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The effect of coccidial infection on iridescent plumage coloration in wild turkeys

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Wild turkeys, *Meleagris gallopavo*, are among the most ornamented birds in North America, displaying vividly coloured fleshy ornaments on their heads and bright, iridescent structural coloration in their plumage. We investigated the effect of experimental inoculation with coccidian parasites on the expression of iridescent structural coloration in yearling male turkeys. Prior to moult of ornamental feathers, we assigned turkeys to three experimental groups: we maintained six turkeys free of coccidial infection, inoculated four turkeys with a single species of coccidial oocysts, and inoculated six turkeys with multiple species of coccidial oocysts. We used reflectance spectrometry to quantify the plumage coloration of wing covert and breast feathers in the breeding plumage of males in each treatment protocol. We found significant treatment-based variation in the iridescent plumage coloration of yearling male turkeys such that infected males showed proportionately less UV reflectance in their wing covert and breast feathers and had duller breast feathers. This is the first experimental evidence that parasites can suppress the expression of structural plumage coloration, and our findings suggest that, in wild turkeys, iridescent coloration could serve as a condition-dependent signal of male health.

The brightly coloured plumages of birds are among the best known and most intensively studied ornamental traits. Until recently, brightly coloured plumage was regarded as a single class of ornament. Comparative studies would frequently score 'overall brightness' of males across families and orders of birds with no distinction between colours that resulted from different mechanisms (e.g. Hamilton & Zuk 1982; Read 1987). It is becoming increasingly clear, however, that colour ornaments produced by different mechanisms can serve as fundamentally different types of displays, each with a distinct signal content (e.g. Owens & Hartley 1998; Badyaev & Hill 2000).

For most species of birds, three primary mechanisms are responsible for bright feather coloration (Fox & Vevers 1960; Brush 1978). Two of these mechanisms involve pigmentation. Carotenoid pigments can be deposited in feathers to make them yellow/orange/red, and melanin pigments can make feathers black/brown/rusty (Brush 1978). Alternatively, a feather can be brightly coloured if its microstructure differentially absorbs and reflects light of different wavelengths (Dyck 1976; Prum 1999). This type of ornamentation, termed structural coloration, can be separated into two categories. Feather microstructure can produce a colour display that is relatively constant regardless of the angle at which the feather is viewed. Alternatively, feather microstructure can produce a colour display that changes markedly in appearance depending on the angle between the light source, the feather surface, and the observer (Dyck 1976; Prum 1999). These latter sorts of colour displays are called iridescent, and iridescent displays account for some of the most striking coloration in birds, including the brilliant blues of peacocks (*Pavo* spp.; see Zi et al. 2003), the purple sheen of starling feathers (*Sturnus vulgaris*; e.g. Cuthill et al. 1999), and the blazing gorgets of many hummingbird species (e.g. Bleiweiss 1994).

The signal content of colour displays has been a major focus of current research in behavioural ecology. Extensive work on carotenoid-based colour displays in birds has shown that this type of ornamental coloration is condition dependent (Hill 2002). Expression of carotenoid coloration is a function of a bird's access to specific carotenoid pigments (e.g. Hill 1992; McGraw et al. 2001;

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Blount et al. 2003), access to good nutrition (Hill 2000), and history of infection by specific parasites (Thompson et al. 1997; Brawner et al. 2000; McGraw & Hill 2000). In contrast, there is mounting evidence that expression of melanin pigmentation is relatively insensitive to parasite infection and nutritional condition (McGraw & Hill 2000; McGraw et al. 2002, 2003). Instead, expression of melanin pigments seems to relate to the social status of the individual (Senar 1999; McGraw et al. 2003).

