Among the 85 centromere positions that could be classified, 38 were unambiguously assigned to HSBs, of which 28 (74%) occurred at the boundaries of evolutionary breakpoints. Furthermore, all 216 nonhuman telomeres appeared at the boundaries of evolutionary breakpoints or at the ends of computed ancestral chromosomes. These observations are logical given the requirement that the viability of a gamete containing the breakage is dependent on proper chromosome segregation in daughter cells as well as in subsequent meioses in an offspring. Another apparently related phenomenon is the joint clustering of centromeres and telomeres around evolutionary breakpoints. For example, there are 20 positions of clustering of telomere/centromere positions across the entire multispecies comparative landscape (fig. S1). Of these, 11 are clusters found in multiple species. Most of the centromeres that appear at evolutionary breakpoints as defined on the human genome are associated with the formation of acrocentric centromeres in other species.

The association between reuse breakpoints and the positions of centromeres or telomeres was significant ($\chi^2 = 14.5$, $P < 0.001$, 1 df). When telomeres and centromeres were analyzed separately, only centromeres were found to be significantly associated with reuse breakpoints ($P < 0.01$; table S8). This observation suggests a possible mechanism for chromosome evolution and the appearance of reuse breakpoints, whereby these evolutionary breakages preferentially occur at sites of ancestral centromeres or neocentromeres in independent lineages. Alternatively, reuse breakpoints may represent unstable chromosomal sites that, after breakage, will tend to form a new centromere or telomere.

We have shown that tremendous evolutionary activity exists at breakpoint regions, including reuse, increased gene density, segmental duplication accumulation, and the emergence of centromeres and telomeres. Taken together with our identification of reuse breakage occurring at the highest frequency between species with the most accelerated rates of chromosome evolution, our data suggest that there exist a limited and nonrandom number of regions in mammalian genomes that can be disrupted by these various dynamic processes. Given sufficient evolutionary time, these sites become "recycled" in different species. Future challenges lie in more fully interpreting the structure and function of breakpoint regions across a broader range of mammalian taxa, with the use of whole-genome sequence-based maps from phylogenetically divergent species.

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Extreme Reversed Sexual Dichromatism in a Bird Without Sex Role Reversal

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Brilliant plumage is typical of male birds, reflecting differential enhancement of male traits when females are the limiting sex. Brighter females are thought to evolve exclusively in response to sex role reversal. The striking reversed plumage dichromatism of *Eclectus roratus* parrots does not fit this pattern. We quantify plumage color in this species and show that very different selection pressures are acting on males and females. Male plumage reflects a compromise between the conflicting requirements for camouflage from predators while foraging and conspicuousness during display. Females are liberated from the need for camouflage but compete for rare nest hollows.

The operational sex ratio and sexual differences in potential reproductive rate lead to gender-biased mate competition, gender-biased sexual selection, and sexual dimorphism (*1*, *2*). These, along with ecological factors such as limited nesting sites (*3*), can result in sex role reversal (SRR), in which males care for offspring and females compete for mates (*2*, *4*). Reversed sexual dichromatism (females brighter than males) is usually associated with SRR and often with reversed size dimorphism (females larger than males (*5*), because sexual selection is stronger on females in SRR species (*1*, *4*). Phalaropes, sandpipers, and button quail are examples (*4*). Here we describe a case of extreme reversed sexual dichromatism in *Eclectus* parrots (*Eclectus roratus*), which is not associated with classic SRR but results from sex-based differences in visual predation and female competition for nest hollows.

The green male and bright red and blue female *E. roratus* are so different that they were originally regarded as separate species

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(6), and their unusual dichromatism has puzzled biologists for decades (7, 8). SRR does not explain the brilliant plumage of the females. Unlike most classic SRR birds (1, 9), the reproductive rate of female *E. roratus* is limited because they have retained the role of incubating eggs and protecting young, and do not lay again until their chicks have fledged. The operational sex ratio may also be male-biased as a result of a strongly biased adult sex ratio (approximately 67% males) caused by higher mortality of juvenile females (10). Thus, *E. roratus* challenges the existing view of the evolution of reversed sexual dichromatism (8).

Our 8-year study in northern Australia has revealed a rare polygynandrous mating system in which males and females have diverged from the social monogamy and shared parental duties seen in most parrots (6, 11) into entirely separate roles during breeding. *E. roratus* compete vigorously with both their own and other species for scarce nest hollows (approximately one hollow per square kilometer) (12, 13). Intrasexual competition is intense in both sexes; females compete for nest hollows and males for access to breeding females. Females remain in their nest tree for up to 11 months each season (mean = 9.30 ± 0.11 SE, *n* = 212 female years), and apart from periods of display in the canopy, spend most of this time guarding their hollows from conspecifics that attempt to crush eggs or kill large chicks (14). Females may kill each other in disputes over hollows (14). Up to five males (mean = 1.97 ± 0.18 SE, *n* = 208 nest years) attend each nest, and they travel many kilometers to fruiting trees to provide all food for the females and their young over the breeding period (10).

