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Behavioural Processes 65 (2004) 123–132

BEHAVIOURAL PROCESSES

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Bill colour and correlates of male quality in blackbirds: an analysis using canonical ordination

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Received 15 October 2002; received in revised form 25 April 2003; accepted 4 August 2003

Abstract

Carotenoid-dependent plumage displays are widely assumed to be honest indicators of individual health or quality, which are used as cues during mate choice and/or agonistic signalling. Despite the fact that red, yellow and orange pigmentation of bills is common, and also variable between individuals, comparatively little is known about bill colouration as a condition-dependent trait. Furthermore, many studies of avian colouration are confounded by the lack of objective colour quantification and the use of overly simplistic univariate techniques for analysis of the relationship between the condition-dependent trait and individual quality variables. In this study, we correlated male blackbird bill colour (a likely carotenoid-dependent sexually selected trait) with body/condition variables that reflect male quality. We measured bill colour using photometric techniques, thus ensuring objectivity. The data were analysed using the multivariate statistical techniques of canonical ordination. Analyses based on reflectance spectra of male blackbird bill samples and colour components (i.e. hue, chroma and brightness) derived from the reflectance spectra were very similar. Analysing the entire reflectance spectra of blackbird bill samples with Redundancy Analysis (RDA) allowed examination of individual wavelengths and their specific associations with the body/condition variables. However, hue, chroma and brightness values also provided useful information to explain colour variation, and the two approaches may be complimentary. We did not find any significant associations between male blackbird bill colour and percent incidence of ectoparasites or cloaca size. However, both the colour component and full spectral analyses showed that culmen length explained a significant amount of variation in male blackbird bill colour. Culmen length was positively associated with greater reflectance from the bill samples at longer wavelengths and a higher hue value (i.e. more orange-pigmented bills). Larger males may have larger territories or be better at defending territories during male–male interactions, ensuring access to carotenoid food sources. Future studies should elucidate the relationship between bill colour and behavioural measures such as aggressiveness, territory size, song rate and nest attendance.

Keywords: Blackbird; Condition-dependent traits; Canonical ordination; Carotenoid colouration; Male quality; *Turdus merula*

1. Introduction

Bright colouration of plumage and integumentary structures is particularly common among male birds. Red, yellow and orange colours, commonly produced by carotenoid pigments (Fox and Vevers, 1960; Brush, 1978), dominate ornamental display. Carotenoids are

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doi:10.1016/j.beproc.2003.08.003

also important physiological modulators and have a range of health-related functions (e.g. free radical scavengers, stimulants of the immune system, protective agents against cancer; Lozano, 1994; Olson and Owens, 1998). Birds are incapable of synthesising carotenoids, so must obtain them from their diet; they may then be modified for colour production once ingested (Goodwin, 1984). Several studies have shown that foraging ability, physical condition and parasite resistance are positively correlated with the extent of carotenoid-dependent colouration of the bearer (e.g. Hill, 1991, 1992; Hill and Montgomerie, 1994; Sundberg, 1995; Thompson et al., 1997; Zahn and Rothstein, 1999). Carotenoid-dependent colour displays are widely assumed to be honest indicators of individual health or quality, which are used as cues during mate choice (see review by Hill, 1999; Møller et al., 2000) and/or agonistic signalling (Pryke et al., 2001; Pryke and Andersson, 2003).

In the majority of studies investigating carotenoid-coloured, condition-dependent traits (see references above), individual variation in plumage pigmentation has been measured. However, red, yellow and orange bill pigmentation is also very common, and variable between individuals (e.g. Burley et al., 1992). Comparatively little is known about carotenoid-dependent bill colouration (versus plumage colour) as a condition-dependent trait in birds. The type of condition-dependent trait may affect the information being revealed, and consequently the predictions that can be generated (Lozano, 1994). The physiological processes and metabolic costs associated with the production and colouration of bills and feathers will vary. Furthermore, the outer layers of a bird's bill are continuously being replaced, while new feathers are produced only during moult and are potentially constrained by the condition of the bird at that time (Negro et al., 1998). The colour of bills may be a reflection of more recent physiological events, and hence have the potential to be an indicator of the current physical condition of the individual (Burley et al., 1992; Lozano, 1994; Blount et al., 2003; Faivre et al., 2003).