Fewer studies have considered the role of environmental challenges in determining expression of structural plumage coloration. In blue grosbeaks, *Passerina caerulea* (Keyser & Hill 1999) and blue-black grassquits, *Volatinia jacarina* (Doucet 2002), there is a significant relationship between the rate at which males grow their feathers, which is constrained by nutritional condition (Grubb 1991; Hill & Montgomerie 1994), and the brightness of structural plumage displays. In a study of brown-headed cowbirds, *Molothrus ater*, captive males that were subjected to periods of fasting during moult, which created nutritional stress, grew duller iridescent body plumage than males not subjected to fasting (McGraw et al. 2002). These studies suggest that expression of structural coloration, like carotenoid coloration, may be dependent on nutritional condition during moult. Although two correlational field studies suggest that structural plumage coloration may be influenced by parasite load (Harper 1999; Doucet & Montgomerie 2003), the effect of parasites on the expression of structural plumage coloration remains to be tested experimentally in any species.

We studied the effect of coccidial infection on the expression of iridescent coloration in the feathers of male wild turkeys, *Meleagris gallopavo*. Wild turkeys are among the most highly ornamented birds in North America. They have brightly coloured fleshy ornaments on their heads and necks that are used in female mate choice and male–male competition (Buchholz 1995, 1997, 2004), and the size of these ornaments is negatively influenced by coccidial infection (Buchholz 1995). Wild turkeys also have elongated tail plumes and display striking iridescent green/copper contour feathers and purplish wing bars and tail covert spots. Although the signal function of the iridescent plumage of wild turkeys has not been investigated, iridescent plumage coloration appears to be sexually selected in this species, as this striking visual display is most prominent in the plumage of males. When males court, they orient their iridescent feathers towards the hen. The contour feathers of the breast are erected and vibrate as the male struts past the female. The male's wings are spread downward so that the coverts are more visible as the male drags his primaries on the ground. Dragging of the primaries produces a scraping sound that might draw the hen's attention to the wing coverts. The banded tail of the male pivots so that it is oriented towards the hen as the male passes her. Breast and wing feathering would also be apparent to other males during intrasexual battles (Healy 1992).

We conducted an experimental test of the effect of parasites on iridescent colour display. Yearling male wild turkeys were randomly assigned to one of three experimental groups: one group maintained free of coccidian parasites, a second group inoculated with a single species of coccidian parasite, and a third group inoculated with multiple species of coccidian parasites. Several months after the acute infection, males underwent moult into their breeding plumage and we used reflectance spectrometry to investigate the spectral properties of the iridescent breast and wing covert feathers. We predicted that if iridescent coloration in male wild turkeys serves as a signal of parasite load, then males infected with coccidian parasites would grow less colourful feathers than males maintained free of infection.

METHODS

Rearing Conditions

Wild turkeys were hatched from the artificially incubated eggs of 15 male–female pairs housed at the Avian Research Facility at the University of Mississippi Field Station. Routine faecal sampling showed coccidia to be absent in the breeder colony. The hatchlings were reared indoors in steam-cleaned, wire-floored, heated poultry brooders. For the first 2 weeks they were fed a gamebird 'starter' ration ad libitum and thereafter were fed gamebird 'developer' feed that was limited to the amount that they could consume in 4 h. When males were isolated (see below) they were fed an amount equivalent to three times their average resting metabolic rate at room temperature (Buchholz 1996) to simulate the energy intake of wild poults obtaining their own food. Water was available ad libitum. Individuals from different parents were distributed randomly among treatment groups, so effects of parentage were randomized with respect to experimental treatment.

Infection Procedures

At 4–6 weeks of age, the wild turkey poults were weighed and assigned at random in equal numbers ($N = 14$) to one of three treatment groups: single infection, mixed infection, control. Birds assigned to different treatment groups were kept in separate cages. Assignment to treatment groups was adjusted so that each treatment group had similar means and ranges of body masses (single: 392 g, range 240–610; mixed: 380 g, range 200–610; control: 391 g, range 200–600). The sexes of the chicks were not known during group formation.