The divergence in life-style between the sexes suggests that male *E. roratus* are more likely to be targeted by visually mediated predators than are females. Whereas males forage in the canopy for several hours every day throughout the year, breeding females only face this risk while they display before nesting and when they forage for themselves during the short nonbreeding period. Thus, one possible explanation for the divergence in color between the sexes is that it reflects the male's need for crypsis when foraging and the female's need to be conspicuous during displays of hollow ownership. Human vision is entirely different from that of birds, so it is important to score color objectively and from the observers' (conspecifics' and predators') perspective (15, 16). To assess visibility to conspecifics and predators, we collected optical data on birds and their backgrounds. We applied established models of avian vision and calculated a disparity index that estimates the difference or visual contrast between two color patterns (17, 18).

The analysis confirmed that males and females differ very strongly in their color patterns as sensed by birds. It unexpectedly revealed that females are more conspicuous than males against a visual background of leaves but not against trunks. Females occupied their nest trees up to 45 days before egg-laying (mean = 22.2 ± 1.92 SE, *n* = 174 female years). Before their confinement to the hollow during breeding, they preferred to display in branches high in the canopy, where other birds viewed them against a leafy rather than woody background (mean proportion of displays against leaves = 0.84 ± 0.032 SE, *n* = 10 females, 9 to 17 observations per individual). Birds flying toward the nest tree generally get their first view of the hollow owner from above. Females were more conspicuous from this angle against both visual backgrounds (Fig. 1, A and B). They were also significantly more conspicuous in open/cloudy light conditions (19) than in the woodland shade lower in the tree (Fig. 1, C and D). This choice of light and background colors by females to maximize conspicuousness during display is similar to that shown by males of some neotropical lekking species (20). However, females continued to call and show themselves from the entrance of the nest hollow throughout incubation. Although females are also conspicuous against tree trunks, our data suggest that their red and blue colors have been selected because these spectra are complementary to leaf green and therefore provide the greatest contrast against the background preferred for displays.

In contrast, males are more conspicuous against tree trunks than against leaves and are more conspicuous than females against tree trunks. Their color appears to serve the dual function of being conspicuous in intrasexual conflict near trunks but relatively inconspicuous when foraging. Most male competition for females occurred at the entrance to the nest hollow, where they displayed, fought, and physically dislodged each other (mean proportion of displays against tree trunk = 0.85 ± 0.033 SE, *n* = 11 males, 7 to 15 observations per individual). At most other times, especially while foraging, they either fly above or sit among foliage. Like females, they are more conspicuous from the angle at which arriving competitors first see them (from above, against tree trunks). Unlike females, they are less conspicuous from the angle at which aerial predators might observe them (from above, against leaves) (Fig. 1, A and B). The plumage of males against leaves is also less conspicuous to raptors than to other parrots (Fig. 1, E and F), suggesting that their colors are selected to exploit the difference between their color vision and that of their aerial predators (21). This appears to be adaptive because more of their lifetime is spent potentially being seen by predators than is spent by females, and more of this time will be against leaves than against trunks. Juvenile males and females both display adult colors, probably in readiness for breeding as early as their second year (10). The male-biased sex ratio among adults may reflect high mortality of juvenile females, who do not have the protection of their own nest hollows.

Fig. 1. (**A** and **B**) Effect of the observer's view (17) against leaves and trunks for females and males [linear mixed model, 3-way interaction, X^2_1 = 269.5, $P <$ 0.001, standard error of difference (SED) = 0.004]. Disparity is a measure of the overall visual contrast between the two color patterns (17). (**C** and **D**) Effect of light environment (linear mixed model, 3-way interaction, X^2_1 = 27.8, $P <$ 0.001, SED = 0.006). (**E** and **F**) Effect of parrot versus raptor eye model (linear mixed model, 3-way interaction, X^2_1 = 6.8, P = 0.009, SED = 0.006). An asterisk above adjacent bars indicates that they are significantly different. Males and females differ significantly in all cases.
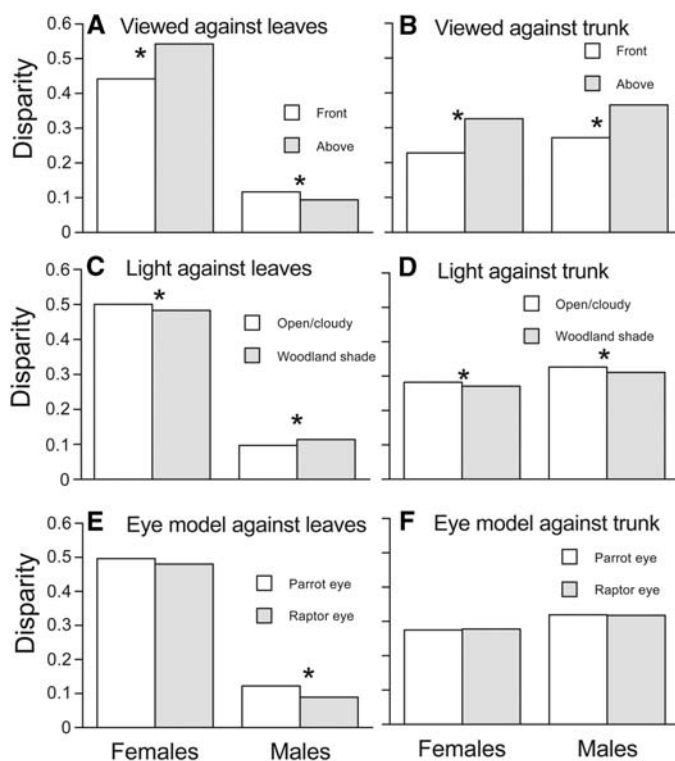
Our analysis offers insights into the selective forces that shape coloration. Unlike open-nesting birds, in which the incubating females need to be inconspicuous to avoid predation, females of hollow-nesting species usually have similar colors to males. The sharing of parental duties and similar exposure to predation (during incubation and foraging) suggest that natural selection affects color similarly in both sexes in most species (*22, 23*). In contrast, the colors of male and female *E. roratus* appear to be under independent selection. Whereas females are more conspicuous than males against leaves, they also have the nest hollow nearby as a refuge against predators. However, foraging males cannot retreat to a nest hollow whenever a predator approaches, and consequently their colors need to be less conspicuous against the leafy background. Ready access to a refuge from predators may also explain why females are not less conspicuous from above (Fig. 1A) or why they do not have colors that are significantly less conspicuous to their aerial predators (Fig. 1E).

