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Distribution of unique red feather pigments in parrots

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In many birds, red, orange and yellow feathers are coloured by carotenoid pigments, but parrots are an exception. For over a century, biochemists have known that parrots use an unusual set of pigments to produce their rainbow of plumage colours, but their biochemical identity has remained elusive until recently. Here, we use high-performance liquid chromatography to survey the pigments present in the red feathers of 44 species of parrots representing each of the three psittaciform families. We found that all species used the same suite of five polyenal lipochromes (or psittacofulvins) to colour their plumage red, indicating that this unique system of pigmentation is remarkably conserved evolutionarily in parrots. Species with redder feathers had higher concentrations of psittacofulvins in their plumage, but neither feather colouration nor historical relatedness predicted the ratios in which the different pigments appeared. These polyenes were absent from blood at the time when birds were replacing their colourful feathers, suggesting that parrots do not acquire red plumage pigments from the diet, but instead manufacture them endogenously at growing feathers.

Keywords: plumage colouration; Psittaciformes; psittacofulvins; sexual selection

1. INTRODUCTION

The brilliant colours of bird feathers are generated by two primary mechanisms: the presence of pigments and the microstructural arrangement of feather tissues (Fox & Vevers 1960). Carotenoid and melanin pigments are the main feather pigments across avian orders (Brush 1978), but these are by no means the only chemical colourants of plumage. For example, porphyrins (With 1957, 1978) and iron oxides (Negro *et al.* 1999) also can confer colour on bird feathers.

Parrots (Aves: Psittaciformes) are among the most spectacularly coloured animals, displaying a spectrum of ultraviolet to red hues in their feathers (Nemesio 2001; Eaton & Lanyon 2003; Hausmann *et al.* 2003; Pearn *et al.* 2003*a*). The function of gaudy plumage colouration in parrots has attracted attention recently, principally as sexually selected signals of quality (Pearn *et al.* 2001, 2003*b*; Arnold *et al.* 2002; Masello & Quillfeldt 2003). Despite several decades of work on the pigments that bestow beautiful colours on parrot feathers (Kruckenberg 1882; Völker 1936, 1937; Hudon & Brush 1992), we still know very little about their biochemical nature. Stradi *et al.* (2001) recently described a series of four new lipochromes (referred to as psittacofulvins) from the red feathers of a scarlet macaw (*Ara macao*).

Here, we use high-performance liquid chromatography (HPLC) to survey the red pigments found in the plumage of 44 species of parrots. We selected a broad sample of parrots of different age, sex, colour and phylogenetic relatedness (spanning the three major families of parrots: Psittacidae—the true parrots, Loriidae—the lories, and Cacatuidae—the cockatoos; Forshaw 1977) to understand the diversity of pigmentation systems within this lineage. We also measured plumage reflectance to examine how the variety of parrot colours are created by feather pigments. Last, we sampled blood from parrots at the time they were growing their colourful plumage to learn about the origin of these feather colourants (specifically if psittacofulvins are delivered to peripheral feather sites for colouration).

2. METHODS

Red parrot feathers were acquired in 2002–2003 from a variety of sources, mostly from pet birds but occasionally from zoos, aviculturists, pet stores and museum specimens (table 1). When possible, we noted the subspecies, sex and rearing conditions (captive bred or wild caught) of feather donors and the body region from which feathers came. At collection (either by removing shed feathers from cage floors or by plucking from museum skins), feathers were stored in the dark in sealed envelopes at room temperature for later analysis (which never exceeded six months post-collection).

Biochemical analyses generally follow those for carotenoids (also lipid-soluble molecules) in McGraw *et al.* (2003), with a few modifications. Feathers were first washed sequentially in ethanol and hexane to remove surface lipids and then blotted dry. Pigmented barbules were trimmed off, weighed to the nearest 10^{-6} g with an electronic balance, and added to a 9 ml glass tube containing 1 ml acidified pyridine (Hudon & Brush 1992). We filled the headspace of the tube with argon to minimize pigment oxidation and held the tube at 95 °C for 3 h. After cooling to room temperature, we extracted the lipids by adding 1 ml distilled water and 3 ml *tert*-butyl methyl ether and shaking vigorously for 2 min. We centrifuged the tube for 5 min at 3000*g*, transferred the coloured supernatant to a clean tube, and evaporated the solvent to dryness under a stream of nitrogen. The pigment residue was re-suspended in 200 µl of HPLC mobile phase (methanol : acetonitrile : chloroform, 46 : 46 : 8) prior to analysis.