Wild and domestic turkeys are susceptible to seven, host-specific species of *Eimeria* (Prestwood et al. 1971; Edgar 1986). Prestwood et al. (1971) detected coccidia infections in 50% of wild-caught poults, and speculated that such infections may contribute to the high mortality of wild poults by starvation and predation. Very little is known of the epidemiology of coccidiosis in free-living wild turkeys (Davidson & Wentworth 1992), but domestic turkeys acquire immunological resistance to new coccidia inoculations after primary exposure or with age (Chapman 1996; Aiello 1998). Generally, *Eimeria* sporozoites are released from ingested oocysts and infect cells lining the gastrointestinal tract, where they reproduce asexually, eventually causing repeated cycles of cell destruction

and infection of neighbouring cells (Long 1982). Lethargy, hypophagia and bloody or mucous-covered faeces are symptomatic of acute coccidia infection (Aiello 1998). Unsporulated coccidia oocysts are released to the intestinal lumen and are shed in the host turkey's faeces beginning 95–120 h (Edgar 1986) after infection. Coccidia can be difficult to identify and isolate to species. We used two oocyst source cultures provided by P. Augustine, Parasite Biology, Epidemiology and Systematics Laboratory, U.S. Department of Agriculture, because they were described and readily available. The poults in the single-species infection group were each fed by mouth, approximately 12 000 oocysts of *Eimeria adenoeides* suspended in a dilute sucrose solution. This coccidia species infects the lower small intestine, caeca and large intestine (Edgar 1986). The poults in the mixed-infection group were each given 6000 oocysts of *E. adenoeides* from the first culture, mixed with 6000 oocysts from a second culture source containing *E. adenoeides*, *E. gallopavonis*, *E. meleagrimitis*, and maybe *E. dispersa*, so that the entire digestive tract posterior to the gizzard would be a suitable habitat for at least one of these species (Edgar 1986). Turkey coccidia species overlap considerably in oocyst size, making it possible to identify the species present but difficult to know the proportion of each species in the mixed culture. The inoculum quantity is equivalent to the consumption of approximately 0.25 g of faeces (that is, a small beak-full) from a heavily parasitized wild turkey (Buchholz 1995), and much lower than the number of oocysts (50 000–500 000) typically used in studies of the effects of coccidia on domestic turkey production (Anderson et al. 1976; Chapman 1996). Control chicks were fed equivalent volumes of the sucrose solution only.

To prevent inadvertent infection, poults in the control group were given water containing 0.020% amprolium (Amprol 128, Merck & Co. Inc., Rahway, New Jersey). Amprolium is a competitive thiamine antagonist that halts coccidia reproduction primarily by acting on the first generation schizont to prevent merozoite production (Lindsay & Blagburn 2001). At the dosage used in this study, amprolium should have no negative effects on turkeys (Aiello 1998). During cage cleaning, sanitary procedures were followed to prevent inadvertently exposing control poults to faecal matter from infected chicks or exposing single-species infected chicks to faeces from the mixed-infection poults.

We did not monitor oocyst shedding by individual chicks, but we confirmed that the treatment was effective by microscopic examination of pooled faecal samples from the droppings tray below each treatment cage. Daily visual inspection of all chicks in each treatment did not reveal any control chicks that looked sickly, or any infected poults that remained healthy. Infected poults were droopy, ruffled their feathers and ate little for 3–5 days after infection. Faecal production virtually ceased after the poults stopped eating, and then was followed by diarrhoea, often spotted with blood, for less than 48 h. The total amount of blood was small and did not exceed daily blood collection guidelines for birds (Gaunt et al. 1997). In accordance with our Institutional Animal Care and Use protocol approval from the University of Mississippi, we were prepared to intercede medically if our infected subjects remained severely ill. However, by 10 days postinfection and thereafter, all the infected chicks appeared to behave and function normally. No poults died from infection.

Six weeks after treatment both infected groups were released into one roofed, outdoor flight pen ($10 \times 5 \times 3$ m) and the uninfected control groups were released into a separate but similar cage at the University of Mississippi Field Station. At this time it was necessary to euthanize five individuals from across all rearing groups because of leg abnormalities that were most likely the result of rearing turkeys on wire floors (Julian 1988). Because single-species and mixed-species treated birds were combined at this stage, there was the opportunity for coccidia other than *E. adenoeides* to infect the single-species birds, although the hosts' age and cross-immunity to antigens shared by the coccidia species may have made this unlikely. At 7–8 months of age, all 16 males were removed from the group cages and housed individually to prevent mortality due to male aggression.