In this study, we investigated correlations between bill colour in the male blackbird, *Turdus merula*, and body/condition variables that may reflect male attributes. The blackbird is an ideal subject with which to examine the relationship between bill colour and male quality variables. The male and female are sexually dimorphic, defend territories and form a long-term pair bond. The male's yellow/orange bill develops upon sexual maturity (Snow, 1958) and varies from dull yellow to bright orange (Gurr, 1954; Heather and Robertson, 1996). Recent evidence suggests that male blackbird bill colour honestly signals male health (Faivre et al., 2003) and can be reliably used as a cue of individual quality (Faivre et al., 2001; Hatchwell et al., 2001; Bright and Waas, 2002).

Many studies of avian colouration are confounded by the lack of objective colour quantification (see Endler, 1990; Bennett et al., 1994). Also, the majority of studies use univariate techniques for analysis of the relationship between the condition-dependent trait and individual quality variables. Univariate techniques may be overly simplistic—by using multivariate techniques, it becomes possible to examine suites of variables and interactions between them. In this study, we measured male blackbird bill colour with photometric equipment, ensuring objectivity of colour quantification (Bennett et al., 1994). The data were then analysed using the multivariate statistical techniques of canonical ordination, which, unlike univariate statistics, produced visual and statistical information on the relationships between bill colour and male quality variables.

2. Materials and methods

This study was conducted on the 80 ha campus of The University of Waikato, Hamilton, New Zealand, from September to December 1999 (the time of year, in the Southern Hemisphere, when the majority of blackbirds breed; Gurr, 1954). Observations and sampling sessions were conducted in woodland areas, which surround the sports fields and faculty buildings. The woodland areas include a mixture of native and exotic trees and shrubs of consistent density and size throughout the campus. The light environment for University of Waikato blackbirds is characteristic of "woodland shade" (Endler, 1993). The population of blackbirds on campus was estimated at 200 birds. Altogether, 26 males were captured, banded and monitored for the purposes of this study.

2.1. Body measurements

Measurements of the left tarsus, wing length, bill depth and culmen length (to the nearest 0.01 mm) were taken from all blackbirds using dial calipers. Cloacal protuberance measurements (diameter) were taken at the base of the seminal protuberance (nearest 0.01 mm). Measurements were repeated three times and averaged for each bird (measurements varied by 0–1.00 mm). Diameter measurements of the cloacal protuberance are closely correlated with height (Birkhead et al., 1993) and were more easily obtained than height measurements in this species. Male passerines store sperm in a cloacal protuberance during the breeding season (Wolfson, 1954). Extra-pair paternity is common within broods of blackbird populations (see Creighton, 2001), although extra-pair copulations are rarely observed (Snow, 1958; Birkhead et al., 1993). Males of species which experience more intense sperm competition (measured by copulation frequency) should have relatively larger sperm stores and larger protuberances than those species where sperm competition is less intense (Birkhead and Møller, 1992; Birkhead et al., 1993). A similar relationship has also been observed between individuals *within* a species (Kempenaers et al., 1999). If colour or male quality and copulation rate are correlated (see review in Birkhead and Møller, 1998), we might also expect a relationship between the intensity of carotenoid-pigmented sexually selected traits and cloacal protuberance size in male blackbirds.

On completion of morphometric measurements, the left wing of each bird was extended and held up to ambient light for estimation of ectoparasite abundance. The complete length of the primary feathers was exposed, primary coverts and under wing coverts being moved gently aside if necessary. Each primary feather was scored according to the percent of the feather infested by mite clusters (visible by eye) (derived from Behnke et al., 1995, 1999). The primaries of corpses were photographed under a scanning electron microscope (AgResearch, Wallaceville, New Zealand) and feather mites of the genus *Proctohyllodes* were identified according to Atyeo and Braasch (1996). Finally, the month that each bird was captured, banded, and measured was recorded. Higher values were given to later months (e.g. November = 11; December = 12).