We injected 50 µl of each sample into a Waters 717plus Autosampler HPLC (Millipore Corp., Bedford, MA) fitted with a Develosil RPAqueous RP-30 column (250 × 4.6 mm; Nomura Chemical Co. Ltd, Aichi, Japan) and an Eppendorf TC-50 column heater (Hamburg, Germany) set at 31 °C. We used an isocratic system (Hewlett-Packard 1050 Series Isocratic Pump) at a constant flow rate of 0.75 ml min^{-1} for 30 min. Data were collected from 250 to 600 nm using a Waters 996 photodiode array detector (Waters Corporation, Milford, MA). We identified pigments by comparing their respective retention times (t_R) and absorbance maxima (λ_{max}) to those of extracts from scarlet macaw feathers (Stradi *et al.* 2001) run as external standards. The relative abundance of the various pigments was determined using peak areas that were integrated by MILLENNIUM software, v. 2.1.

Plumage colour was scored with a hand-held Colortron II reflectance spectrophotometer (Light Source Inc., San Rafael, CA; Hill 1998). This 32-band unit quantifies spectral reflectance from 390 to 700 nm and its accompanying COLORSHOP software derives

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Table 1. List of parrot species for which red feather pigments were analysed. We assumed that all birds were captive bred unless otherwise noted.

family	common name	scientific name	*n*	sex[a]	plumage region	source[b]
Psittacidae	eclectus parrot	*Eclectus roratus*[c]	20	8m, 12f	whole body (f), flank/ underwing (m)	PET
	African grey parrot	*Psittacus erithacus*[d]	4	1m, 2f, 1u	tail	PET
	scarlet macaw	*Ara macao*	5	1m, 1f, 3u	whole body	PET (4), SAZ
	greenwing macaw	*Ara chloroptera*	6	2m, 1f, 3u	whole body	PET
	severe macaw	*Ara severa*	1	u	underwing	PET
	blue-fronted amazon	*Amazona aestiva*	1	m	tail	PET
	orange-winged amazon	*Amazona amazonica*	2	1m, 1u	wing	PET
	double yellow-headed amazon	*Amazona ochrocephala oratrix*	1	u	wing	SAZ
	lilac-crowned amazon	*Amazona finschi*	1	f	forehead	PET
	Cuban amazon	*Amazona leucocephala leucocephala*	4	3m, 1f[e]	throat, belly	SDZ
	Amboina king parrot	*Alisterus amboinensis*	1	u	head, belly	PET
	Pesquet's parrot	*Psittrichas fulgidus*	4	1m, 2f, 1u	flanks	SDZ (2), MMZ, SAZ
	eastern rosella	*Platycercus eximius*	1	u	head, breast	AVI
	western rosella	*Platycercus icterotis*	1	u	head, breast	AVI
	green-cheeked parakeet	*Pyrrhura molinae*	1	u	breast, tail	AVI
	Bourke's parakeet	*Neophema bourkii*	1	u	breast	PP
	moustache parakeet	*Psittacula alexandri*	1	f	breast	PET
	red-crowned kakariki	*Cyanoramphus nouaezelandiae*	1	u	crown	PET
	kea	*Nestor notabilis*	3	1m, 1f, 1u	underwings	WPZ
	hawk-headed parrot	*Deroptyus accipitrinus accipitrinus*	1	u	tail	WPZ
Cacatuidae	Leadbeater's cockatoo	*Cacatua leadbeateri*	4	1m, 2f, 1u[f]	crest, breast	PET (2), SDZ (2)
	umbrella cockatoo	*Cacatua alba*	1	f	tail	PET
	moluccan cockatoo	*Cacatua mollucensis*	2	1f, 1u	crest	PET
	slender-billed corella	*Cacatua tenuirostris*	1	m	face, throat	PET
	red-tailed black-cockatoo	*Calyptorhynchus banksii*	4	2m, 2f[f]	tail	PET (2), SDZ (2)
	gang-gang cockatoo	*Callocephalon fimbriatum*	1	m	head	SDZ
Loriidae	red lory	*Eos bornea*[g]	5	2m, 3f	whole body	PET (3), SAZ, AMNH
	blue-streaked lory	*Eos reticulata*	2	2f	whole body	AMNH, PET
	obi lory	*Eos squamata obiensis*	1	u	whole body	SAZ
	blue-eared lory	*Eos semilarvata*	4	3m, 1f	whole body	SDZ
	talaud red and blue lory	*Eos histrio talautensis*	1	m	whole body	SDZ
	dusky lory	*Pseudeos fuscata*	1	m	breast	AMNH
	purple-naped lory	*Lorius domicella*	1	u	neck, vent	AMNH
	collared lory	*Phigys solitarius*	1	m	breast, vent	AMNH
	mindanao lorikeet	*Trichoglossus johnstoniae johnstoniae*	1	u	face	AMNH
	rainbow lorikeet	*Trichoglossus haematodus*[h]	2	2f	breast	AMNH
	red-flanked lorikeet	*Charmosyna placentis placentas*	1	m	throat, flank	AMNH
	stella lory	*Charmosyna papou goliathina*	3	2f, 1m	whole body	SDZ (2), AMNH
	astrolabe mountain fig-parrot	*Cyclopsitta diophthalma coccineifrons*	1	m	head	AMNH
	blue-crowned hanging parrot	*Loriculus galgulus*	1	u	tail	AMNH
	yellow-streaked lory	*Chalcopsitta scintillata*	2	1m, 1u	forehead, tail	AMNH, MMZ

