

Disruptive sexual selection for plumage coloration in a passerine bird

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The theory of sexual selection was developed to explain the evolution of highly exaggerated sexual ornaments¹. Now supported by vast empirical evidence², sexual selection is generally considered to favour individuals with the most extreme trait expression^{2–4}. Here we describe disruptive selection on a sexual ornament, plumage coloration, in yearling male lazuli buntings (*Passerina amoena*). In habitats with limited good-quality nesting cover, the duller and the brightest yearlings were more successful in obtaining high-quality territories, pairing with females and siring offspring, than yearlings with intermediate plumage. This pattern reflects the way that territorial adult males vary levels of aggression to influence the structure of their social neighbourhood. Adult males showed less aggression towards dull yearlings than intermediate and bright ones, permitting the dull yearlings to settle on good territories nearby. Fitness comparisons based on paternity analyses showed that both the adults and dull yearlings benefited genetically from this arrangement, revealing a rare example of sexually selected male–male cooperation^{5,6}.

Lazuli buntings are socially monogamous songbirds that breed in early successional habitats throughout western North America⁷. At our study sites near Missoula, Montana (46° 48' N 114° 57' W), male buntings show dramatic variation in plumage coloration and territory quality, two characteristics that females may seek in their prospective mates^{2,8}. We studied the ecological and social consequences of this variation from 1992–1997. Males defend territories that include patches of shrubs in which the nests are built. Nesting cover is extremely patchy, ranging from single isolated shrubs to extensive areas of dense bushes. As a result, territory characteristics varied greatly among males: percentage shrub cover on territories ranged from 3 to 92%. Older males tend to return to the breeding grounds in the spring before yearling males, and competition among males for the limited areas with dense nesting cover can be intense^{7,9}.

Plumage coloration of males also varied dramatically, ranging from mainly dull brown, female-like plumage, to very bright blue, reddish, and white plumage (Fig. 1). We quantified this variation with a scoring system that yielded an overall index of each male's plumage brightness that is a composite of several measures (see Methods). Plumage scores ranged from 14 for extremely dull males to 36 for extremely bright males (see Fig. 1 for examples). Lazuli buntings exhibit "delayed plumage maturation" in which more than one year is generally required to attain full adult coloration^{10,11}. Thus, on average, yearling males were significantly duller than males of two or more years (hereafter called adults) (Fig. 1e). However, yearlings were also more variable than adults, so that some yearlings were extremely dull (Fig. 1a), whereas others (Fig. 1c) were almost as bright as adult males (Fig. 1d).

Plumage coloration had important reproductive consequences for yearling males (Fig. 2b, d, f), but not for adults (Fig. 2a, c, e). The

pairing success of yearlings showed a clear bimodal relation with plumage brightness: the duller and brightest males obtained social partners while intermediate males had extremely low pairing success (Fig. 2b). Fitness analysis with univariate cubic splines¹² revealed significant disruptive sexual selection for yearling plumage coloration ($P < 0.01$). Disruptive selection is a rare and poorly understood mode of selection^{4,13} and has only been shown to occur twice for a sexually selected trait (body size¹⁴, pheromones¹⁵). Thus, identifying its causes is of broad interest.

Two factors combined to produce the disruptive selection for yearling plumage coloration: (1) the effect of plumage coloration on territory acquisition; and (2) strong female preference for high-quality territories, irrespective of a territorial male's plumage coloration. In yearling males, territory quality (estimated by per-

