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THE EVOLUTION OF BIRD PLUMAGE COLOURATION: A ROLE FOR FEATHER-DEGRADING BARCTERIA?

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SUMMARY.—*The evolution of bird plumage colouration: a role for feather-degrading bacteria?*
Aims: To test the existence of differences in the effects *in vitro* of a feather-degrading bacteria on bird feathers containing different types of pigments, and thus, of different colours.
Methods: Tubes containing feathers from nine bird species and containing three different pigments or no pigments were inoculated with bacteria (*Bacillus licheniformis* isolated from soil) and incubated at 37°C during eight days. Feather damage was monitored daily.
Results and Conclusions: At the end of the experiment nearly all feathers were degraded to dust or fibres. However, melanin-containing feathers suffered from earlier bacterial damage than carotenoid-containing feathers or unpigmented feathers. The feathers last showing signs of bacterial damage were those of a parakeet that contained an unknown green pigment. The pigmentation of a feather, and thus its colour, may determine its susceptibility to bacterial degradation. Therefore if feather degrading bacteria could grow on free-ranging birds, they could play an unsuspected role on the evolution of bird plumage colouration.
Key words: *Bacillus licheniformis*, evolution of bird colour, feather-degrading bacteria, plumage colouration, soil bacteria.

RESUMEN.—*La evolución del color en el plumaje de las aves: ¿podrían tener un papel las bacterias capaces de degradar las plumas?*
Objetivo: El principal objetivo de este trabajo fue testar la existencia de diferencias en la degradación *in vitro* de plumas de aves que contenían distintos tipos de pigmento y que, por lo tanto, presentaban distinto color.
Métodos: Se inocularon tubos con bacterias destructoras de plumas (*Bacillus licheniformis*) aisladas del suelo que contenían fragmentos de pluma de 9 especies de aves con tres tipos de pigmentos diferentes o que eran blancas y no contenían ningún pigmento. Los tubos se incubaron a 37°C durante ocho días. Se observó diariamente la evolución de los daños sufridos por las plumas.
Resultados y Conclusiones: Al final del experimento prácticamente todas las plumas fueron reducidas a polvo o fibras. Sin embargo las plumas que contenían melanina sufrieron daños antes que las plumas que contenían carotenos o que no contenían ningún pigmento. Las últimas plumas en presentar daños producidos por las bacterias fueron las de una cotorra que contenían un pigmento verde desconocido. El pigmento de las plumas y por lo tanto su color parece determinar su susceptibilidad a ser degradada por estas bacterias. Por lo tanto, si estas bacterias pudieran degradar el plumaje de aves salvajes, podrían haber jugado un papel insospechado en la evolución de la coloración del plumaje de las aves.
Palabras clave: *Bacillus licheniformis*, evolución de la coloración en aves, bacterias destructoras de plumas, coloración del plumaje, bacterias del suelo.

INTRODUCTION

The evolution of integumentary colouration in animals, and particularly its relationships with parasite-mediated sexual selection, is a controversial issue that has attracted the interest of numerous researchers (*e.g.* Hill, 1991; Houde & Torio, 1992; Andersson, 1994; Lozano, 1994; Badyev & Hill, 2000). Most studies concern birds, which exhibit an enormous array of colours and patterns unparalleled among vertebrates, yet unexplained by any synthetic theory. Ch. Darwin and A. R. Wallace already contended about bird colours in the 19th century (Cronin, 1991). However, the renewed interest on the evolution of plumage colouration can be traced back to Hamilton & Zuk (1982), who hypothesised that, within bird species, those indi-

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viduals with brighter colouration would be signalling higher heritable resistance to parasites. Other authors have proposed more direct benefits for females in the selection of brightly-ornamented parasite-free males, *i.e.* the «transmission avoidance model» (Freeland, 1976; Borgia & Collins, 1989, 1990; Clayton, 1990; Hamilton, 1990), or the «resource provisioning model» (Hamilton, 1990; Read, 1990).