(*continued on next page*)

Table 1 (*Continued*).

family	common name	scientific name	n	sex[a]	plumage region	source[b]
brown lory	*Chalcopsitta duivenbodei*	1	f	breast	AMNH	
	musk lorikeet	*Glossopsitta concinna*	1	m	forehead	AMNH
	Salvadori's fig-parrot	*Psittaculirostris salvadori*	1	m	breast	AMNH

[a] u, unknown sex.

[b] AMNH, American Museum of Natural History; AVI, aviculturist; PET, pet bird; PP, Pampered Pets of Ithaca; SAZ, San Antonio Zoo; SDZ, San Diego Zoo; WPZ, Woodland Park Zoo (number of birds from each source in parentheses).

[c] Several subspecies sampled, including *aruensis*, *biaki*, *polychloros*, *roratus*, *solomonensis* and *vosmaeri*.

[d] Two Congo subspecies (*P. e. erithacus*), one of each sex, sampled.

[e] One of each sex was wild caught.

[f] One female was wild caught.

[g] One Moluccan lory (*Eos bornea bornea*) of unknown sex was sampled (AMNH).

[h] One bird of unknown sex was sampled from both *T. h. haematodus* and *T. h. rosenbergii* (Rosenberg's lorikeet).

tristimulus scores from the generated reflectance curves. We used the hue, saturation and brightness (HSB) tristimulus scoring system to capture variation in parrot plumage reflectance. Hue represents the wavelength at maximum reflectance, for which COLORSHOP assigns numerical values around a 360° colour wheel (with red starting at 0°). Saturation captures spectral purity and is measured by COLORSHOP as a percentage relative to black and white standards provided by Light Source Inc. (100% = fully saturated, or comprised entirely of one light-wavelength). Brightness is a measure of the total amount of light reflected by a surface (or area under the spectral curve), and again is represented by COLORSHOP as a percentage (with 100% being total reflectance, or white). We selected a central 9 mm^2 area in the pigmented feather barbules and scored its colour twice. For all measurements, the Colortron was held perpendicular to the feather and the foot lever containing the 9 mm^2 reading area depressed firmly against it. Average HSB values are used in analyses (see McGraw & Hill (2001) for repeatability of HSB values using this instrument).

To identify lipid-soluble pigments circulating through blood during feather moult, we obtained frozen plasma samples sent by the veterinarians of eight adult pet parrots, all of which displayed red plumage colour and shed feathers for use in this study—single mated pairs of Eclectus parrots (*Eclectus roratus*), African grey parrots (*Psittacus erithacus*) and scarlet macaws (*Ara macao*), as well as a male blue-fronted Amazon (*Amazona aestiva*) and a female greenwing macaw (*Ara chloroptera*). Lipochromes were extracted and analysed from thawed plasma using HPLC (*sensu* McGraw *et al.* 2002) within a week of blood sampling.

Our data met the assumptions of parametric statistics, so we used two-way analyses of variance (ANOVA) to analyse the effect of sex and parrot family on plumage colour and feather-pigment concentrations and proportions. We used Pearson's correlational tests to compare the relationships between plumage colour, feather-pigment concentration and feather-pigment proportions among species.