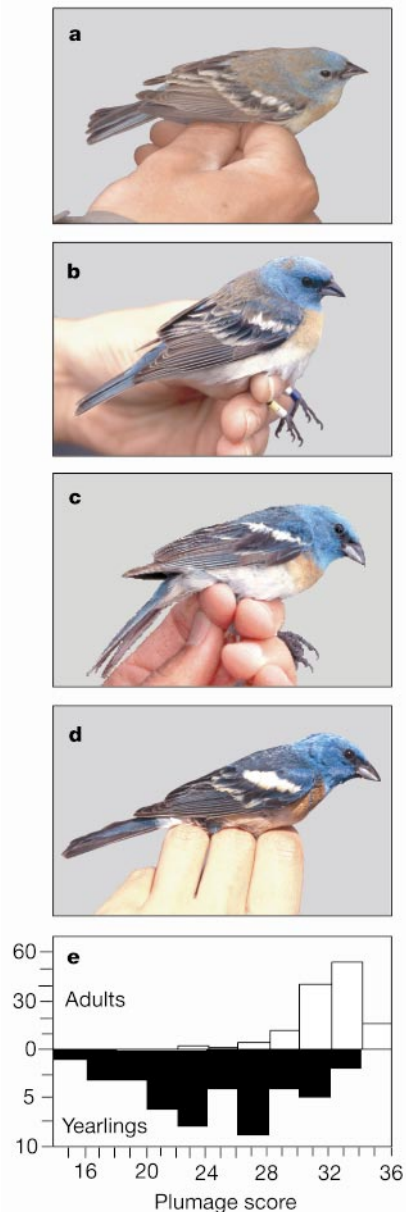


Figure 1 Variation in plumage coloration of male lazuli buntings. **a**, Dull yearling (plumage score, 17.5). **b**, Intermediate yearling (plumage score, 26). **c**, Bright yearling (plumage score, 31). **d**, Bright adult (plumage score, 34). **e**, Distribution of plumage scores of adult males (upper histogram) and yearling males (lower histogram). Yearling males have significantly lower plumage scores (24.9 ± 0.7 (mean \pm s.e.m.), $n = 45$) than adults (32.1 ± 0.2 , $n = 129$; $t = 10.5$, $P < 0.001$); t -test); yearlings also have more variable plumage scores (variance ratio $F = 4.19$, $P < 0.01$).

centage nesting shrub cover) showed a disruptive pattern with plumage coloration (Fig. 2d) that closely parallels the bimodal pairing pattern (Fig. 2b): the dullest and brightest yearling males generally obtained high-quality territories while intermediate yearlings settled in sparsely vegetated areas. This led to the bimodal pattern in pairing success because females preferentially paired with males on high-quality territories: paired males (all ages combined) had significantly more shrub cover on their territories ($47.0\% \pm 1.7$ (value \pm standard error of the mean, s.e.m.), $n = 119$) than unpaired males (25.8 ± 3.4 , $n = 34$; Mann–Whitney z approximation is 4.97, $P < 0.0001$). These findings imply that territorial quality is an essential component of the disruptive selection, but raise the question of why bright and dull yearlings obtained good territories, while intermediate males did not.

The plumage coloration of yearling males influenced their ability to acquire territories by affecting their behavioural interactions with the more abundant adult males. During territory settlement, adult males were more aggressive to colourful males than to dull males (Fig. 3 and ref. 9). To examine the relation between the intensity of adult male aggression and the disruptive pairing and territory quality patterns that we observed for yearling males, we partitioned yearling plumage scores into three plumage classes on the basis of the disruptive pairing pattern (Fig. 2b). Dull plumage scored less than 24; intermediate plumage scored greater than or equal to 24 and less than 28; and bright plumage scored greater than or equal to 28 (other analyses below are also based on these categories). Adult male territory holders behaved significantly more aggressively towards bright and intermediate males than to dull yearling males (analysis of variance (ANOVA), $F_{3,55} = 8.95$, $P < 0.0001$). *Post hoc* paired comparisons (Fisher protected least significant difference (PLSD) tests) revealed significant differences between dull males and all other categories of males (all $P < 0.05$); none of the other paired comparisons differed. Plumage scores of bright yearlings overlapped entirely with adult scores and bright

yearlings were treated as aggressively as bright adults by territory owners (Fig. 3); thus, they probably competed for territories in the same manner as adults. In contrast, dull yearlings were tolerated by adults (Fig. 3), which allowed them to settle nearby in high-quality habitat. The extreme tolerance shown by adult males toward some dull yearlings even suggested social bonds between them: during territorial settlement, some adults and dull yearlings were observed calmly perching or foraging together (Fig. 3). The failure of intermediate yearling males to settle on good territories suggests that they were too bright to be tolerated by adult males, but not aggressive enough to obtain territories by fighting.

