

Ornamental non-carotenoid red feathers of wild burrowing parrots

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Bird plumage colors have the potential to indicate individual quality, condition, health, immunocompetence, or the extent of parental care. Color intensity of feathers has been found to correlate with parameters of individual quality, condition, parental care and breeding success. Psittaciformes are well known for their colorful plumage but the significance of parrot coloration is still poorly understood. Red colors are very common in many parrot species. They are produced by at least four non-carotenoid-based pigments (linear polyenal structure). In the present study, we investigated a collection of red abdominal feathers of a marked population of wild Burrowing Parrots *Cyanoliseus patagonus* in Patagonia, Argentina. The aims of this study were to investigate the ecological significance of the recently described non-carotenoid-based red pigments of Psittaciformes, and the relationships between objectively assessed plumage color and body size, body condition, breeding success and nestling growth in wild Psittaciformes. We found that sexes differed in plumage coloration (sexual dichromatism), that plumage color was a good predictor of female body condition and male size, and we identified the red coloration of the abdominal patch as a signal of individual quality and parental investment.

Key words: breeding success; individual quality; nestling growth; polyene pigments; sexual selection.

Introduction

The evolution of bird coloration is currently an important topic in behavioral ecology. A major focus of current work on color signaling and sexual selection is condition dependence. Recent studies have suggested that particular bird plumage colors have the potential to indicate individual quality, condition, health, immunocompetence, or the extent of parental care (e.g. Fitzpatrick 1998; Perrier *et al.* 2002; Siitari & Huhta 2002; Saks *et al.* 2003). Accordingly, either the color intensity or the extent of the colored feather area have been found to correlate with some parameters of individual quality, condition, parental care, breeding success, etc. (e.g. Ruusila *et al.* 2001; Masello & Quillfeldt 2003a).

Color can be characterized in different ways. The three variables: hue, chroma and value are primarily based on the human perception of color but these variables also reflect physical characteristics of the light reflected by bird plumage (Figuerola *et al.* 1999). The fact that reflectance in the ultraviolet (UV) range of light is not measured using these three variables, is the main objection that has been raised over the use of this method (Bennett *et al.* 1994). Because many bird spe-

cies are tetrachromatic having a fourth single cone type that is sensitive to UV wavelengths (see Bennett & Cuthill 1994; Bowmaker *et al.* 1997; Siitari *et al.* 2002), it might be a problem to ignore UV reflection when one is studying the function and evolution of plumage coloration. There is considerable evidence that many birds use UV cues when making mate choice decisions (see review Cuthill *et al.* 2000). However, as Hunt *et al.* (2001) suggested it is important to consider the role of the UV reflection in conjunction with the rest of the avian visible spectrum. Hill (1998) pointed out that most carotenoid pigments reflect light primarily in the visible spectrum and then, ignoring UV reflection makes little difference in a description of their coloration. As suggested by several studies on House Finches *Carpodacus mexicanus* (e.g. Hill & Montgomerie 1994), if there are no additional reflectance peaks or significant light reflection in the ultraviolet region, then hue,

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chroma and value are a valid way to characterize color (see also Figuerola *et al.* 1999; Senar *et al.* 2002). This might not be valid for other types of plumage that obtain their coloration from structural elements of the feathers or that are pigmented with melanin (see Hill 1998).

A more accurate way of characterizing color is using spectrophotometry (e.g. Bennett & Cuthill 1994; Bennett *et al.* 1994; Perrier *et al.* 2002; Siitari & Huhta 2002; Saks *et al.* 2003). Spectrophotometry objectively characterizes color, but the major obstacle with this technique is the high cost of such equipment and the amount of technical know-how required to use a spectrophotometer to make color measurements.

Psittaciformes are well known for their colorful plumage. Unfortunately, this is probably the main reason why these birds are common pets and have been collected in high numbers from the wild, so endangering many species. Few published studies on the significance of parrot coloration have been carried out (Pearn *et al.* 2001; Arnold *et al.* 2002; Pearn *et al.* 2003). All these studies have been conducted in captive Budgerigars *Melopsittacus undulatus*. However, published studies about the ecological and evolutionary significance of the colorful plumage of wild parrots are still lacking.

Red colors are very common in many parrot species. Stradi *et al.* (2001) found that the red colors of parrots Scarlet Macaws *Ara macao* are produced by at least four non-carotenoid-based pigments (linear polyenal structure). It is thought that these pigments are widespread among Psittaciformes (Stradi pers. comm.), but the ecological and evolutionary importance of this new kind of pigments has not yet been studied.

Burrowing Parrot *Cyanoliseus patagonus* are colonial Psittaciformes. As in Scarlet Macaws, the Burrowing Parrot has a non-carotenoid-based red ornamental coloration (Masello & Quillfeldt 2003a). Burrowing Parrots have a red feather patch in the center of the abdominal region whose extent (surface, length, width) has been identified as a signal of individual quality (Masello & Quillfeldt 2003a).

In the present study, we investigated a collection of red abdominal feathers of a marked population of wild Burrowing Parrots in Patagonia, Argentina. The aims of this study was to investigate the ecological significance of the recently described non-carotenoid-based red pigments of Psittaciformes, and to answer the following questions about Burrowing Parrots: (i) is the red color of adult Burrowing Parrots condition dependent?, (ii) is the red color related to morphological traits of the adult birds?, (iii) is adult red coloration variable between the sexes? and (iv) is the red color of the abdominal patch of Burrowing Parrots a signal of individual quality? and if so, is the red coloration related to nestling growth or breeding success?