3. RESULTS

(a) *Feather pigments*

The same set of five lipochromes was characterized from the solvent extracts of all red parrot feathers (figure 1). These corresponded to the four pigments previously elucidated by Stradi *et al.* (2001)—tetradecahexenal, hexadecaheptenal, octadecaoctenal and eicosanonenal—in addition to small amounts of a fifth, more polar, as-of-yet unidentified psittacofulvin (figure 1), which is also present in the red plumage of scarlet macaws (see fig. 1*a* of Stradi *et al.* 2001). The ratios in which these psittacofulvins appeared in feathers varied substantially among individuals and species, but there was no apparent sex difference or phylogenetic trend, as the three main parrot families did not differ significantly in relative pigment composition (figure 2*a*). However, parrot sexes and families did differ significantly in total psittacofulvin concentration, with feathers from males containing more pigments overall than females and feathers from the Loriidae containing the highest levels of the three parrot families (figure 2*b*). No carotenoid pigments were detected in any feather sample (lower detection limit $= 1\ \mu\text{g g}^{-1}$; analytical methods described in McGraw *et al.* (2004)).

(b) *Feather reflectance*

Red parrot feathers reflected predominantly in the red portion of the spectrum, although there was a smaller UV component (figure 2*c*). The general shape of this reflectance curve in parrots is similar to that of carotenoid-coloured red feathers in other birds (Burkhardt 1989).

Across all parrot species studied here, both the hue ($r = -0.70$, $p = 0.004$) and saturation ($r = 0.65$, $p = 0.002$) of red feathers significantly predicted the total concentration of psittacofulvins present, with redder and more saturated feathers containing the most ($p = 0.24$ for the correlation between pigment concentration and brightness). None of the tristimulus measures were significantly correlated with the proportional composition of feather pigments, however (all $p > 0.05$). Parrot families and sexes differed in plumage colour, specifically with males having feathers of a redder hue than females (two-way ANOVA, $F_{1,39} = 5.0$, $p = 0.03$) and cacatuids having lighter feathers than members of the other two families (two-way ANOVA, $F_{2,39} = 5.4$, $p = 0.009$; *post hoc* Fisher's protected least significant difference test, both $p < 0.005$) (all other $p > 0.1$).

(c) *Fluorescence*

Prior studies of parrot colouration indicated that many yellow feathers fluoresce under ultraviolet light (Völker 1936, 1937, 1942; Boles 1990, 1991; Hausmann *et al.* 2003). There is no indication that red colours in parrots fluoresce, however (Hausmann *et al.* 2003). We confirmed this finding with our large sample of feathers by subjecting them all to both short- and long-wave UV light ($\lambda = 254$ and 366 nm, respectively) using a Minerelight lamp (model UVGL-58, UVP Inc., San Gabriel, CA) and detecting no fluorescence.

(d) *Blood pigments*

We found no evidence of psittacofulvins in any of the plasma samples analysed. The detection limit of these assays was 1 ng, or 0.02 μg pigment per ml plasma.