Different model parasites, both external and internal, have been used to test the Hamilton and Zuk hypothesis but results have been controversial (Møller, 1990; Clayton, 1991; Seutin, 1994). Birds present a vast array of parasites, from lice to nematodes or haematozoa, conforming a wide community where it is hard to find out which ones intervene in sexual selection (Clayton, 1991; Blanco *et al*., 1997). Despite bacteria are present everywhere, its effects on the fitness of their wild-ranging avian hosts remains poorly studied and only recently some researchers have studied these interactions (Burtt & Ichida, 1999; Lombardo *et al*., 1996; Mills *et al*., 1999; Potti *et al*., 2002). However, the possible role that bacteria could play on the evolution of bird colouration (and therefore on a strong aspect of sexual selection) remains almost unstudied (but see Burtt & Ichida, 2004; Goldstein *et al*., 2004).

In 1990, a feather-degrading bacterium (*Bacillus licheniformis*) was isolated from an industrial digester containing poultry waste. This bacterium occurs in soils and could be responsible for the degradation of moulted feathers in the field (Williams *et al*., 1990). In a subsequent study, Burtt & Ichida (1999) isolated feather-degrading bacteria from feathers of 134 wild birds of 34 species. Identification in 14 samples showed that 82-91% was *B. licheniformis*, and that the isolated bacteria were able to fully degrade feathers of domestic chickens. Further studies have identified a wider spectrum of soil bacteria capable of fully degrading feathers even on temperate environments (Lucas *et al*., 2003; Riffel *et al*., 2003). Those studies suggest that there is a complex community of bacteria and fungi capable of fully degrading feathers. Its influence on the evolution of feather traits has not been demonstrated but possible relationships with the timing of feather moult and sexual selection have been suggested (Burtt & Ichida, 1999; Clayton, 1999).

The effects of feather-degrading bacteria on bird feathers containing different pigments were tested *in vitro*, thus focusing on the possible influence of bacteria in the evolution of feather colouration.

Material and methods

Bacteria

A strain of *Bacillus licheniformis* (CMP L5) isolated from soil in California was used. Species identification was carried out at the Environmental Biotechnology Institute of Calpoly State University, California, which kindly supplied bacteria for this study.

Feathers

Feathers were tested from nine bird species containing a selection of different feather pigments (Table 1). The feathers were taken from recent skins (< 20 year-old) deposited in the bird collection of Doñana Biological Station (Sevilla, Spain). Feather samples were taken from four different specimens of each species. One wing covert feather was plucked from each bird, except from the White Storks *Ciconia ciconia* from which two coverts were taken, one white (unpigmented) and one black (with melanin), the Golden Orioles *Oriolus oriolus* from which three small tail undercovert feathers were taken, and the Blue-crowned Parakeets *Aratinga acuticaudata* from which a secondary feather was taken. All samples were of approximately the same surface area (2 cm^2). As feathers were treated with chemical substances to preserve the museum specimens from the action of insects, bacteria or fungus, it was assumed that those feathers had been free from any external alteration since the birds were collected. The feathers were carefully rinsed with distilled water in order to eliminate these chemical products. Following Burtt & Ichida (1999), the tip of each feather, which could have suffered from abrasion, was removed and discarded. The following 2 cm were placed in glass test tubes for bacterial culture (feathers from each specimen were introduced in individual tubes). Later, the tubes containing the feather fragments were sterilised by autoclaving

TABLE 1

Colour and pigment in the feathers used in a feather-degrading experiment with *Bacillus licheniformis*. The species from which the feathers were obtained are also given.
[Color y pigmento que contienen las plumas utilizadas en el experimento de degradación de plumas con Bacillus licheniformis*, así como la especie a la que pertenecían.]*