Methods

Study species and site

Burrowing Parrots are highly gregarious colonial birds that can form large flocks and roosts, sometimes in excess of 1000 birds. In Argentina, the species occurs from the Andean slopes in the north-west to the Patagonian steppes in the south (Darrieu 1980; Bucher & Rinaldi 1986). Burrowing Parrots generally inhabit open grassland, but are also reported from wooded valleys with cliffs and farmland (Juniper & Parr 1998). The breeding birds occupy the colonies between 1 or 2 months before egg laying and leave the breeding site gradually as the young fledge. Southern populations migrate then to the north, sometimes reaching as far as Uruguay (Bucher & Rodríguez 1986). Burrowing Parrots excavate their own nest burrows by tunneling into the faces of sandstone, limestone or earth cliffs (Leonardi & Oporto 1983). The nesting pairs use burrows that they have dug in previous seasons, but they enlarge the burrows every year. Each burrow is occupied by a single pair. Burrowing Parrots do not use nesting material but rather, deposit their eggs on the sandy bottom of the nest chamber (Mey *et al.* 2002). Burrowing Parrots lay one clutch per breeding season (Masello & Quillfeldt 2002). The female incubates the eggs for approximately 24 days (de Grahl 1985) while the male provides food (Masello *et al.* 2002). Clutch size varied from two to five eggs. The young hatch asynchronously with an interval of 2 days between subsequent nestlings. Nestlings from a brood fledged also asynchronously, with an interval of 2 to 3 days between nestlings (Masello & Quillfeldt 2002). Burrowing Parrots have a socially and genetically monogamous breeding system with intensive biparental care (Lubjuhn *et al.* 2002; Masello *et al.* 2002; Masello & Quillfeldt 2003a). The nestlings remain in the nest for approximately 60 days (Masello & Quillfeldt 2002). After fledging, the young are fed by the adults for approximately 4 months (Westen 1995).

The study was carried out from October 1998 to February 1999 in the largest and most important colony of Burrowing Parrots, located in a sandstone cliff at the Atlantic coast in the province of Río Negro, Patagonia, Argentina. The colony covers 9 km of cliffs (Masello unpubl. data, see also Yorio & Harris 1997). The easternmost kilometer of the colony (41°3'S, 62°48'W) is by far the most densely populated with 6750 active nests (Masello *et al.* 2001; Masello & Quillfeldt 2003b). The habitat in the surroundings of the colony is primarily Patagonian steppe.

The diet of Burrowing Parrots of central Argentina comprises of seeds and fruits, with fruits predominating during the summer (Bucher *et al.* 1987). In the north

of Patagonia, we observed Burrowing Parrots eating during the breeding season seeds of the giant thistle *Carduus marianus*, the thistles *Xanthium spinosum* and *X. kravanilesii*, furthermore seeds of other wild plants such as *Avena fatua*, *Rumex crispus*, and berries of wild shrubs like *Condalia microphylla*. For the study region, Forshaw (1973) mentioned berries of *Empetrum rubrum*, *Lycium salsum* and *Discaria* spp. as part of the Burrowing Parrot diet, and also described the habit of Burrowing Parrots to feed on soft parts of plants. We observed buds and other soft vegetable matter in crop contents of nestlings especially during the first weeks of nestling rearing (November–middle December, J. F. Masello and P. Quillfeldt unpubl. data). Burrowing Parrots can sometimes feed on grain crops, but the damage to agriculture is a locally limited phenomenon (Bucher 1984; Bucher & Rinaldi 1986).

Study methods

According to accessibility, 79 nests were selected and marked in the densest sector of the colony as part of an ongoing study of the breeding behavior of the species. Nests were inspected every 5 days by climbing the cliff face. Burrowing Parrots tend to desert in response of disturbance during the incubation period (de Grahl 1985) and during the first week after hatching (Masello *et al.* 2002). In order to reduce observer influence, nests were not disturbed until approximately 5 days after the estimated hatching date of the last nestling of a clutch. Clutch size was determined by visual inspection of the nests using a torch, and without capturing the adults. At the time of the first measurement, when nestlings were still clearly different sizes, the hatching rank was determined, and nestlings were individually marked. Nestlings lighter than 100 g were first marked with nail enamel on their claws. When the nestlings reached 100 g, they were ringed with numbered steel rings.

When one or two adults were present during nest control, they were captured, ringed with numbered steel rings and measured. During the breeding season 1998–1999, a total of 46 adults were captured at the nest: 22 males and 24 females.

Blood samples (approximately 50 μ l) of Burrowing Parrots were taken by puncture of the brachial vein. Samples were immediately suspended in 70% ethanol (Arctander 1988) and stored at 4°C for 4 to 12 weeks and thereafter at –20°C until processing. DNA was extracted using standard procedures modified according to Miller *et al.* (1988; for additional details see Lubjuhn & Sauer 1999). Adult Burrowing Parrots were sexed using polymerase chain reaction (PCR) amplification of a highly conserved W-linked gene according to Griffiths *et al.* (1996), modified for Biometra-Thermocycler T Gradient (Biometra, Goettingen,

Germany). PCR conditions were adjusted and PCR products digested with *Hae* III overnight. Fragments were separated using agarose gel electrophoresis (gel size 7 \times 10 cm, 3% agarose, 9 V cm⁻¹).

The Servicio Meteorológico Nacional of Argentina provided precipitation data. For information on La Niña event 1998 see Legeckis (1998).