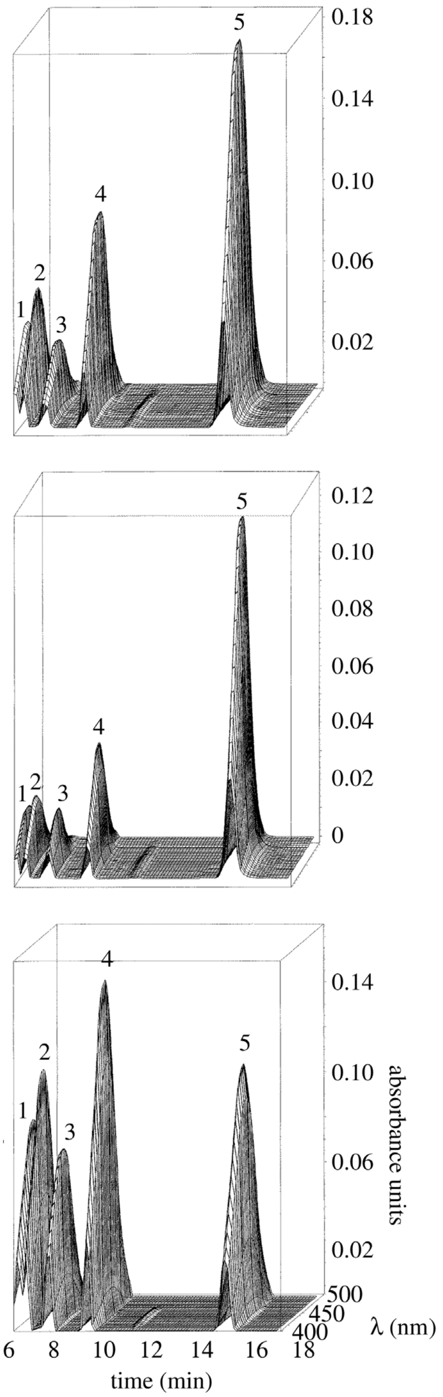

Figure 1. Representative three-dimensional HPLC chromatograms from one species in each of the three parrot families: (*a*) male African grey parrot (*Psittacus erithacus*, Psittacidae), (*b*) male red lory (*Eos bornea*, Loriidae) and (*c*) male red-tailed black cockatoo (*Calyptorhynchus banksii*, Cacatuidae). Note the presence of the same set of five psittacofulvins in each: (i) unidentified pigment, $t_R=6.4$ min, $\lambda_{max}=438$ nm; (ii) eicosanonenal, $t_R=6.7$ min, $\lambda_{max}=438$ nm; (iii) octadecaoctenal, $t_R=7.9$ min, $\lambda_{max}=424$ nm; (iv) hexadecaheptenal, $t_R=9.6$ min, $\lambda_{max}=443$ nm; (v) tetradecahexenal, $t_R=15.8$ min, $\lambda_{max}=443$ nm. The *z*-axis is truncated at 375 nm in all panels because these pigments showed no absorbance peaks in the UV.

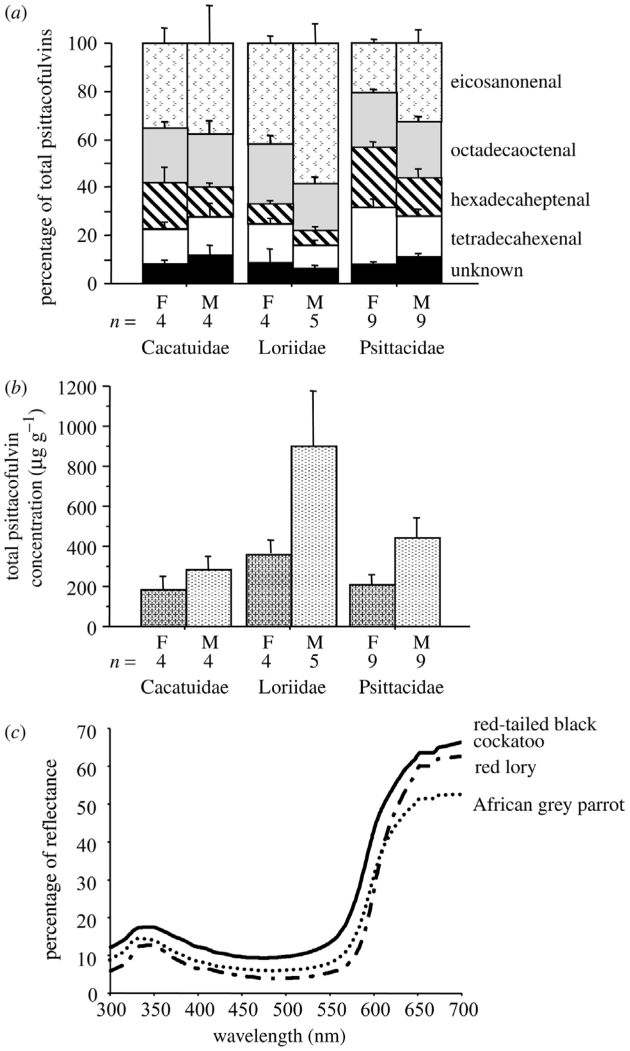

Figure 2. Psittacofulvin composition of red feathers from parrots found in each of the three main parrot families. Standard errors are shown above each bar, which denotes the species means (n=number of species) for each pigment type within a family. In separate two-way analyses of variance for the five psittacofulvins, we found no effect of sex (all $p>0.07$), family (all $p>0.15$), or sex-by-family interaction (all $p>0.35$) on the percentage (*a*) of total pigments that each comprised. We did, however, find that there was a significant effect of sex ($F_{1,39}=4.0$, $p=0.04$) and family ($F_{2,39}=7.4$, $p=0.02$) on (*b*) total feather-pigment concentration (no sex-by-family interaction; $p>0.3$). *Post hoc* tests revealed that male feathers contained more pigments than females (Fisher's PLSD, $p=0.01$) and that lory feathers contained more than feathers of psittacids and cockatoos (Fisher's PLSD, both $p<0.02$; $p=0.25$ for pairwise comparison between psittacids and cockatoos). (*c*) Representative UV–VIS reflectance spectra for the red feathers of the three species for which HPLC chromatograms are shown in figure 1. See Siefferman & Hill (2003) for these spectrophotometric methods.