Why would territorial adult males show such tolerance to dull males¹⁶, effectively permitting them to settle nearby? The possibility that yearling males dupe adult males by mimicking females (the “female mimicry hypothesis”¹⁰) was previously rejected experimentally⁹. Alternatively, the lack of aggression toward dull yearlings could reflect a form of male–male cooperation^{5,6} whereby both the dull yearling and adult male benefit. If females seek extra-pair matings on the basis of male plumage coloration^{17,18}, adult males might reduce their risk of cuckoldry by allowing less attractive (that is, dull) males to settle nearby¹⁹, and might also enhance their opportunities for obtaining extra-pair fertilizations^{16,20}.

Paternity analyses, using DNA fingerprinting, revealed a high level of extra-pair paternity in this socially monogamous species. Overall, 49% of nests ($n = 41$) contained at least one chick not sired by the resident male. These paternity analyses confirmed that adult males derive genetic benefits by having dull males as neighbours. First, dull males served as paternity buffers for adult males. The realized fitness of adult males was positively correlated with the proportion of their immediate territorial neighbours that were dull yearlings (Fig. 4a; Spearman rank correlation coefficient (r_s) = 0.40, $n = 22$, $P < 0.05$); this was due to a decreasing probability of fitness loss through extra-pair young (Fig. 4b: $r_s = -0.41$, $n = 22$, $P < 0.05$). In fact, from an adult male’s perspective, having all dull neighbours was genetically similar to having no immediate neighbours at all, a situation in which realized fitness tends to be high (Fig. 4a, right panel) and loss of paternity through extra-pair young tends to be low (Fig. 4b, right panel).

In addition, females paired with dull yearlings probably also provided a source of extra-pair paternity for adult males. This is because the plumage characteristics of a male influenced the likelihood that their nests contained extra-pair young: dull yearlings

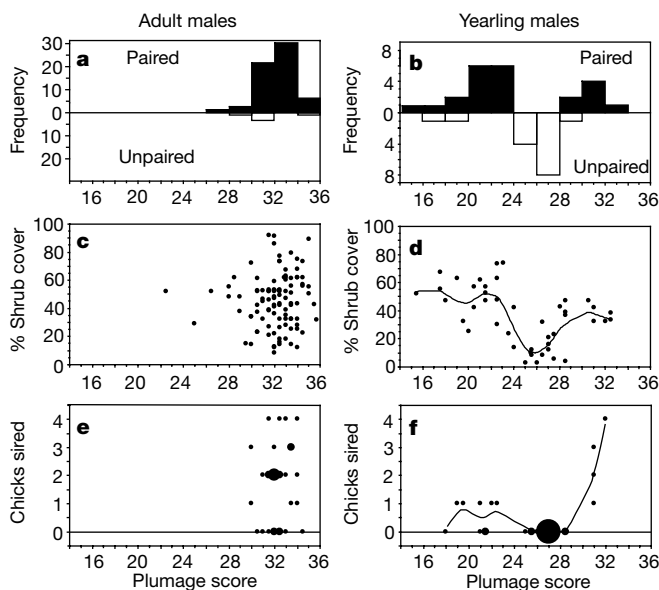


Figure 2 Social and genetic consequences of plumage variation in males. Left panels, adult males; right panels, yearling males. **a, b**, Distribution of plumage scores for males who obtained social mates (above) and those who did not (below). **c, d**, Relation between plumage score and territory quality. **e, f**, Relation between plumage colour and number of chicks sired in a male’s own nest, assessed by DNA fingerprinting. Unpaired males with no nests were assigned zeros. None of the comparisons for adult males were significant (all $P > 0.1$). All three comparisons for yearlings showed significant disruptive relations; univariate cubic splines were used to assess the form of phenotypic selection¹² (splines shown in **d** and **f**), and analysis with 100 bootstrapped splines¹² revealed significant minima ($P < 0.01$) in all three comparisons.