Breeding and morphometric parameters

The following parameters of breeding success were recorded: (i) clutch size, the number of eggs laid per nest, (ii) number of eggs hatched, (iii) brood size, at the time of hatching of the last nestling, and 10, 20, 30, 40 and 50 days after, and (iv) number of fledglings.

Five morphometric parameters of the nestlings and attending adults were recorded each time the nest was inspected: (i) Body mass, using a digital balance to the nearest 1 g, (ii) tarsus length and (iii) bill length, using calipers to the nearest 0.1 mm, (iv) wing length, the distance from the anterior surface of the radio carpal joint to the tip of the longest primary, using a wing rule to the nearest 1 mm, and (v) length of the internal tail feather using a feather rule to the nearest 1 mm.

Pre-fledging measurements of the nestlings were taken the last time they were found in the nests (i.e. 1–4 days before fledging). To ensure that only true pre-fledging data were included in the analyses, only data of nestlings older than 55 days were included.

Individual wing and tail growth rates of nestlings were determined for the linear phase of the growth curves (see Masello & Quillfeldt 2002). The beginning and end of the approximately linear phase of both wing growth and tail growth were defined in terms of wing and tail lengths. For each nestling, growth rates were calculated using the time elapsed between these measurements. Tarsus growth rate could not be determined because most of its linear growth phase occurs during the first 10 days after hatching. Observations were avoided during these 10 days because of the possibility of adult nest abandonment.

The ages of nestlings whose hatching dates were not known were calculated from a growth curve for the bill length of known-age nestlings as described in Masello & Quillfeldt (2002).

Feather samples and color assessment

The first time the adults were captured in the nest, one feather of the center of the abdominal red patch was sampled for further analysis. In order to investigate the feathers color objectively, we employed a modified version of the RGB (red, green blue) method of Gerald *et al.* (2001). This method uses digital images of the feathers and Adobe Photoshop, (San Jose, California, USA) a software application that manipulates images

and customizes color. Digital images maintain the true integrity of color while with the use of Adobe Photoshop it is possible to characterize color by specifying numeric measures of the three-color components: hue, value, and chroma. Hue refers to the colloquial color term, and is measured by assessing pixel brightness in the three-color channels: red, green, and blue. Channel measures are graphically represented in a color diagram. Hue units are grads ($^{\circ}$). Value, also known as brightness, refers to the relative darkness lightness⁻¹ in the color sample (1% = dark, 100% = light). Chroma indicates the degree to which the sample is saturated with the hue in question (amount of hue relative to white, 100% = saturated).

To assess color we first obtained digital images of the feathers using a scanner with determined properties in Adobe Photoshop (resolution: 200 dpi, contrast: 0%, descreen: none, filter: none, shadow: 0, highlight: 255, midtone: 1.00, exposure: 0%). The scanning of all feathers was carried out in a single session in order to standardize conditions. Feather images were saved as tiff files and magnified up to 800% to improve detection of color variability and image resolution and to facilitate pixel selection. Hue, value and chroma were measured in 10 pixels located in an horizontal line 4 mm from the distal tip of the red feather, using the 'Info' function of Adobe Photoshop and selecting the HBS (hue, brightness, saturation) palette option. The mean hue, chroma and value were then calculated for each individual. Only the distal region of the red feathers of the abdominal patch of Burrowing Parrots is in fact red, while the medial region is increasingly yellow, and the basal region is greyish. The region we measured (4 mm of the distal tip) was chosen because it assured that the measurement is taken in the center of the red zone. We measured the width of the red region (*d*) as the distance between the distal tip of the feather and the first pixel that reached or exceeded a hue of 25 $^{\circ}$.

Statistical procedures

As body mass is partly the result of structural body size and does not necessarily reflect the quantity of body reserves, we scaled body mass to body size as a condition index. Males and females were considered separately because of the size dimorphism previously found in Burrowing Parrots (Masello & Quillfeldt 2003a). To determine body condition, stepwise linear regressions of male and female body mass as dependent variables with wing, tarsus and bill length as predictors, were carried out. The best fit was achieved with the following regressions: expected female body mass = 11.23 * tarsus length - 64.05 ($n = 64$, $R = 0.447$, $F = 15.195$, $P < 0.001$), expected male body mass = 8.54 * bill length + 41.71 ($n = 48$, $R = 0.318$, $F = 6.396$, $P = 0.014$).

Body condition was then calculated as the ratio between observed body mass and expected body mass (see also Masello & Quillfeldt 2003a).

All analyses of nestling growth included only nestlings that survived to fledging. In order to exclude the influence of hatching order, analyses of growth parameters of nestlings were carried out on first hatched nestlings. Further details of the influence of hatching order are discussed elsewhere (Masello 2002).

Data were analysed using Sigma Stat 2.03 (San Rafael, California, USA) (Jandel Scientific 1995) and SPSS 10.0 (SPSS Inc. 1999, Chicago Illinois, USA). Throughout this study all means are given \pm SE. The significance level used is $P < 0.05$. Note that sample sizes for different analyses varied as not all measurements could be taken on all birds.

Results

The relationships between four color parameters of the red feathers of the abdominal patch of adult Burrowing Parrots (hue, chroma, value, and extent of the red region of the feathers) and nine adult condition and morphological parameters (body condition, mass, wing, tarsus, and bill length, bill width, surface, length and width of the red abdominal patch) were studied using Pearson correlations (Table 1). Also using Pearson correlations, the relationships between the mentioned color parameters of adult Burrowing Parrots and seven parameters of breeding success (hatching date of first nestlings, clutch size, number of eggs hatched, brood size 30 and 40 days after the time of hatching of the last nestling, number of nestlings dead in the nest, and number of fledglings; Tables 2 & 3) and nine parameters of growth of first hatched nestlings (peak mass, pre fledging mass, pre fledging wing length, pre fledging tarsus length, pre fledging bill length, pre fledging tail length, maximum tarsus, wing growth and tail growth) were studied (Tables 4 & 5).