2.2. Bill colour

One or two small flakes (2 mm × 2 mm) from the bill (middle of the upper left mandible) of each adult male were scraped off the outer surface with a scalpel. There were no noticeable behavioural effects associated with sampling subjects in this way (A. Bright, personal observations) and the majority of birds were observed again around the campus in the following months.

Spectral curves derived from flakes were representative of those obtained from whole bills (based on visual examinations of the actual spectra; A. Bright, unpublished data). Spectral reflectance from these flakes was measured using a Zeiss spectrometer (MMS-1 Carl Zeiss Corporation, Jena, Germany) and a 10 W halogen lamp (LS1, Ocean Optics, FL) by AB at HortResearch, Hamilton, New Zealand within 2 months of collection. A fibre optic interactance probe (Ocean Optics) positioned at a 90° angle to the bill sample was used to direct the illumination and collect the light scattered by the small samples. Measurements were taken at 15 ms integration time (309–700 nm) and expressed relative to a white Teflon reflectance standard for all 26 adult male blackbirds. This Teflon standard performs similarly to the Spectralon 99% white reflection standard (Labsphere, Congleton) across all measured wavelengths (A. McGlone, HortResearch, Hamilton, unpublished data). Dark current and white standard reference measures were taken before every tenth sample in order to minimise error associated with drift of the light source and sensor. All bill samples were measured twice and there was little variation between spectra. Reflectance spectra were averaged from 20 scans and recorded in 3.3 nm wavelength bands, which were later reduced to 7 nm wavelength bands because of software and memory limitations. The reflectance curves were transformed (Standard Normal Variate) to correct for geometric differences between samples, caused by variation in probe and sample distance (i.e. variation in the thickness of bill flakes). From the corrected spectral reflectance curves (309–700 nm), we also computed hue (spectral positions of maximum slope), chroma (ratio between maxima and minima reflectance) and brightness (total reflectance).

2.3. Statistical analysis

The data were analysed using the multivariate statistical techniques of canonical ordination. Canonical ordination is a combination of ordination and multiple regression, typically used by ecologists for relating the species composition of communities to their environment. In ecology, ordination is applied to species data, typically the abundance of a set of species. Variation in species data is then explained by environmental variables (for more information on this analysis see ter Braak, 1986).

Our data were analysed using Redundancy Analysis (RDA). RDA, or least-squares reduced-rank regression, is the canonical form of a Principal Components Analysis. The results of RDA can be displayed in an ordination diagram or biplot. This species–environment biplot gives a display of approximate values of correlations between species and environmental variables. The amount of the species data explained by the environmental variables for each ordination axis (a theoretical explanatory variable) in the biplot is given by the eigen value (between 0 and 1); only axes 1 and 2 are used in the biplots (for further information on constructing and interpreting biplots see ter Braak, 1986; Jongman et al., 1987; ter Braak and Šmilauer, 1998). Environmental variables with long arrows are the most important in the analysis. The longer the arrow the more confident one can be about the inferred correlation. The direction of the arrow indicates the association between environmental variables and species data, and the arrow can be extended on either side to form a line. Arrows pointing in roughly the same direction indicate a positive correlation between environmental variables and species data; arrows at right angles indicate zero correlation (ter Braak, 1986).

In this study, bill colour data replace the species information, and body/condition measurements of adult male blackbirds the environmental variables.

Culmen length, cloaca size and percentage of ectoparasites were entered as body/condition variables in the model. Culmen length was used to represent blackbird body size, as we found it to be the most repeatable measurement and therefore more accurate and objective than tarsus length, wing length and bill depth. Culmen length is representative of body size in blackbirds (Gurr, 1954), as in other species (Guglielmo and Burns, 2001). Month of collection, tarsus length, wing length and bill depth were however, classified as covariables (ter Braak and Šmilauer, 1998) (i.e. there were no independent correlations of these variables with the bill colour data). Including or excluding covariables in our analyses did not change which variables were most important in explaining bill colour variation. Forward selection and Monte Carlo permutation tests (using 199 unrestricted permutations) were performed to identify the body/condition variables that were statistically significant in determining the variations in bill colour data. RDA and associated analyses were performed using CANOCO v. 4.0 (ter Braak and Šmilauer, 1998).