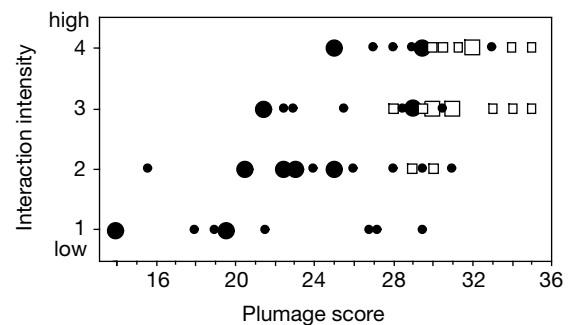


Figure 3 Relation between plumage coloration of an intruding male and the maximum intensity of aggressive interactions with adult male territory holders during territory settlement. Filled circles denote interactions with yearling intruders, open squares interactions with adult intruders. All points represent different pairs of interacting males: small symbols represent one interaction; larger symbols indicate two overlapping points. Aggression categories, in increasing levels of aggression, are (1) males perched less than 2 m apart with no visible sign of aggression; (2) males engaged in countersinging but no chases; (3) territory owner chased intruder, but no physical contact; and (4) territory owner chased intruder and physical contact observed. Aggression from adult male territory holders was positively correlated with plumage coloration of intruders ($r_s = 0.62$, $n = 59$, $P < 0.0001$).

(plumage score less than 24) were more than twice as likely as all brighter males to have at least one extra-pair nestling in their nests (87.5% of 8 nests versus 39% of 33 nests of brighter males; $G = 4.43$, $P < 0.05$). Consequently, dull males also had significantly more extra-pair young in their nests (1.5 ± 1.1 , $n = 8$) than brighter males (0.76 ± 1.1 , $n = 33$; Mann–Whitney $U = 191$, $P < 0.001$). If extra-pair matings primarily involve close neighbours²¹, adult males would increase their probability of siring extra-pair young by allowing dull yearlings to settle nearby. Thus, by tolerating dull yearlings, adult males shape the composition of their social neighbourhood to their own genetic advantage.

Dull yearlings also appear to benefit from their interactions with adult males, as they experience high pairing success (Fig. 2b). But given their high cuckoldry rates, do they actually increase their fitness through this interaction? Additional selection analysis on yearling plumage coloration, based on the number of chicks that males sire in their own nests, confirms that they do benefit. The significant minimum on the fitness surface (Fig. 2f, $P < 0.01$) indicates that dull yearlings sired more chicks than intermediate males.

Thus, settling in high-quality habitat increased the pairing success of the dull yearlings more than enough to compensate for the high levels of extra-pair paternity in their nests. This analysis also provides additional, even stronger evidence for disruptive selection on plumage, given that the number of chicks sired is a more accurate measure of fitness than pairing success. Dull yearlings also gained future benefits from settling in high-quality habitat: yearling territory quality was positively correlated with the quality of their territory the following year (correlation between percentage shrub cover on yearlings' territories and the percentage cover during the next year, $r = 0.71$, $n = 17$, $P < 0.05$). By demonstrating that both adult and dull yearling males benefited from their close proximity in high-quality habitat, our results provide rare evidence for sexually selected male–male cooperation^{5,6}.