Color parameters of males and females

Male and female Burrowing Parrots showed differences in hue and in the extent of the red region of the feathers of the red abdominal patch. Male feathers were redder (i.e. lower hue) than females feathers (paired samples test $t = 3.724$, d.f. 17, $P = 0.002$): while male feathers had a mean hue of $19.4 \pm 0.6^{\circ}$ (range 13.9–24, $n = 21$) females had a mean hue of 23.0 ± 0.8 (range 16.7–34.2, $n = 22$). The red region of male feathers was larger than that of female feathers (paired samples test $t = 3.478$, d.f. 17, $P = 0.003$). The mean width of the red region was 0.68 ± 0.03 cm (range 0.41–0.87 cm, $n = 21$) for male feathers and 0.56 ± 0.04 cm (range 0.19–0.91 cm,

Table 1 Pearson correlations between four color parameters of the red feathers of the abdominal patch of adult Burrowing Parrots, adult condition, and adult morphological parameters

Parameter	Sex	<i>n</i>		Hue	Chroma	Value	Extent of red
Body condition	Females	22	<i>R</i>	-0.384	-0.217	0.525	0.579
			<i>P</i>	0.078	0.333	0.012	0.005
	Males	21	<i>R</i>	-0.00006	0.154	-0.303	-0.190
			<i>P</i>	1.000	0.506	0.182	0.410
Body mass	Females	22	<i>R</i>	-0.401	-0.340	0.443	0.543
			<i>P</i>	0.064	0.121	0.039	0.009
	Males	21	<i>R</i>	-0.039	0.117	-0.363	-0.253
			<i>P</i>	0.866	0.613	0.106	0.268
Wing length	Females	22	<i>R</i>	-0.139	0.086	0.301	0.316
			<i>P</i>	0.537	0.705	0.174	0.152
	Males	21	<i>R</i>	-0.273	-0.256	0.373	-0.019
			<i>P</i>	0.232	0.262	0.095	0.936
Tarsus length	Females	22	<i>R</i>	-0.198	-0.373	-0.004	0.105
			<i>P</i>	0.378	0.088	0.985	0.643
	Males	21	<i>R</i>	-0.663	-0.435	0.053	0.312
			<i>P</i>	0.001	0.049	0.820	0.169
Bill length	Females	21	<i>R</i>	-0.005	-0.290	-0.082	-0.366
			<i>P</i>	0.983	0.202	0.724	0.103
	Males	21	<i>R</i>	-0.187	-0.146	-0.227	-0.229
			<i>P</i>	0.417	0.527	0.322	0.318
Bill width	Females	22	<i>R</i>	-0.146	-0.168	0.087	-0.0522
			<i>P</i>	0.518	0.454	0.700	0.818
	Males	21	<i>R</i>	0.122	-0.121	0.150	0.070
			<i>P</i>	0.600	0.603	0.515	0.764
Red patch surface	Females	22	<i>R</i>	-0.173	0.095	0.243	0.359
			<i>P</i>	0.442	0.674	0.277	0.100
	Males	21	<i>R</i>	0.011	-0.291	0.297	0.091
			<i>P</i>	0.964	0.201	0.191	0.696
Red patch length	Females	22	<i>R</i>	-0.086	-0.107	-0.004	0.074
			<i>P</i>	0.705	0.635	0.984	0.744
	Males	21	<i>R</i>	-0.032	0.246	0.021	0.016
			<i>P</i>	0.892	0.282	0.927	0.945
Red patch width	Females	22	<i>R</i>	-0.185	0.267	0.276	0.378
			<i>P</i>	0.410	0.230	0.213	0.083
	Males	21	<i>R</i>	0.050	-0.350	0.212	0.043
			<i>P</i>	0.829	0.120	0.357	0.853

$n = 22$) for female feathers. Mean chroma for males was $26.1 \pm 1.0\%$ (range 18.8–32.2%, $n = 21$) while for females was $27.1 \pm 0.9\%$ (range 20.2–35.8%, $n = 21$). Mean value for males was $95.6 \pm 0.4\%$ (range 91.4–97.6%, $n = 21$) while for females was $96.1 \pm 0.2\%$ (range 93.1–97.8%, $n = 21$). No significant correlations have been found for hue, chroma, value, and the extent of the red region of the feathers, between the male and the female of a pair (for hue, $R = 0.0423$, $P = 0.868$, $n = 18$; for chroma, $R = 0.400$, $P = 0.1$, $n = 18$; for value, $R = 0.324$, $P = 0.190$, $n = 18$; for extent of the red region of the feathers, $R = 0.242$, $P = 0.333$, $n = 18$).

Feathers with lower hue had larger red regions. There was a statistically significant negative correlation between the hue of the red feathers and the extent of the red region: $R = -0.649$, $P < 0.001$, $n = 43$ feathers.

The extent of the red region of the feathers of females strongly correlated with body condition and mass of

females (Table 1). Value (brightness) of female feathers also correlated with body condition and mass (Table 1). Some color parameters of male feathers correlated with morphological measurements of males. The hue of male feathers negatively correlated with tarsus length, while chroma (saturation) correlated with tarsus length and tail length of male Burrowing Parrots (Table 1).