4. DISCUSSION

Parrots are a monophyletic but diverse group of nearly 350 species, with over 80% displaying red in their plumage (Forshaw 1977). In this first examination of the variety of colourful pigments present in parrot feathers, we studied 44 parrot species from 27 genera and found that they all use the same set of five lipochromes to colour their feathers red. Our sample spanned each of the three main psittaciform families and included one of the most primitive of all parrots—Pesquet's parrot (*Psittrichas fulgidus*; Smith 1975). Consistent pigment signatures were also found in spite of the fact that we analysed parrots of different age, sex and rearing conditions. These results suggest remarkable conservation of pigmentation systems across parrots. Groups of birds and other animals that colour themselves with red carotenoids, for example, use a wide array of pigments, all of which are never found in any given species (Stradi 1998, 1999).

Red parrot feathers also differ in colour intensity, from the light-pink hue of several cockatoos to the deep red of red lories (*Eos bornea*). We sought to understand the relationship between colour and pigment composition as well as how both covary with the sex or phylogenetic relatedness of parrots. The five psittacofulvins occurred in different ratios in feathers across species, but these ratios were not linked to sex, family or plumage colouration. Instead, it was total pigment concentration that best predicted these variables, with male parrots and parrots from the Loriidae displaying redder and more pigment-laden plumage than females and other parrot families (e.g. cockatoos), respectively. Parrot plumage is not generally recognized as sexually dichromatic (with a few exceptions, such as the Eclectus parrot, *Eclectus roratus*, where females are red and males are green), but rigorous spectrophotometric methods have yielded similar 'cryptic' dichromatism in other avian colour patches (Hunt *et al.* 1998; Mahler & Kempenaers 2002).

The only reports of these pigments in nature are from parrot feathers. We were interested in searching for a potential dietary source of these compounds or an internal anatomical site at which parrots may be constructing these molecules. We sampled blood from birds that were growing their colourful feathers to obtain a record of the pigments assimilated from the diet and/or formed at sites in the body (e.g. the liver) where they are then delivered to feathers for pigmentation. We found that all blood samples lacked psittacofulvins. From this, we conclude that parrots most probably synthesize these straight-chain hydrocarbons *de novo* and do so locally at maturing feather follicles. There are several other lines of evidence that point to a non-dietary origin of these pigments, including (i) the absence of these pigments from diet samples of certain captive parrots (K.J.M., personal observation) and (ii) the ability of parrots to maintain striking plumage colouration in captivity despite tremendous variation in diet (which is not the case for diet-derived carotenoid colouration; reviewed in Stradi *et al.* 2001). Stradi *et al.* (2001) supposed that parrots derive these acyclic polyenal lipochromes either by the addition of acetate units to acetyl CoA or by fatty-acid desaturation. What remains unclear is why parrots are the only group of organisms capable of manufacturing/harbouring these colourants.

Much of the recent work on the evolutionary significance of parrot colouration has focused on the budgerigar (*Melanopsittacus undulatus*), which like many other parrots displays yellow plumage colouration. We set out in this study to characterize yellow pigments from parrot feathers as well, but these have proven more difficult to resolve chromatographically. What is clear from our preliminary work is that, like red psittacofulvins, these yellow pigments are lipid-soluble and produced endogenously, but unlike the red pigments they can fluoresce under UV light. Nonetheless, whether produced by similar or different pathways, both red and yellow pigmentary colours can serve as sexual signals of attractiveness or condition in parrots (Pearn *et al.* 2001; Arnold *et al.* 2002; Masello & Quillfeldt 2003). Having identified the basic set of parrot plumage pigments in the present study, we can now begin to investigate the pathways associated with lipochrome production to determine if they really are as elaborate or costly as some have suspected (Arnold *et al.* 2002).

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