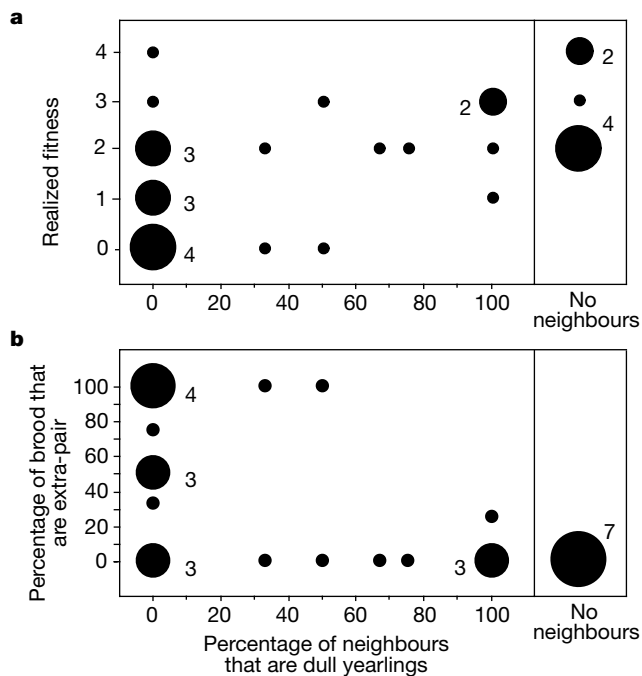


Figure 4 Dull yearling neighbours are paternity buffers for adult males. **a**, Relation between realized fitness in nests of adult males and the percentage of their immediate male neighbours (that is, those that shared a territory boundary) that were dull yearlings (plumage score less than 24). **b**, Relation between fitness loss through extra-pair young in the nest of adult males and the proportion of their male neighbours that were dull yearlings. Smallest points represent a single nest; sample sizes of nests indicated beside larger points. Panels on the right show data for adult males with isolated territories, sharing no territory boundary with another male.

The disruptive phenotypic selection on yearling plumage coloration thus resulted from plumage-dependent differences among males in their ability to acquire high quality territories, either involving cooperation or conflict with adult males. Extreme variation in yearling plumage was an important prerequisite, raising questions about the underlying proximate causes and maintenance of this variation. Two explanations are possible: the variation is largely genetic and is maintained as adaptive variation, or it is largely environmental and is maintained due to constraints^{2,10,11,22}. With respect to the former, strong disruptive selection can lead to equal-fitness alternative tactics¹⁴.

However, fitness comparisons reveal that the dullest yearling males (scoring below 24) had lower reproductive success (Fig. 2f; 0.56 ± 0.18 (s.e.m.) chicks sired in own nest, $n = 9$) than the brightest yearlings (2.5 ± 0.64 chicks sired, $n = 4$; Mann–Whitney $U = 33.5$, $P < 0.05$), a finding that is consistent with a constraint explanation. Moreover, the high frequency of males with intermediate plumage, despite selection against their phenotype, further suggests that the plumage variation is due largely to environmental factors (for example, hatching date, time of moult, condition during moult), and does not have a strong genetic basis. Finally, lazuli buntings breed in a wide variety of habitats⁷, and the pattern of selection may vary with habitat. For example, in habitats with extensive dense nesting cover, there is little competition among males for the unlimited high quality territories, and plumage coloration does not influence a yearling male's ability to acquire a good territory (B.E.L. and E.G., unpublished data). Thus, environmental factors may explain why many yearling males are unable to obtain an optimal plumage coloration. However, the behavioural flexibility to deal with this constraint mitigates some of the fitness losses; cooperation with adult males enables the dullest yearlings to make the best of a bad situation.

We found that complex patterns of mating success, in a species with an apparently simple mating system of social monogamy, derived ultimately from variation in territory quality, an ecological factor that mattered to females and led to striking spatial structure among males. Such spatial structuring may be widespread in other species that occur in variable habitats. Differences among species in variation in territory quality might also help explain currently puzzling variation in mating systems, such as differences in the frequency and distribution of extra-pair copulations. Historically, the study of mating systems focused on the ecological factors that shape social behaviour^{23,24}, but more recently emphasis has shifted away from ecology, to the social and particularly the genetic aspects of mating systems^{25,26}. Our findings suggest that some of the complexities of mating systems can best be unravelled by a combination of these approaches. □