Color parameters of adults and nestling growth

Some color parameters of the red abdominal feathers of adult Burrowing Parrots correlated with parameters of nestling growth (Table 2). The extent of the red region of the feathers of males correlated with the pre-fledging body mass of nestlings. Male Burrowing Parrots with larger red region had first hatched nestlings with the highest pre-fledging masses (Fig. 1a, Table 2). The hue of the red feathers negatively correlated with

Table 2 Pearson correlations between four color parameters of the red feathers of the abdominal patch of male Burrowing Parrots, and nine parameters of growth of first hatched nestlings

Growth parameters	<i>n</i>		Hue	Chroma	Value	Extent of red
Peak mass	17	<i>R</i>	−0.251	0.128	−0.127	0.141
		<i>P</i>	0.331	0.624	0.627	0.588
Pre-fledging mass	15	<i>R</i>	−0.230	−0.372	0.128	0.579
		<i>P</i>	0.410	0.173	0.649	0.024
Pre-fledging wing length	15	<i>R</i>	−0.076	−0.104	−0.204	−0.025
		<i>P</i>	0.787	0.712	0.466	0.93
Pre-fledging tarsus length	15	<i>R</i>	−0.248	−0.347	−0.198	0.429
		<i>P</i>	0.372	0.206	0.478	0.110
Pre-fledging bill length	15	<i>R</i>	−0.010	−0.391	0.181	0.152
		<i>P</i>	0.972	0.149	0.519	0.589
Pre-fledging tail length	15	<i>R</i>	0.066	−0.067	0.379	−0.237
		<i>P</i>	0.814	0.813	0.163	0.396
Maximum tarsus	15	<i>R</i>	−0.310	−0.140	−0.005	0.446
		<i>P</i>	0.261	0.619	0.985	0.095
Wing growth	12	<i>R</i>	−0.660	−0.477	−0.100	−0.206
		<i>P</i>	0.019	0.117	0.757	0.521
Tail growth	14	<i>R</i>	−0.037	−0.085	−0.173	−0.247
		<i>P</i>	0.899	0.772	0.554	0.396

Table 3 Pearson correlations between four color parameters of the red feathers of the abdominal patch of female Burrowing Parrots, and nine parameters of growth of first hatched nestlings

Growth parameters	<i>n</i>		Hue	Chroma	Value	Extent of red
Peak mass	17	<i>R</i>	−0.100	−0.104	0.100	0.245
		<i>P</i>	0.704	0.691	0.702	0.343
Pre-fledging mass	15	<i>R</i>	−0.232	−0.184	0.352	0.303
		<i>P</i>	0.405	0.512	0.198	0.272
Pre-fledging wing length	15	<i>R</i>	0.064	0.352	−0.119	−0.094
		<i>P</i>	0.821	0.198	0.671	0.739
Pre-fledging tarsus length	15	<i>R</i>	−0.063	0.159	−0.002	0.097
		<i>P</i>	0.823	0.571	0.996	0.732
Pre-fledging bill length	15	<i>R</i>	−0.173	−0.380	0.172	−0.041
		<i>P</i>	0.537	0.162	0.540	0.885
Pre-fledging tail length	15	<i>R</i>	−0.431	−0.264	−0.093	−0.053
		<i>P</i>	0.109	0.342	0.740	0.852
Maximum tarsus	14	<i>R</i>	−0.010	−0.267	0.232	−0.086
		<i>P</i>	0.973	0.356	0.424	0.771
Wing growth	13	<i>R</i>	0.058	−0.159	0.155	0.071
		<i>P</i>	0.85	0.605	0.612	0.818
Tail growth	14	<i>R</i>	0.110	−0.103	0.110	−0.075
		<i>P</i>	0.709	0.727	0.708	0.800

the wing growth of nestlings. The wings of the first hatched nestlings of males with redder feathers (i.e. lower hue) grew faster (Fig. 1c, Table 2). No correlations have been found between color parameters of the red abdominal feathers of female Burrowing Parrots and parameters of nestling growth (Table 3).

Color parameters of adults and breeding success

Some color parameters of the red abdominal feathers of female Burrowing Parrots showed relationships with

parameters of breeding success (Table 4). The hue of female feathers correlated with clutch size. Females with redder feathers (i.e. lower hue) had smaller clutches (Fig. 2a, Table 4). Chroma correlated with hatching success. Females with more saturated feathers hatched more eggs (Fig. 2c, Table 4). The extent of the red region of the feathers of females correlated with the brood size 30 and 40 days after the hatching of the last nestling of a brood (Fig. 2d). Female Burrowing Parrots with larger red region had smaller broods (Table 4). No correlations have been found between

Table 4 Pearson correlations between four color parameters of the red feathers of the abdominal patch of female Burrowing Parrots, and parameters of breeding success

Parameters of breeding success	<i>n</i>		Hue	Chroma	Value	Extent of red
Hatching date of first nestlings	21	<i>R</i>	−0.134	0.220	−0.003	0.219
		<i>P</i>	0.562	0.339	0.991	0.34
Clutch size	19	<i>R</i>	0.551	0.140	0.160	−0.296
		<i>P</i>	0.0144	0.568	0.512	0.219
No. eggs hatched	19	<i>R</i>	0.311	0.460	0.064	−0.295
		<i>P</i>	0.195	0.046	0.794	0.221
Brood size <i>t</i> = 30	16	<i>R</i>	0.311	0.086	−0.161	−0.723
		<i>P</i>	0.241	0.753	0.55	0.002
Brood size <i>t</i> = 40	16	<i>R</i>	0.348	−0.063	0.122	−0.643
		<i>P</i>	0.186	0.818	0.654	0.007
No. nestlings dead in the nest	19	<i>R</i>	0.265	0.449	0.152	0.155
		<i>P</i>	0.273	0.054	0.534	0.526
No. fledglings	22	<i>R</i>	−0.013	−0.162	−0.074	−0.246
		<i>P</i>	0.954	0.471	0.745	0.270

Brood size *t* = 30 and brood size *t* = 40 are respectively, brood size 30 and 40 days after the time of hatching of the last nestling.

