

to pollute the population with grey members. In contrast, the grey high-inclination objects, with perihelion distances merging with those of the scattered-disk objects, may have participated in dynamical evolution with the Plutinos and Centaurs.

An alternative theory would allow some dynamical exchange between populations of KBOs, but argue that some physical process ensures that surfaces become redder whenever objects are confined to the ragged edge of the Solar System beyond 40 AU. What this process could be is unclear. An object in the Kuiper belt is so far from the Sun that being at 38 AU rather than 42 AU would appear to make little difference to how much sunlight it receives. Clearly, photometric and orbital

investigations of more KBOs are needed. Nonetheless, in this first attempt at combining the two, KBO studies have come of age. ■

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Behavioural ecology

Why are some males dull?

Tore Slagsvold

Birds vary extensively in plumage colour, both between and within species. The males of a species are usually brighter than the females, and older males tend to be brighter than younger birds. But males of the same age within a single population may also show great variety in colour. In such cases, the more brightly coloured males are usually socially dominant and are the mating partners of choice for females¹. Why, then, hasn't natural selection eliminated the duller varieties?

On page 1000 of this issue, Greene and colleagues² suggest one explanation to the puzzle. They studied the lazuli bunting (*Passerina amoena*), a beautiful small finch of North America. Adult lazuli bunting males have turquoise-blue upper parts with a pale cinnamon colour across the breast and sides. Some yearling males are also brightly coloured, but many are dull brown and female in appearance, while still others have intermediate brightness (see the photographs on page 1000). Greene *et al.* show that both the brightly coloured and the dull yearling males sire more chicks than yearlings of intermediate colours. It seems that nature favours the extremes at the expense of those in between. This phenomenon is called disruptive selection, and has been seen only a few times in animals.

Why did the brightly coloured and dull birds succeed where those of intermediate colouring failed? Greene *et al.* found that both bright and dull yearling males occupied territories that included suitable shrub cover, whereas the intermediate yearlings settled on sparsely vegetated areas, where hardly any female would breed. Brightly coloured yearling males succeeded because they possessed the fighting ability necessary

to occupy a good territory in the face of competition from adult males. In contrast, dull yearlings obtained a good territory because adult males tolerated their presence. Yearlings of intermediate colouring were too bright to be tolerated by adult males, but were not aggressive enough to fight their way to a good site.

The next question, then, is why adult males tolerated dull yearling males. One possibility is that those adults in possession of good territory had problems in recognizing the true sex of prospecting dull males. But no support for this 'female mimicry' hypothesis³ has yet been found in the lazuli bunting⁴. Instead, the authors suggest that dull males were accepted because they represented no threat to the mating success of adult males, or to the number of chicks that adult males sired. The dull males might also act as a buffer against even brighter males, which females tend to prefer.

Because of this bias in female preference, adult males may even sire extra young by copulating with the mates of their drab male neighbours. Indeed, DNA 'fingerprinting' showed that the number of chicks sired by adult males was positively correlated with the proportion of immediate neighbours that were dull yearlings. So, both parties seem to benefit from this peculiar system — adult males by 'paternity insurance' and by siring extra young, and dull males by being allowed to occupy a high-quality territory and thereby obtain a mate. In addition, previous occupancy of a good territory helped drably coloured owners to obtain a high-quality territory in the subsequent year. The study provides rare evidence for cooperation between males — a territorial arrangement that



100 YEARS AGO

In the *Atti dei Lincei*, ix. 5... Prof. Grassi describes experiments carried out by a committee with the assistance both of the Italian Government and of the Mediterranean Railway Company, with a view to the prevention and cure of malaria in infected districts. The experiments were carried out in the plains about Paestum, which have long been known as a hotbed of malaria ("malaricissima" is the epithet Grassi applies to the region), and fell into two categories, namely, cure of the disease by the use of quinine, and protection from the bites of *Anopheles claviger* by the use of wire gauze as a covering for windows, doors and even chimneys of houses, the inhabitants of which were required to remain indoors from before sunset till after sunrise, or to go about covered with veils at night. By thus preventing mosquito bites, it was found that the malarial regions could be safely inhabited even at the season when the fever was at its height, and under such conditions the district might be made as healthy as any part of Italy. From *Nature* 25 October 1900.

50 YEARS AGO

An article in the *South African Archaeological Bulletin* (5, No. 18; June 1950) makes sad reading. At Saulspoort, in the Bethlehem district, rock-shelter paintings occur and an important 'gisement' was identified... The work of excavation was begun; but during a period of the workers' absence intruders arrived who just 'hogged' the site and left a yawning pit where the section should have been. The problem of controls is a difficult one. Too rigid rules defeat their own object. It is, in a subtle way, the general interest in archaeology among all classes that makes the subject live and enables the few professionals to continue the study. Without this general interest the subject would in practice wither. A certain freedom to explore must therefore be given to the amateur; but, of course, stories such as this one are major tragedies. Perhaps the problem could best be tackled through the schools. If the young folk were taught to realize that Stone Age sites are not innumerable and should be respected, that 'hogging' sites is a crime and that excavations should only be attempted either under a competent excavator or after having already had experience in digging, then such grievous happenings as occurred at Saulspoort would no longer occur. From *Nature* 28 October 1950.

increases the reproductive success of both parties.