Ethical Note

Experimental investigation of parasite-mediated sexual selection requires that study subjects be exposed to ecologically relevant disease conditions, but scientific ethics require that we minimize and mitigate the pain and suffering of our study subjects. In concert with the university veterinarian, we developed a protocol to meet both these scientific needs. Although these steps appear separately in other sections of this paper, we summarize them again here for emphasis. In the weeks previous to infection, the turkey poults were given high protein feed to ensure that they were in the best condition to survive infection. We used a relatively low number of oocysts to infect our subjects in an infection scenario based on field data. The chicks were maintained in social groups to minimize their distress and supplemental heating was provided so that the chicks would be more comfortable. Although parasite-induced damage did result in some blood in the faeces at the peak of infection, the amount was small and within established guidelines for blood collection in birds. The treatment groups were carefully observed twice per day to ensure that chicks were able to stand and to walk normally. If infected poults had become incapacitated, or failed to recover and function normally, we were prepared to provide supplementary medical care or euthanasia. Veterinary intervention due to infection was never necessary, although we did humanely euthanize several poults later for reasons unrelated to infection. In accordance with U.S. federal law, all procedures were conducted only after review by and approval from the University of Mississippi Institutional Animal Care and Use Committee.

Colour Quantification

After males had grown their first basic plumage, the ornamental coloration used in their first breeding season,

we collected two greater secondary covert feathers (numbers 5 and 6) and two contour feathers from a position on the breast that was consistent across males. The covert feathers have a distinct patch of iridescent coloration on the exposed side of the vane (i.e. the side not overlapped by other feathers), and we took spectral readings from the centre of this coloured patch. Breast feathers have a distinct band of iridescent coloration about 1 cm from the distal end, and we took spectral readings from this coloured band.

We used an Ocean Optics S2000 spectrometer and a deuterium-tungsten-halogen light source (Ocean Optics, Dunedin, Florida) to quantify spectral reflectance. As expected from iridescent colours, the shape of the spectral curves varied with the angle of observation. Thus, to allow for independent modification of illumination and reflection angles, we used separate illumination and reflection fibre-optic probes mounted in an angled fibre-optic probe holder (Avantes, The Netherlands). The distance between the end of the probes and the feather surface was set so that a region 2 mm in diameter was illuminated. Exploratory investigation of illumination/reflection angle combinations revealed that the most saturated (most 'peaky') reflectance curves were obtained by positioning the illumination probe at a 90° angle to the feather surface and the reflection probe at a 45° angle to the feather surface (Osorio & Ham 2002), so we conducted all spectral measurements using this angle combination.

All spectral measurements were taken with the reflectance probe at the proximal end of the feathers. Feathers were placed on black cardboard during measurements, although the background had no effect on spectral measurements due to the large size of the feathers and tight overlapping of the barbules. We measured two secondary coverts and two breast feathers for each individual. We took three measurements from the coloured portion of each feather, moving the probe at least 2 mm between measurements. To reduce noise in the measurements, each reading was composed of an average of 20 reflectance curves taken at 100-ms intervals. We then averaged the three readings for each feather, and averaged these within feather type for each male, which resulted in one average spectrum for coverts and one average spectrum for breast feathers for each male in our analyses.

To summarize overall variation in reflectance into three orthogonal variables, we performed principal components analysis (PCA) on reflectance spectra (Endler 1990; Hunt et al. 1998; Cuthill et al. 1999). We began by summarizing mean reflectance values into 33.3-nm-wide bins, resulting in 12 mean reflectance values between 300 and 700 nm for each spectrum. We then ran PCAs on these values for all 16 males in our experiment. Factor rotation did not facilitate interpretation of the PC scores, so we used unrotated PCs. We performed two separate PCAs, one for each body region that we measured.