Species *[Especie]*	Feather Colour *[Color de la pluma]*	Pigment *[Pigmento]*
Greater Flamingo *(Phoenicopterus ruber)*	Pink *[Rosa]*	Carotenoid *[Carotenoides]*
Roseate Spoonbill *(Platalea ajaja)*	Pink	Carotenoid
Scarlet Ibis *(Eudocimus ruber)*	Red *[Rojo]*	Carotenoid
Golden Oriole *(Oriolus oriolus)*	Yellow *[Amarillo]*	Carotenoid
American White Ibis *(Eudocimus albus)*	White *[Blanco]*	No pigment *[Sin pigmentos]*
Little Egret *(Egretta garzetta)*	White	No pigment
White Stork *(Ciconia ciconia)*	White	No pigment
White Stork *(Ciconia ciconia)*	Black *[Negro]*	Melanin *[Melanina]*
Raven *(Corvus corax)*	Black	Melanin
Blue-crowned Parakeet *(Aratinga acuticaudata)*	Green *[Verde]*	Unknown *[Desconocido]*

(120°C at 15 lb for 20 min), to exclude any possible bacterial contamination.

Media and culture conditions

The basal medium for growth of the feather-degrading bacteria was the one previously used by Williams *et al*. (1990), that contained the following (in grams per litre): NH_4Cl, 0.5; NaCl, 0.5; K_2HPO_4, 0.3; KH_2PO_4, 0.4; MgCl $6H_20$, 0.1; yeast extract, 0.1. pH was adjusted to 7.5. Ten ml of the basal medium were added to the fragment of the sterilised feathers placed in glass tubes and inoculated with the pure bacterial culture grown in Columbia agar (Oxoid). All tubes were inoculated with the same amount of bacteria (100 µl of a bacterial suspension containing approximately 10^5 ufc/ml). Tubes were incubated at 37°C with shaking at 125 rpm during 8 days (mean degradation time according to Burtt & Ichida, 1999).

To confirm that bacterial growth in the medium was dependent on the feathers, four control tubes with the same medium but without feathers where inoculated with bacteria. Two test tubes containing feather fragments and medium were not inoculated to provide additional controls. Bacterial growth was first monitored visually three days after inoculation and then daily from the fifth day onwards (always starting at 17.00H). All alterations suffered by the feathers were recorded. At the end of the experiment, a sample of every tube was cultured in Columbia agar to test whether growth was due to the same bacteria that had previously been inoculated.

Statistical analysis

Five consecutive categories of feather degradation were defined after the experiment (Table 2). A Kruskal-Wallis ANOVA was used

to assess possible differences in degradation between differently pigmented feathers. A factor with four categories according to the pigment contained in the feather was defined (carotenoid, unpigmented, melanin, and unknown pigment). Differences were tested for on the first day in which the feather was «clearly deteriorated» (see Table 2) and on the final degradation status of the feather depending on the pigment that it contained.

RESULTS

Feathers were affected by bacterial activity in all the tubes that were inoculated ($n = 40$) indicating that the products used to prepare the specimens (borax or corn flour) was removed when the feather fragments were rinsed and autoclaved.

At the end of the experiment the *Bacillus* had degraded nearly all the feathers to dust or fibres. The first signs of damage produced by bacterial activity were detected between the third and the sixth day in most feather samples. Feathers seemed to be the only bacterial growing substrate as there was no bacterial growth in any of the control tubes. In addition, the feathers placed in medium with no bacteria showed no sign of damage. The time needed by the bacteria to degrade the feathers was within the range reported by Burtt & Ichida (1999).

Statistical differences were found between the differently pigmented feathers in the first day in which the feather presented clear signs of deterioration (Chi-Square = 30.61, df = 3, $P < 0.001$). The first feathers to present clear evidence of damage were those pigmented with melanin, followed by unpigmented and carotenoid pigmented feathers and finally those with the unknown pigment of the Blue-crowned Parakeet (Fig. 1). The feathers also differed on their final status at the end of the experiment (Chi-Square = 2505, df = 3, $P < 0.001$). The melanin pigmented feathers were the only ones where all samples were reduced to dust. Unpigmented (white) feathers were more deteriorated than the ones containing carotenoids and closer to the melanin-pigmented feathers final status. The feathers of the Blue-crowned Parakeet were as deteriorated as carotenoid pigmented feathers when the experiment ended (Fig. 2).