The continuous occupation of the nest hollow by female *E. roratus* is atypical for parrots (*11*) but strikingly similar to that seen in hornbills (Bucerotiformes) (*24*). Females in most hornbill species are sealed into the nest hollow during the incubation and nestling phases and are fed by their mates and other group members. However, strong sexual dichromatism is rare in this group (*24*). Unlike *E. roratus*, most hornbill species (25 out of 33 known) are territorial, and the males and females of all 41 species on which sufficient data have been gathered have been observed to locate, prepare, and defend the nest site together. Further, female hornbills often leave the nest and help provision young before the young have fledged (*24*) and overall do not remain at the hollow for as long (66 to 142 days as compared with 279 days in *E. roratus*) (*24*). Similar sex roles both before and during breeding, and less total time spent at the nest by females, may reduce any independent selection on each sex in hornbills.

In *E. roratus*, a rare combination of intrasexual competition for a scarce resource in females, the separation of parental duties, and visually mediated predation appears to have shifted the balance of natural and sexual selection from the expected monomorphism in hollow nesters toward reversed dichromatism. These parrots provide an example of how conspicuous colors, like complex song (*25*), can result from strong intrasexual competition. The dichromatism of these parrots is also highly unusual among birds (*8*) because the sexes have acquired different color patterns for different purposes, and each is more conspicuous under specific conditions. Females compete for nest hollows and males compete for females at nest hollows, and thus both sexes are conspicuous against the tree trunks. However, males differ from females by spending a much larger proportion of their time foraging among the rainforest canopy. This favors reduced visibility to predators against leaves and, as a result, the balance between sexual selection and predation (*26, 27*) differs in the two sexes and represents a reversal of the usual pattern. Although theory successfully predicts the direction of sexual selection (*9, 26–29*), and mutual mate choice can account for similarly adorned sexes (*30*), *E. roratus* shows that bright coloration can evolve independently and simultaneously in both sexes. *Erectus* parrots emphasize the crucial interaction between natural selection and the lifestyle of males and females in modifying colors, even if they primarily result from sexual selection.

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14. We found eggs crushed but not eaten in 33 out of 421 clutches. In seven cases, the crushed eggs were found immediately after we saw an intruding female leave the nest hole. Ovicide was inferred in the remaining 26 cases. A 21-day-old nestling was found dead with wounds apparently inflicted by a parrot beak after an intruding male left the nest. We inferred infanticide in 15 further nests where nestlings aged from 1 to 15 days were found dead with similar wounds. One adult female was found dead in her hollow with extensive wounds on her head after an extended fight with an intruding female. Thirteen other uneaten corpses of adult females were found in the vicinity of nest trees in 210 female-years. Ten of these had wounds consistent with fighting.
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Independent Codes for Spatial and Episodic Memory in Hippocampal Neuronal Ensembles

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Hippocampal neurons were recorded under conditions in which the recording chamber was varied but its location remained unchanged versus conditions in which an identical chamber was encountered in different places. Two forms of neuronal pattern separation occurred. In the variable cue-constant place condition, the firing rates of active cells varied, often over more than an order of magnitude, whereas the location of firing remained constant. In the variable place-constant cue condition, both location and rates changed, so that population vectors for a given location in the chamber were statistically independent. These independent encoding schemes may enable simultaneous representation of spatial and episodic memory information.

Hippocampal neuronal ensemble activity appears to play an important role in the establishment of both spatial and nonspatial episodic memories, but there has long been controversy as to which of these parameters best characterizes the role of the hippocampal formation in mnemonic processes (*1, 2*). Although hippocampal neurons fire in a sparse