To facilitate the interpretation of our principal component scores, we calculated six commonly used colourimetric variables relevant to the three dimensions of animal colour vision (brightness, hue and saturation; Hailman 1977) and compared these to our PC scores. We calculated total brightness as the average percentage of reflectance from 300 nm to 700 nm. We calculated hue as the wavelength at maximum reflectance. We calculated four measures of chroma (UV, blue, green, red) to approximate variation in saturation across the entire bird-visible spectrum. We selected wavelength ranges for these chroma calculations by considering the intersection of lines describing predicted spectral sensitivities for the violet-sensitive, short-wavelength-sensitive, medium-wavelength-sensitive, and long-wavelength-sensitive cone types in domestic turkeys (Hart et al. 1999). Thus, we calculated UV chroma as the proportion of total reflectance occurring between 300 and 450 nm, blue chroma as the proportion of total reflectance occurring between 450 and 500 nm, green chroma as the proportion of total reflectance occurring between 500 and 550 nm, and red chroma as the proportion of reflectance occurring between 550 and 700 nm. Although the peak sensitivity of the violet-sensitive cone type in turkeys occurs at longer wavelengths than that of most passerines (approximately 426 nm), the associated oil droplets and ocular media have high transmission at short wavelengths, and thereby confer considerable UV sensitivity in this species (Hart et al. 1999).

Statistical Analyses

The final sample comprised six males in the control group, four males in the single-species inoculation group, and six males in the multiple-species inoculation group. Because of the incremental nature of our three treatment groups (uninfected, inoculation with one species of coccidian parasite, inoculation with multiple species of coccidian parasites), we categorized our treatments as three ordinal variables (0, 1, 2, respectively) and used ordinal logistic regressions to investigate treatment-based variation in structural plumage ornamentation.

RESULTS

Colour and Interpreting PC Scores

The reflectance spectra of wing coverts generally increased across the bird-visible spectrum (Fig. 1a), whereas the reflectance spectra of the breast feathers were unimodal, peaking at 603 $\pm$ 7.48 nm (Fig. 1b). For the PCA on wing coverts, PC1 explained 72% of the variation in reflectance, PC2 explained 20% of the variation, and PC3 explained 5% of the variation. For the PCA on breast feathers, PC1 explained 62% of the variation in reflectance, PC2 explained 22% of the variation, and PC3 explained 10% of the variation. For both body regions, the factor loadings for PC1 were moderate and positive across the entire bird-visible range (Fig. 1c, d), suggesting an association with achromatic brightness (Endler 1990). Indeed, PC1 was highly correlated with brightness for both body regions (Table 1). In contrast, factor loadings for PC2 and PC3 varied in direction and magnitude at different wavelengths (Fig. 1c, d), suggesting an association with hue and saturation (Endler 1990). For wing coverts, PC2 was negatively associated with short