TABLE 2

Feather degradation categories defined to quantify the differences in the level of degradation of the differently coloured feathers.
[Categorías de degradación de las plumas definidas para cuantificar las diferencias en el nivel de degradación de las plumas con distintos pigmentos.]

Degradation category *[Categorías de degradación]*	Description *[Descripción]*
1 intact feather *[1 pluma intacta]*	No alteration in the feather *[Pluma sin alteración alguna]*
2 partially damaged *[2 pluma parcialmente dañada]*	The contour of the feather fragment shows signs of damage *[El contorno del fragmento de pluma muestra signos de daño]*
3 clearly deteriorated *[3 pluma claramente dañada]*	The feather presents clear evidence of bacterial degrading activity (broken barbules and some fibers) *[La pluma presenta claras evidencias de actividad degradadora por la bacteria (bárbulas rotas y algunas fibras)]*
4 fibres *[4 fibras]*	The feather has been reduced to long fibres that float in the culture medium *[La pluma ha sido reducida a largas fibras que flotan en el medio de cultivo]*
5 dust *[5 polvo]*	The feather has been reduced to particles deposited at the bottom of the vial *[Las plumas están reducidas a particulas depositadas en el fondo del tubo]*

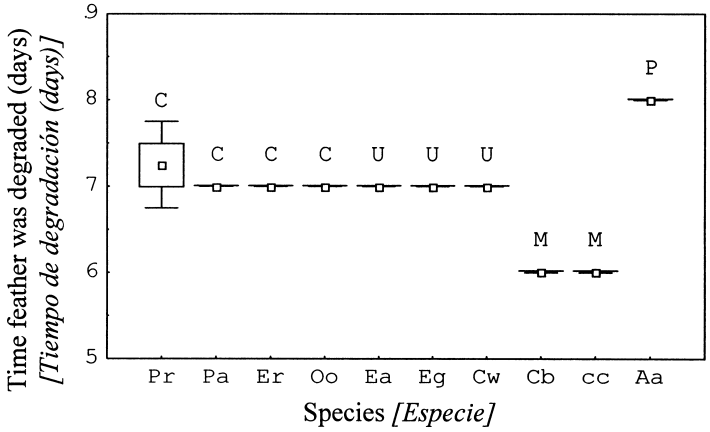

FIG.1.—First day of the experiment in which the feather presents clear evidence of bacterial degrading activity (broken barbules and some fibres) for each species. Species abbreviations are: Pr = *Phoenicopterus ruber*, Pa = *Platalea ajaja*, Er = *Eudocimus ruber*, Oo = *Oriolus oriolus*, Ea = *Eudocimus albus*, Eg = *Egretta garzetta*, Cw = *Ciconia ciconia* (white feathers), Cb = *Ciconia ciconia* (black feathers), Cc = *Corvus corax*, Aa = *Aratinga acuticaudata*. The letters over the bars indicate the pigments that those feathers contain, C = Carotenoids, U = No pigment, M = Melanin, and P = Unknown parakeet pigment.
[Primer día del experimento en el que se observaron claras evidencias de degradación de las plumas debido a la acción de las bacterias (bárbulas rotas y algunas fibras) para cada especie. Las abreviaciones de cada especie corresponden a: Pr = Phoenicopterus ruber, *Pa* = Platalea ajaja, *Er* = Eudocimus ruber, *Oo* = Oriolus oriolus, *Ea* = Eudocimus albus, *Eg* = Egretta garzetta, *Cw* = Ciconia ciconia *(plumas blancas), Cb* = Ciconia ciconia *(plumas negras), Cc* = Corvus corax, *Aa* = Aratinga acuticaudata. *Las letras encima de las barras indican el pigmento que contenían las plumas, C = Carotenoides, U = sin pigmento, M = Melanina y P = pigmento desconocido de la cotorra.]*