Table 5 Pearson correlations between four color parameters of the red feathers of the abdominal patch of male Burrowing Parrots, and parameters of breeding success

Parameters of breeding success	<i>n</i>		Hue	Chroma	Value	Extent of red
Hatching date of first nestlings	20	<i>R</i>	0.222	0.148	0.244	−0.127
		<i>P</i>	0.348	0.533	0.300	0.593
Clutch size	18	<i>R</i>	0.231	0.061	−0.350	−0.313
		<i>P</i>	0.356	0.811	0.155	0.206
No. eggs hatched	18	<i>R</i>	−0.068	0.064	−0.118	0.143
		<i>P</i>	0.788	0.802	0.641	0.571
Brood size <i>t</i> = 30	16	<i>R</i>	0.078	0.017	−0.101	−0.138
		<i>P</i>	0.775	0.951	0.710	0.611
Brood size <i>t</i> = 40	16	<i>R</i>	0.247	0.177	−0.213	−0.215
		<i>P</i>	0.357	0.511	0.429	0.425
No. nestlings dead in the nest	18	<i>R</i>	0.206	0.372	0.164	−0.064
		<i>P</i>	0.412	0.128	0.516	0.802
No. fledglings	21	<i>R</i>	−0.022	−0.184	−0.307	−0.008
		<i>P</i>	0.924	0.426	0.176	0.973

Brood size *t* = 30 and brood size *t* = 40 are respectively, brood size 30 and 40 days after the time of hatching of the last nestling

color parameters of the red abdominal feathers of male Burrowing Parrots and parameters of breeding success (Table 5).

Discussion

This paper reports color parameters of the plumage of genetically sexed adult Burrowing Parrots and, to our knowledge, is the first study of the relationships between objectively assessed plumage color and body size, body condition, breeding success and nestling growth in wild Psittaciformes. It is also the first study of the ecological significance of the newly described non-carotenoid-based pigments (linear polyenal structure, Stradi *et al.* 2001) responsible of the red coloration of the plumage of Psittaciformes. We found that sexes

differed in plumage coloration, that plumage color was a good predictor of female condition and male size, and we identified the red coloration of the abdominal patch of adult Burrowing Parrots as a signal of individual quality and parental investment.

Color variation between sexes

Although Burrowing Parrots are not obviously dichromatic, we observed differences between the sexes in hue and in the extent of the red region of the abdominal patch, males being highly significantly redder and with larger red areas than females (Table 1).

Sexual dichromatism is a common phenomenon in birds, males being in many species gaudily colored, while females show few or no color ornaments. Sexual dichromatism has often been used as a measure of the

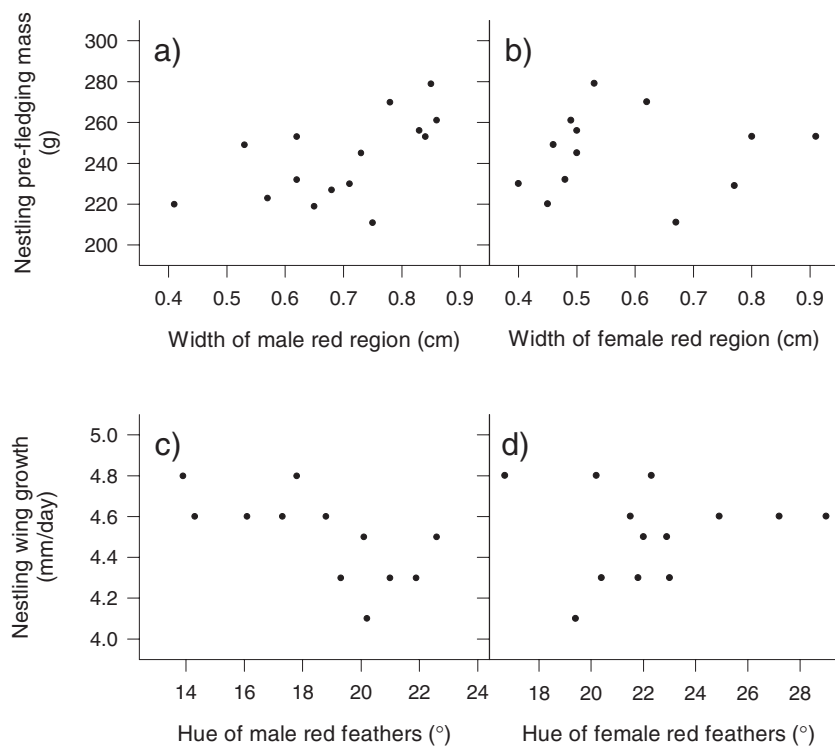


Fig. 1. Relationship for color parameters of the red feathers of the abdominal patch of adult Burrowing Parrots and parameters of growth of first hatched nestlings: width of the red region of the red feather of (a) males and (b) females and pre-fledging mass of nestlings; mean hue of the red feathers of (c) males and (d) females and nestling wing growth (hue = 14 is more red than hue = 24).

intensity of sexual selection (e.g. Møller & Birkhead 1994; Owens & Hartley 1998). In many polygamous birds, the more competitive sex develops more ornate than the choosy sex, whereas large differences between the sexes in parental care lead to the development of more cryptic plumage in the caring sex. Monogamous species usually are less dichromatic. Thus, the variation in the extent of sexual dimorphism among bird species is traditionally attributed to differences in social mating system. Large plumage dichromatism is usually associated with high levels of extra-bond paternity (Møller & Birkhead 1994; Owens & Hartley 1998). But genetically monogamous species like Burrowing Parrots (Masello *et al.* 2002) should display little sexual dichromatism. This has been found in the present study, indicating mutual mate choice, which is consistent with the monogamic breeding system and biparental care commonly observed in Psittaciformes (Collar 1997).