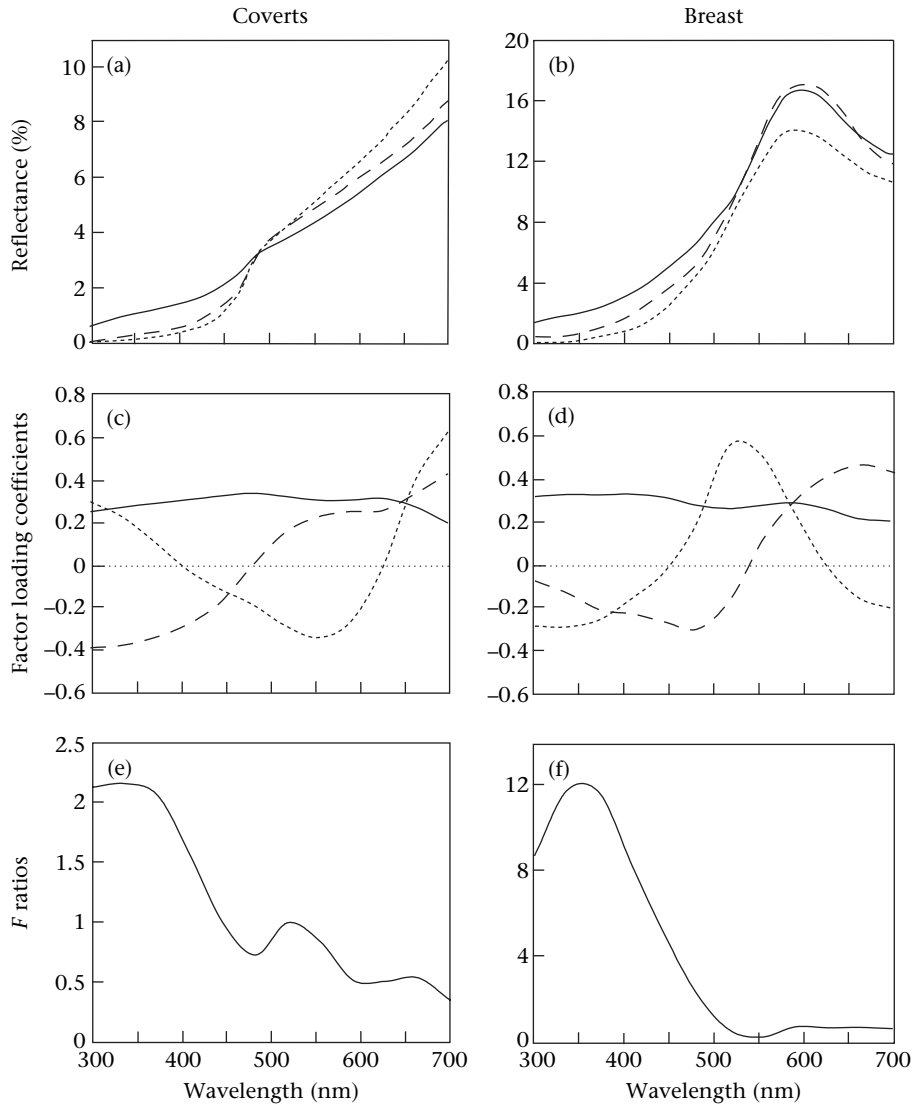

Figure 1. Average spectral reflectance curves for wing coverts (a) and breast feathers (b) of yearling male wild turkeys, *Meleagris gallopavo*. Solid lines represent uninfected males ($N = 6$), dashed lines represent males inoculated with a single species of coccidia ($N = 4$), and dotted lines represent males inoculated with multiple species of coccidia ($N = 6$). Association between principal component factor-loading coefficients PC1 (solid lines), PC2 (dashed lines) and PC3 (dotted lines) and wavelength for wing coverts (c) and breast feathers (d). *F* ratios, calculated from binned reflectance values (see text), showing the regions of the spectrum for which treatment group differences in plumage reflectance were greatest for wing coverts (e) and breast feathers (f).

Table 1. Correlation between principal component (PC) scores and colourimetric variables for two different body regions of yearling male wild turkeys, *Meleagris gallopavo*

	Hue	Brightness	UV chroma	Blue chroma	Green chroma	Red chroma
Wing coverts						
PC1	−0.31	0.98**	0.79**	0.81**	0.01	−0.83**
PC2	−0.38	0.17	−0.59*	−0.29	0.27	0.51
PC3	0.52*	0.06	0.08	−0.28	−0.85**	0.12
Breast feathers						
PC1	−0.32	0.93**	0.72**	−0.01	−0.34	−0.26
PC2	0.22	0.36	−0.47*	−0.94**	−0.58*	0.95**
PC3	−0.73**	0.08	−0.35	−0.07	0.61*	−0.11

PC scores were derived from a principal components analysis on the reflectance spectra of 16 male turkeys (see text).
*$P < 0.05$.
**Significant after Bonferroni correction for multiple tests ($P < 0.0028$).

wavelengths and positively associated with long wavelengths, whereas PC3 was highly negatively associated with intermediate wavelengths and positively associated with short and long wavelengths (Fig. 1c, d, Table 1). For the breast feathers, PC2 was negatively associated with intermediate (blue) wavelengths and positively associated with longer (red) wavelengths, whereas PC3 was highly positively associated with intermediate (green) wavelengths (Fig. 1c, d, Table 1). PC3 for breast feathers was also negatively associated with hue (Table 1).

