biology of eclectus parrots—in particular, their polyandrous mating system. Polyandry is the rarest of avian mating systems and occurs when a single female pairs with 2 or more males during a breeding season.[11] Polyandry falls into 2 distinct categories, depending on whether the females mate sequentially with single males who then care for the clutch alone (classic polyandry[12]) or with multiple males who care for the clutch cooperatively.[13] Classic polyandry entails sex role reversal with all or most parental care given by males and aggressive competition between females for territories and mates. Typically, as soon as 1 clutch is laid, the male assumes incubation duties and the female seeks to lay further clutches with additional males.[6]

In contrast, cooperative polyandry occurs when 2 or more males form stable social units with single females and share paternity in a single brood or season. In some species it appears that groups of males can defend territories better than a lone male, and that the benefits from sharing paternity can outweigh the costs.[14–16] In others, space use can differ between the sexes, with variable mating systems arising depending on the extent of overlap of male and female territories.[17–19] In both circumstances, the mating system can become polygynandrous if the males mate with additional females.

The numbers of males observed feeding female eclectus parrots was much larger (up to 7 males per female) than any other polyandrous mating system,[9] and it has also been established that their sex roles are not reversed, as is generally the case for reverse dichromatic birds (see above). Throughout the long period in which females guard their hollows, all of their food is provided by the males, who forage for fruit over large home ranges of approximately 30 km^2. Multiple matings have been observed in quick succession, with little apparent aggression between rival males, but in other cases, males fight vigorously for access to the females.[9]

Molecular markers known as DNA microsatellites were used to establish the extent of kinship between the attending males. Microsatellites map out variable loci present in nuclear DNA from blood samples and are especially useful for identifying close family members, such as siblings and parents and offspring. Importantly, the data showed that the social groups are not composed of family members, which rules out any possibility that the extra males are grown offspring that have failed to disperse. Instead, it appears that all group males are seeking direct reproduction. Although most broods of 2 nestlings had just 1 father, further group males became fathers in later nesting attempts, and some males only gained paternity at irregular intervals with the same female over multiple years. For example, 1 male sired 2 different young with the same female, but these were 7 years apart.[10]

Radio-tracking from light aircraft also showed that males had very large home ranges that encompassed many nest trees. Known individual males were observed to spend time with several different females, and the molecular data indeed confirmed that some became fathers at very widely dispersed nest trees (the maximum distance recorded was 7.2 km).[10] The authors thus concluded that the eclectus mating system regularly includes both polyandry (females mate with more than 1 male) and polygynandry (males mate with more than 1 female and females mate with more than 1 male). Both types of mating system are very rare among parrots, and the polygynandrous component described for eclectus parrots is played out over the largest distances recorded for any bird. DNA collected from feathers left in the nest also confirmed that females monopolize their breeding hollows over multiple years; 2 females retained their nest hollows exclusively for the entire 8-year study period.[10]

Biased Sex Allocation

The final key aspect of this study has been to investigate the apparent ability of eclectus parrots to manipulate the sex of their offspring. The females typically lay 2 eggs but often only manage to fledge 1 of their chicks. Although the overall sex ratio of fledglings is close to 50:50, some captive females that were brought to my attention produced long unbroken runs of 1 sex over many clutches before switching to producing the other sex. The maximum from 1 female was 20 sons in a row before she switched to producing daughters. A statistical analysis showed that these long runs of 1 sex of offspring were highly improbable under the assumption that males and females are produced in equal numbers, as happens for most birds and mammals.[20]

Evolutionary theory predicts various benefits to parents of producing 1 sex of offspring over the other, but clear examples in birds have been rare. The few reported instances suggest that parents might produce 1 sex earlier in the season if it helps that sex begin breeding earlier in its life (ie, kestrels, *Falco* species),[21] or they might vary the order of the sexes within a clutch if that helps 1

sex to survive better (ie, kookaburras, *Dacelo* species).[22] In perhaps the most celebrated example of the ability to bias offspring sex, Seychelles warblers (*Acrocephalus sechellensis*) in small family groups have been shown to produce the sex (females) that stays and helps raise further broods but to produce the dispersing sex (males) when conditions are too crowded.[23]

Before analyzing the mating system, it was believed that the social groups observed around each nest tree comprised parents with their grown offspring, and it was hypothesized that the parents used their ability to manipulate the sex of offspring to skew output toward males because they help at the nest. However, the finding that the additional males are all unrelated to the breeders and likely to father chicks suggests different reasons for biased sex allocation.[10] This component of the long-term study has not yet been analyzed, but the current working hypothesis is that breeding females only produce male offspring, which are larger and hence more energetically expensive, when they have good hollows and many mates feeding them.

Conclusion

Each of the unusual traits of the eclectus parrot discussed here is ultimately linked to the scarcity of their nesting hollows. Field observations have also shown that the hollows they use vary markedly in quality. Some are low in smaller trees and therefore prone to ground-based predators such as monitor lizards (family Varanidae) or scrub pythons (*Morelia amethistina*), and many are also prone to flooding in heavy rain. If a hollow floods easily, then the period when it is useable could be very short. I have observed even large chicks drown in the torrential downpours that occur mid-breeding season.[9] In eclectus parrots, a rare combination of intense competition between females for breeding resources, the separation of parental duties and therefore selective pressures on the sexes, and the effects of trying to hide from predators appear to have pushed these birds away from a monogamous mating system and the monomorphic colors found in most parrots. Instead, they have evolved a ''free-for-all'' polygynandrous mating system and totally divergent plumage colors in the males and females. Although theory successfully predicts the direction of sexually selected colors in most species, eclectus parrots show that bright coloration can evolve independently and simultaneously in both sexes.

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