A comparable result was found in a previously published study on Burrowing Parrots (Masello & Quillfeldt 2003a), where sexual dimorphism was analysed. Burrowing Parrots are slightly dimorphic, males being approximately 5% bigger than females. Slight sexual dimorphism is usually associated with biparental care (Owens & Hartley 1998).

Plumage color, female condition and male size

In the present study we found that female Burrowing Parrots with larger red region in the feathers of the

abdominal patch had highly significantly higher body conditions and body masses, and that redder males had highly significantly longer tarsus (a measurement of structural size) (Table 1). This suggests that the red coloration of the abdominal patch of Burrowing Parrots might reflect individual quality in this species, as it was found for the size of the abdominal patch in a previously published study (Masello & Quillfeldt 2003a).

Many bird species advertise their quality with secondary sexual characteristics. The topic has been intensive investigated in the last two decades and at the present, there is evidence that structural coloration of feathers, melanin- and carotenoid-based plumage colors operate in sexual selection (e.g. Andersson 1994; Fitzpatrick 1998; Badyaev & Hill 2000). Carotenoid-based plumage coloration has been found to be a condition dependent trait indicating the nutritional status and foraging ability of the bearer (e.g. Badyaev & Hill 2000). Evidence of condition dependence of structural (e.g. Fitzpatrick 1998; Doucet 2002) and melanin-based (e.g. Siitari & Huhta 2002) plumage coloration has recently been found. A correlation between male coloration and tarsus length has also been found in the Ruff *Philomachus pugnax* (Höglund & Lundberg 1989), but this relationship was not clearly linked with individual quality.

The red colors of parrots are produced by at least four non-carotenoid-based pigments with a linear polyenal structure and, unlike carotenoids, they did not depend on dietary input of precursors (Nemésio