Methods

Colour scoring

Males were captured in mist nets (Banding Permit no. 21830 to E.G.), and a standard series of photographs were taken showing all body parts. Adult and yearling males were aged by the colour of their primary wing covert feathers²⁷. Plumage scores were derived by summing scores from nine distinct areas on the head, breast, back and wings (details available at <http://biology.umt.edu/faculty/greene>, or as a colour figure provided on request from E.G.). Unlike other species whose plumage reflects strongly in the near-ultraviolet²⁸, the peak intensity of the blue feathers of lazuli buntings is at 500–575 nm in the visible portion of the spectrum (measured by reflectance spectrophotometry with an Ocean Optics S2000 fibre optic spectrometer with deuterium-halogen and tungsten illumination). Thus, our scoring does not miss brightness in the ultraviolet. This plumage scoring system is highly repeatable²⁹ by individuals (repeatability index, $r = 0.95$, $n = 24$ males), and among different individuals ($r = 0.93$, $n = 24$ males). The plumage of 18 males observed in aggressive interactions were scored in the field using a telescope. Plumage scores are very similar for birds scored from both photographs and through a telescope ($r = 0.91$, $n = 43$ males).

Territory quality

The percentage shrub cover on each male's territory was estimated in the field by averaging the percentage shrub cover estimated for four randomly placed 20 m × 20 m quadrats. At this study site, average territory size was 1.4 hectares (range 0.6–4.7 hectares, $n = 116$

territories⁷). Thus, four quadrats sample about 11% of a territory of average size, and this was found to characterize the overall shrub cover well.

Aggressive interactions

Five-minute observations of interactions between territorial adult males and intruders were made during territory establishment during the 1994–1997 breeding seasons, and the maximum intensity of interaction was scored. Only one five-minute observation period was used to characterize levels of aggression between pairs of interacting males (that is, there was no pseudoreplication).

DNA fingerprinting

To assess parentage we used standard multilocus DNA fingerprints, based on restriction enzyme *HaeIII* and probes Per and Jeffreys 33.15 (following the protocols described in ref. 30). Autoradiographs were scored by eye. A chick was considered illegitimate if it had three or more unique bands and a bandsharing coefficient, *D*, of less than 0.35 with respect to the putative father. In all cases of extra-pair parentage, the male was excluded as the parent, never the female.

Statistical analyses

P values reported with splines indicate the number of times (out of 100 bootstrapped spline fits) that the resultant spline was not disruptive (that is, there was no clear minimum).

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An area for vergence eye movement in primate frontal cortex

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To view objects at different distances, humans rely on vergence eye movements to appropriately converge or diverge the eyes and on ocular accommodation to focus the object^{1,2}. Despite the importance of these coordinated eye movements (the 'near response') very little is known about the role of the cerebral cortex in their control. As near-response neurons exist within the nucleus reticularis tegmenti pontis³, which receives input from the frontal eye field region of frontal cortex^{4–6}, and this cortical region is known to be involved in saccadic^{7–9} and smooth-pursuit eye movements^{10–12}, we propose that a nearby region might play a role in vergence and ocular accommodation. Here we provide evidence from rhesus monkeys that a region of frontal cortex located immediately anterior to the saccade-related frontal eye field region is involved in vergence and ocular accommodation, and in the sensorimotor transformations required for these eye movements. We conclude that the macaque frontal cortex is involved in the control of all voluntary eye movements, and suggest that the definition of the frontal eye fields should be expanded to include this region.

Over the past decade, there has been significant progress in elucidating the anatomy and physiology of the subcortical pathways involved in the control of vergence eye movements and ocular accommodation in non-human primates^{13–15}. However, the areas of cerebral cortex involved in controlling these eye movements have remained elusive. On the basis of previous studies^{3–12}, we hypothesized that the frontal eye fields or an adjacent region within the frontal cortex might play a role in controlling vergence and ocular accommodation. To investigate this possibility, we recorded from the frontal cortex of two, trained, rhesus monkeys while they performed vergence, saccadic and smooth-pursuit eye movements. We encountered saccade-related neurons within the anterior bank of the arcuate sulcus⁸. In addition, in the prearcuate cortex rostral to the saccade-related region, we recorded from 34 neurons (22 from one animal and 12 from the other) displaying activity that was significantly correlated with both vergence and accommodation. Of these neurons, 25 increased their activity for near viewing, and 9 increased their activity for far viewing. As vergence and accommodation are highly correlated under normal viewing conditions, we related neuronal activity to the vergence eye movements. But previous studies^{16,17} suggest that some of the 34 neurons that we identified in this study are likely to be related to ocular accommodation as well