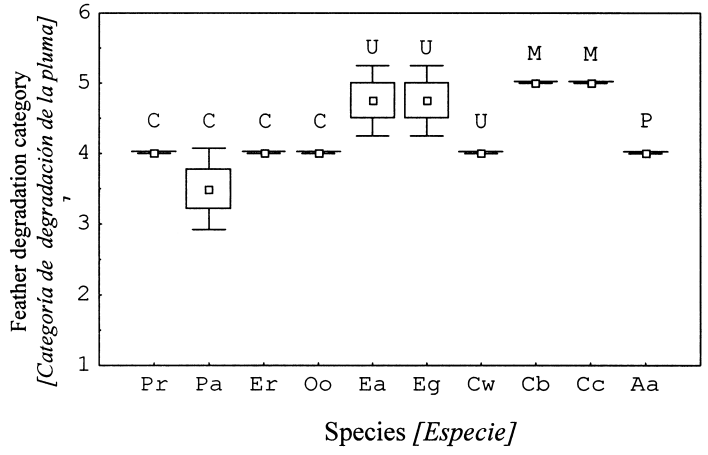

FIG.2.—Final state of each species feathers when the experiment ended. Codes for the degradation stage of the feather: Intact feather = 1, Partially damaged = 2, Clearly deteriorated = 3, Fibres = 4, and Dust = 5. Species and pigment codes as in Fig. 1.
[Estado final de las plumas de cada especie al final del experimento. Los códigos para cada estado de degradación son: pluma intacta = 1, Parcialmente dañada = 2, Claramente deteriorada = 3, Fibras = 4, y polvo = 5. Los códigos de las especies y los pigmentos son los mismos que en la Fig. 1.]

DISCUSSION

Feather colours and bacteria

Several aspects of the results reinforce the idea that the different pigmentation of the feathers influences the rate of feather degradation by feather-degrading bacteria. First, despite the difference in size between the original feather from which the samples were taken (compare, *e.g.*, the oriole feathers with those from the Greater Flamingo *Phoenicopterus ruber* or the Roseate Spoonbill *Ajaia ajaja*), the degradation of the feathers followed similar patterns among the feathers containing the same pigment. Second, excepting a few cases, the feathers from every species containing the same pigment were degraded at the same time and with the same intensity. Finally, the pattern of degradation of unpigmented and melanin-containing feathers from white storks followed the same pattern as the feathers from other species with the same pigment. White feathers from the stork were as degraded as the white feathers from other species, but differently so compared with black feathers from the same individuals, that were degraded in the same way as Raven *Corvus corax* feathers (Figs. 1 and 2).

The dramatic effect *in vitro* of *B. licheniformis* on bird feathers suggests that feather-degrading bacteria are a potential selective force in the evolution of feather characteristics. The experiment was specifically designed to test whether there were differences in the degradation rate of feathers containing different pigments and therefore of different colouration. According to these results, the colour of a feather, and thus the pigment that it contains, seems to determine its susceptibility to bacterial degradation. This means that some species or some parts of a bird are more susceptible than others to bacterial attack because of their composition, and not only due to species-specific requirements of habitat, as previously suggested (Burtt & Ichida, 1999). Similarly, in species with sexual or age dichromatism, one sex or age class, can be more at risk of bacterial degradation than others.