Strong disruptive selection, such as that seen here, sometimes leads to individuals with alternative tactics having equal reproductive success. A good example is that of coho salmon (*Oncorhynchus kisutch*), in which some small males persist in the population because they sneak in to fertilize eggs when females spawn on the territories of large males⁵. By contrast, the duller yearling male lazuli buntings sired fewer young than the brightest yearlings. From this finding, and from the fact that most yearling males had an intermediate and apparently suboptimal plumage colour, the authors suggest that genetics plays a small part in male coloration. They propose that environmental constraints — such as the condition of the bird during moulting — are important in determining coloration.

The study by Greene *et al.*² was a success thanks to their integration of behavioural, ecological and genetic analyses, which enabled them to link variation in plumage colour with variation in an ecological factor (territory quality) and with complex patterns of mating success. This approach should be followed in the future. Another question for future studies is whether an association with bright males in a socially monogamous species — such as the lazuli bunting — increases the mating success of the dull males in the way predicted by the so-called hotshot model⁶. In this model, bright males (hotshots) often attract several females, some of which might settle with the dull males.

Greene *et al.*'s work offers an explanation for intrasexual variety in male sexual traits in one species. But their explanation may not be universally applicable. In the lazuli bunting there is a high level of 'extra-pair' paternity — dull yearling males sire fewer young by their mates as a result of competition from brighter males. But this particular pattern of cuckoldry does not occur in all species that exhibit variation in male sexual traits^{7,8}. Greene *et al.* suggest that the heritability of coloration is low in the lazuli bunting, a phenomenon that has been found in some other birds but not in others¹. Explaining such differences between species will be a great challenge. One thing we need to know more about is how genes interact and are expressed in different genetic and ecological environments. For instance, do genes that enhance sexual attractiveness have positive or negative effects on survival^{9,10}? And are there any mutations that are beneficial to one sex but harmful to the other¹¹? ■

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El Niño

Clues from corals

Robert B. Dunbar

Weather forecasters now enjoy increasingly accurate predictions of climate events linked to the El Niño/Southern Oscillation system (ENSO), ranging from powerful hurricanes in the Atlantic to devastating droughts in southern Africa and Indonesia. Lead times of up to a year can make a big difference in assessing and preparing for economic and agricultural risks. Yet surprises still come with every El Niño. The magnitudes of the two largest events of the twentieth century, in 1982–83 and 1997–98, were not readily forecast (or hindcast for that matter), nor was the extended mild El Niño of 1990–94. One ingredient still missing from the recipe for prediction is a knowledge of the nature and consequences of decadal and longer climate variability.

On page 989 of this issue, Urban *et al.*¹ provide an intriguing view of tropical variability from an unexpected source — a coral record spanning the past 155 years. The authors find that the timescale of the ENSO cycle is not only highly irregular but also that its irregularity may be linked to subtle changes in the mean background or time-averaged state of the ocean.

In the 34 years since Jacob Bjerknes first proposed a mechanistic link between ocean temperatures in the equatorial Pacific and much larger-scale patterns of atmospheric circulation², one of the great triumphs of research into climate dynamics has been the formulation of predictive models of the ENSO system. The basic physics of ENSO became clear after the introduction in the 1980s of a costly but effective monitoring

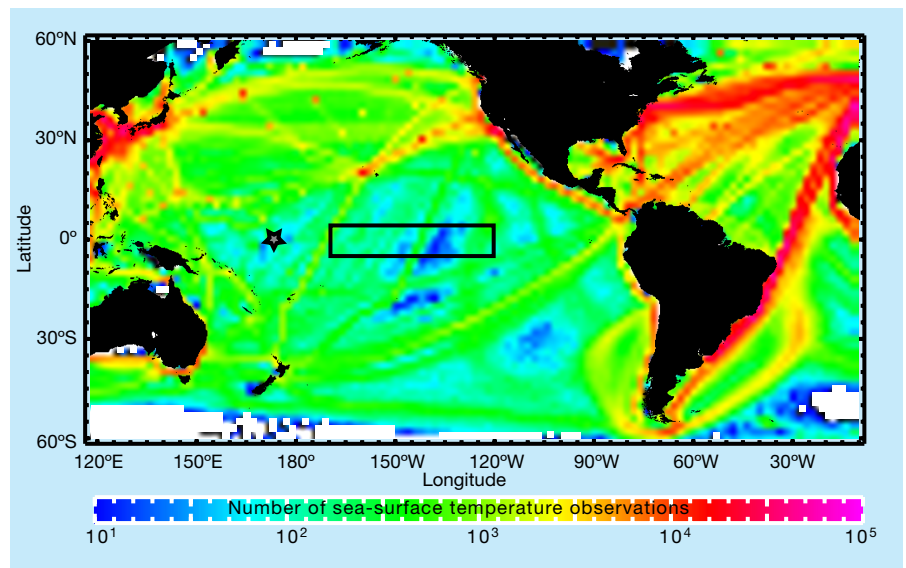


Figure 1 Taking the temperature of the oceans. Number of ship-based observations of sea surface temperature taken between 1900 and 1950 for each 2° latitude by 2° longitude cell of the global ocean. These observations form the core of our instrumental record of surface-ocean variability. Surface water temperatures at the Maiana Atoll (star) and the Niño 3.4 region (rectangle) are particularly sensitive to the state of the El Niño cycle, and temperatures at Niño 3.4 are increasingly used in forecasting. Instrumental records are most common along early twentieth-century shipping lanes and throughout most of the North Atlantic. Within most of the equatorial Pacific there are far fewer measurements over the same period. In any case, highly reliable records of tropical ocean variability extend back only 30 to 50 years. Studies of longer-term interannual to decadal climate variability will rely increasingly on biological archives, such as the coral skeletons from the Maiana Atoll described by Urban *et al.*¹.

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