Effect of Experimental Manipulation on Colour

There was a significant effect of treatment group on the reflectance of both wing coverts and breast feathers (Table 2). For wing coverts, the only significant predictor of treatment group was PC2 (Table 2). The wing coverts of birds infected with coccidian parasites had less reflectance in the UV portion of the spectrum and greater reflectance at longer wavelengths (Fig. 1a, c) in the direction predicted by the severity of each treatment (Fig. 2a). For the breast feathers, only PC1, a positive correlate of brightness and UV chroma (Table 1), significantly predicted treatment group (Table 2), although variation in PC3 approached significance (Table 2). Birds infected with coccidian parasites had duller breast feathers with less UV reflectance than uninfected birds (Fig. 1b, d), again in the direction predicted by the severity of the treatments (Fig. 2b). For both body regions, treatment-based differences were greatest at short (UV) wavelengths (Fig. 1e, f).

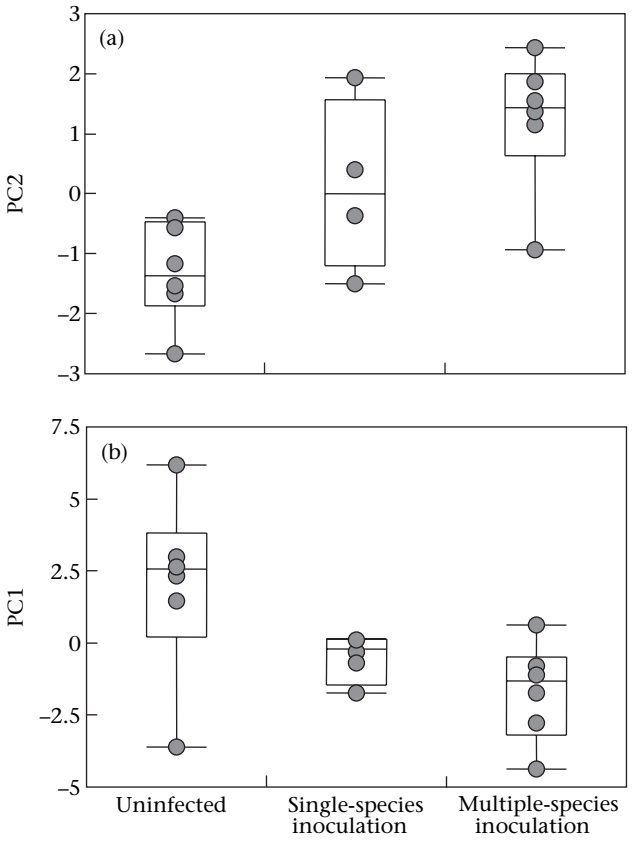

Figure 2. Box plots illustrating variation in plumage reflectance scores (PC1, PC2) for wing coverts (a) and breast feathers (b) based on different treatment groups (uninfected, infected with a single species of coccidia, infected with multiple species of coccidia) of yearling male wild turkeys, *Meleagris gallopavo*. Box plots show 10th, 25th, 50th, 75th and 90th percentiles with horizontal lines. Individual data points are also shown.

DISCUSSION

We found a clear effect of coccidial infection on the spectral reflectance of iridescent feathers of male wild turkeys. Males infected with coccidia grew covert feathers with less UV reflectance and greater reflectance at long wavelengths than males that were not infected. Infected males also grew duller breast feathers with less UV reflectance than uninfected males. Additional effects of parasitism on plumage reflectance may occur in this species, but with a small number of birds in each treatment group, some of our statistical tests had low power and consequently, we could detect only large effects of parasites on the iridescent plumage coloration.

Infection by *Eimeria* coccidia is widespread in wild populations of turkeys. Prestwood et al. (1971) reported a 50% incidence of *Eimeria* oocysts among wild turkey poults and 17% prevalence in juveniles and adults. Forty per cent prevalence in adult wild turkeys was described in another study (Kozicky 1948), although the intensity of infection was not described. Buchholz (1995) found that infected male wild turkeys show considerable individual differences in mean coccidia burden (range 10–30 000 oocysts/g of faeces). It seems likely that, as in our captive experiment, coccidia will have an important influence on the expression of ornamental coloration among free-living turkeys. Thus, just as degree of eimerian infection was found to be closely correlated with the expression of the sexually selected fleshy head ornaments of turkeys in the wild (Buchholz 1995), these parasites might also be affecting female choice and male–male competition via reflective properties of ornamental plumage.