Bird plumages, apart from their insulating properties, convey important visual information useful for species or sex recognition, as well as for assessment of mate quality (Andersson, 1994). The relative importance as signals of different feather colours has recently been stressed. Thus, carotenoid-dependent pigments, necessarily obtained from the diet and also consumed for non-pigmentary bodily functions, may have a higher signalling power than those based on melanin, which is synthesised by the individual (Badyev & Hill, 2000). In this study it has been shown that carotenoid-containing feathers resisted bacterial degradation longer than melanin-containing feathers. This may contribute to explain why these pigments are so prevalent in body areas that are used for sexual communication or as warning colours (such as the crown, the rump, breast or belly, depending on the species, Møller *et al.*, 2000). If the information conveyed is important, individuals would benefit from keeping the quality of the signal for as long as possible. Curiously enough, white unpigmented feathers were degraded later and to a lesser degree than melanin pigmented feathers. Melanin itself could provide nutrients to bacteria, making it even more susceptible to damage than the white unpigmented feathers. Alternatively, the structure of the barbules in feathers containing melanin may facilitate bacterial activity. However, contrary to these results, Goldstein *et al.* (2004) have reported that melanin-containing feathers degraded more slowly than white unpigmented hen feathers. They quantified the concentration of β-keratin oligopeptids dissolved on the culture medium but made no observational description of the way in which the feathers were degraded. Therefore, their results cannot be directly compared with those presented here .

If the concentration of β-keratin oligopeptids correlated with the visual categories defined, the contradictory results could be related to the conservation status of the feathers, which was different in the two studies. Perhaps melanic feathers of museum specimens were selectively affected by some unknown factor which did not affect the remaining feathers. However, this is felt to be unlikely and it is thought that the more reasonable explanation is that different *Bacyllus* strains have been used. It is known that different bacterial strains may act differently under de same conditions. For example, not all the strains isolated by Burtt & Ichida (1999) had keratinolitic activity, or the strains from arid zones had less keratinolitic activity than the ones from humid zones (Burtt

& Ichida, 2004). This points to the necessity to replicate this kind of experiments with different strains and conditions before deriving possible evolutionary implications of bacterial activity on bird feather coloration.

At a regional scale, the warm and humid conditions, which facilitate feather degrading bacteria growth, are typical of tropical areas (especially rain-forest) and wetlands. Therefore bird species inhabiting those environments may be more exposed to bacterial action.

It has been suggested that the brightest plumages are shown by bird species living in tropical areas (Bailey, 1978; Simmons, 2000). Curiously enough, the feathers resisting bacterial degradation longer in this experiment were those of a tropical parakeet. These highly coloured birds do not present carotenoids in their plumage, but a different type of poorly known pigments (Brush, 1981). Contrary to carotenoids, the feather pigments in the *Psittacidae* do not fade in captivity and thus they not seem to depend on the diet. As most parrots live precisely in hot and humid forested tropical areas, it is possible that their very peculiar feather pigments have been selected under the pressure of feather-degrading bacteria.

Looking for evidences of bacterial action

Potentially linked to feather-degrading bacteria are some odd bird behaviours not yet well explained, such as anting (Clayton & Wolfe, 1993), red-soil bathing (in Bearded Vultures, *Gypaetus barbatus*, Negro *et al*., 1999; Negro & Margalida, 2000), or addition of green plants with antibiotic properties to the nest (Clark & Mason, 1985; Clayton & Wolfe, 1993; Petit *et al*., 2002). It would be worthwhile to re-examine all these behaviours in the light of the actions of feather-degrading bacteria.

Direct protection against bacterial activity could be the spreading of the plumage with the secretions of the uropygial gland. Jacob & Ziswiler (1982) proposed that these secretions contain fatty acids that eliminate potential pathogens and more recently Shawkey *et al*. (2003) have confirmed that uropygial oil inhibits the growth of at least several feather degrading bacteria. Reneerkens *et al*. (2002) have reported that several sandpipers change the composition of their preen wax secretion during their pre-nuptial migration. Most of these birds change from a mostly whitish or greyish winter plumage to a rufous summer plumage (Hayman *et al*., 1986). It would be highly informative to examine waders and other birds that experience seasonal colour shifts for the presence of feather-degrading bacteria (and, if possible, to test the potential antibiotic properties of their uropygial gland secretions).

It is still unknown whether feather-degrading bacteria are active on the plumage of live birds, or only act on shed feathers. More research is needed to determine whether bacteria degrade feathers *in vivo*, and if so, whether they play a prominent role in the evolution of bird colours.

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