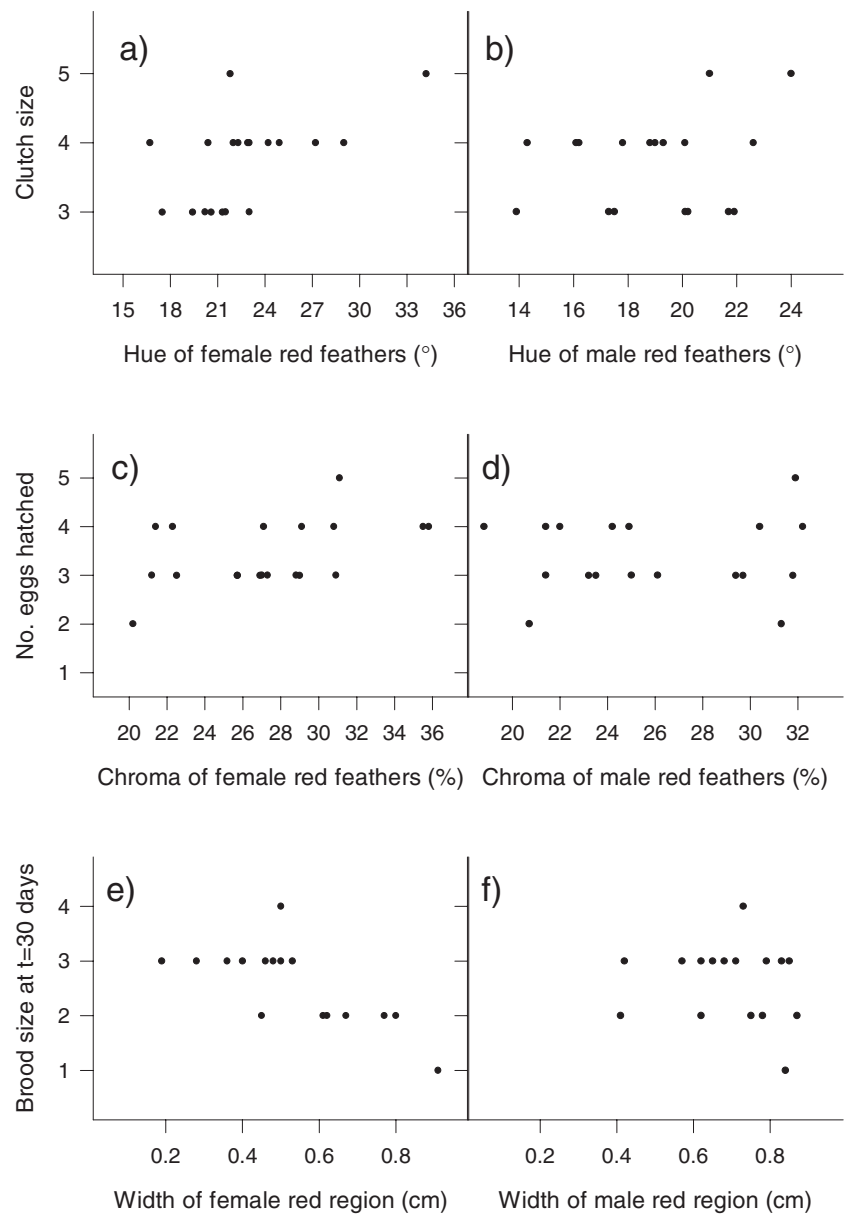


Fig. 2. Relationships for color parameters of the red feathers of the abdominal patch of female adult Burrowing Parrots and parameters of breeding success and growth of first hatched nestlings: mean hue of the red feathers of (a) females and (b) males and clutch size; mean chroma of the red feathers of (c) females and (d) males and the number of eggs hatched; width of the red region of the red feathers of (e) females and (f) males and brood size 30 days after the hatching of the last nestling.

2001; Stradi *et al.* 2001). If the polyene pigment-based plumage is an honest signal, it should be costly to produce. But the mechanisms and costs of the production of the involved non-carotenoid pigment remain to be identified.

Plumage color of adults and nestling growth

We found that male Burrowing Parrots with larger red region in the feathers of the abdominal patch fledged nestlings with higher pre-fledging body masses (Fig. 1a, Table 2), and that redder males had nestlings which made their wings grow faster (Fig. 1c, Table 2). In other words, more ornamented male Burrowing Parrots had larger fledglings, which also grew faster, than did

nestlings of less ornamented males. A similar result was obtained in a previous study on Burrowing Parrots, when only the size of the ornamental red patch of adult and nestling growth, but not its color, was considered (Masello & Quillfeldt 2003a).

Plumage coloration is an indicator of parental quality, a trait that influences immediate reproductive success (Hill 1998). Nestlings that are larger at fledging have a better chance to survive the critical period of high juvenile mortality that Burrowing Parrots have to confront immediately after fledging (Masello & Quillfeldt 2002). Thus, more ornamented male Burrowing Parrots had a greater probability of breeding success than less ornamented males. Relationships between parental quality, expressed in terms of ornamental

feathers, and nestling growth have so far only been studied in the Blue Tit *Parus caeruleus* (Senar *et al.* 2002), but to our knowledge, not in Psittaciformes.

Whether male Burrowing Parrots plumage coloration acts as a signal to prospective partners for direct (e.g. good parents) or indirect (e.g. good genes) benefits in sexual selection (Andersson 1994) remains uncertain. Cross-fostering experiments and data of more years of different environmental conditions would be necessary in order to answer this question.

Plumage color of adults and breeding success

During the months before and during the studied breeding season, a severe drought occurred in the region of the studied Burrowing Parrot colony as a consequence of a strong La Niña event (see Spear *et al.* 2001). The study site is located in Patagonia on the Atlantic coast of southern South America, a region experiencing dry conditions during the La Niña phase of the El Niño Southern Oscillation phenomenon (ENSO, see Holmgren *et al.* 2001). At the beginning of the breeding season, in October 1998, only 5% of the long-term mean of rain fell (Masello & Quillfeldt 2003a). Precipitation is the main limiting factor of primary production in arid and semi-arid zones like the Patagonian steppe (see Golluscio *et al.* 1998). The strong La Niña event initiated in May 1998 caused an important food shortage. Most of the crops in the region frequented by the parrots failed, and large sectors of the steppe burned as a consequence of the dry conditions (J. F. Masello pers. observ.). During these unfavorable conditions of La Niña only 65% of the hatched nestlings survived to fledging (Masello & Quillfeldt 2003a) while during an average precipitation year (1999–2000) 91% of the hatched nestlings fledged (Masello & Quillfeldt 2002). No predation of nestlings occurred in the nests, thus nestling mortality was entirely due to starvation (Masello & Quillfeldt 2002, 2003a).

We found that redder female Burrowing Parrots had smaller clutches (Fig. 2a, Table 4). Female Burrowing Parrots with larger red regions in the feathers of the abdominal patch had highly significantly smaller brood sizes 30 and 40 days after the hatching of the last nestling of a brood (Fig. 2d, Table 4). These results suggest that more ornamented female Burrowing Parrots invested less heavily in current reproduction than less ornamented females, in the study season of unfavorable conditions. The allocation of energy between reproduction and self-maintenance has been recognized as one of the most important trade-offs affecting variation in reproductive effort (Stearns 1992). Heavy investment in current offspring can be associated with reduced chances of survival and future reproductive success.

Therefore we would expect a trade-off between the resources allocated to offspring and the resources used for adult body maintenance in any breeding season, resulting in parent-offspring conflict when the resources are limited (Stearns 1989). Animals with a short reproductive life-span are expected to invest more heavily in current offspring, while those with a long reproductive life-span should allocate more resources to their own survival and thus to future offspring. Psittaciformes are long-lived birds, and adults should therefore use scarce resources mainly for body maintenance. In contrast to females, males did not show a trade-off between ornamentation and breeding success. A possible explanation can be found in mate choice. If male breeding partners are chosen by females, then they cannot afford to reduce the expression of the ornamental signal even under adverse environmental conditions. An equivalent scenario has been found in a previous study on Burrowing Parrots, when only the size of the ornamental red patch of adult and nestling growth, but not its color, was considered (Masello & Quillfeldt 2003a).

At present, our data do not allow us to conclude why more ornamented females invested less heavily in the present offspring than less ornamented females. Data of several breeding seasons, which include good and poor foraging conditions, will be necessary.

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