No previous studies have experimentally tested the effect of coccidia, or any parasite, on structural coloration.

Table 2. Ordinal logistic regressions using three principal component (PC) colour scores to predict infection levels (uninfected, infected with a single species of coccidia, infected with multiple species of coccidia) of 16 yearling male wild turkeys, *Meleagris gallopavo*

	Wing coverts*		Breast feathers†	
Predictors	χ^2_1	*P*	χ^2_1	*P*
PC1	0.63	0.43	5.76	0.016
PC2	6.72	0.009	1.52	0.22
PC3	0.07	0.79	3.54	0.059

See Table 1 for interpretation of PC scores.
*Whole model: $\chi^2_3 = 14.5$, $N = 16$, $P = 0.002$.
†Whole model: $\chi^2_3 = 11.7$, $N = 16$, $P = 0.008$.

Eimerian coccidia have previously been shown to negatively affect the skin colour of chickens (Bletner et al. 1966; Marusich et al. 1972). Similarly, coccidia in the genus *Isospora* have been shown to depress expression of carotenoid but not melanin coloration in the plumages of cardueline finches (Hill & Brawner 1998; Brawner et al. 2000; McGraw & Hill 2000). One could argue that we subjected birds to a severe infection in this experiment and that it was a foregone conclusion that systems for creating microstructural coloration would fail along with many other systems within the animals' bodies. To the contrary, however, exposure to coccidia did not simply degrade the general quality of feathers. The size, shape and integrity of feathers appeared unaffected, and only certain aspects of the iridescent coloration, namely, brightness and ultraviolet reflectance, were altered by coccidial infection. Moreover, it should not be assumed that plumage coloration will be affected even when birds are very ill during feather growth. When American goldfinches were subjected to a debilitating coccidial infection, melanin pigmentation was unaffected (McGraw & Hill 2000). Our observation that parasite infection during moult suppresses expression of iridescent coloration suggests that structural coloration in male wild turkeys is a condition-dependent trait that reliably signals the health of an individual.

A key question concerns the mechanism by which structural coloration can be condition dependent. The condition dependency of carotenoid coloration results from the scarcity of carotenoid pigments in the diets of animals and the cost of utilizing dietary carotenoids and expressing them as integumentary pigments (Hill 2002). The mechanism by which structural colours could be dependent on condition during moult was, until recently, less clear. However, Shawkey et al. (2003) recently showed that in noniridescent structural colours, variation in the number and size of keratin rods in the barbs can influence the hue and saturation of these feathers. Poor nutrition during feather growth may corrupt the production or arrangement of the microstructural feather elements required for maximum colour display (Shawkey et al. 2003). Parasites could affect structural coloration in a similar manner by causing energy to be diverted from feather production to immune defence or by directly suppressing food intake and hence acting indirectly through nutritional condition. No comparable study has investigated the proximate cause of intraspecific variation in reflectance in iridescent structural colours. Unlike the three-dimensional matrix of keratin rods and air spaces that produces noniridescent structural colours, iridescent structural colours are produced by stacked arrays of melanin granules and/or air vacuoles suspended in barbule keratin (Prum 1999; Zi et al. 2003). Interspecific comparisons suggest that variation in the number and/or size of the reflective layers might influence the colour of iridescent feathers (Dyck 1976), possibly providing another avenue for research investigating the microstructural effects of nutrition and parasites.

Our study demonstrates the potential for the expression of iridescent structural coloration to be affected by parasites. Future studies will need to assess whether these colour displays are used in male–male competition or female mate choice in wild turkeys. Another key area of research will involve assessing the relative importance of parasites, nutrition and genes on the expression of iridescent structural coloration in captive and wild birds.

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