3. Results

3.1. Spectral reflectance curves

The spectral reflectance curves from bill samples at 15 ms integration time are shown in Fig. 1. There are two regions of maximum reflectance, the first in the Ultra Violet-A waveband (UVA; 309–350 nm) and a second in the visible spectrum (550–700 nm).

The biplot based on RDA analysis of the spectral reflectance curves of bill samples with respect to body/condition variables is shown in Fig. 2. Solid arrows represent wavelength spectra and are labelled with nm values; dashed arrows represent body/condition variables. Longer wavelengths were negatively associated with axis 1, and shorter wavelengths positively so. UVA wavelengths were positively associated with axis 2. Forward selection and associated Monte Carlo permutation tests of the significance of body/condition variables (Table 1)

Table 1
Results of forward selection and Monte Carlo permutation tests from RDA on male blackbird bill sample spectral reflectance curves and body/condition variables

	Lambda-1	Lambda-A	*P*	*F*
Culmen length	0.13	0.13	0.05	4.15
Cloaca size	0.02	0.01	0.45	0.58
Percentage of ectoparasites	0.02	0.02	0.48	0.50

The lambda-1 column lists the body/condition variables in order of the variance they explained singly (i.e. when that particular variable was used as the only body/condition variable). The variance was in addition to the variance explained by covariables. The lambda-A column lists the body/condition variables in order of their inclusion in the model, together with the additional variance each variable explains at the time it was included and, the significance of the variable at that time (*P* value) together with its test statistic (*F* value). Eigen values: axis 1 = 0.142; axis 2 = 0.010.

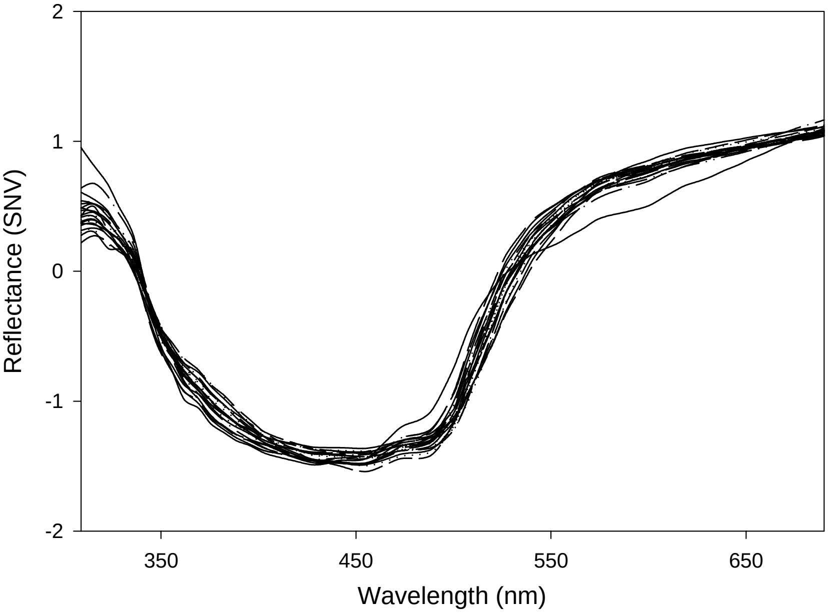

Fig. 1. Reflectance spectra from bill samples of 26 adult male blackbirds measured at 15 ms integration (309–700 nm). Reflectance spectra were post-transformed by Standard Normal Variate.

showed that culmen length explained the largest proportion of the variability in bill colour ($P = 0.05$). After addition of culmen length to the ordination, the subsequent additions of cloaca size and percentage of ectoparasites did not make significant contributions ($P \geq 0.45$) to explaining the additional variation in bill colour data. Culmen length was strongly negatively associated with axis 1 and positively associated with longer wavelength spectra; therefore larger birds had more orange-pigmented bills than smaller birds.

3.2. Spectral reflectance hue, chroma and brightness values

Three individual colour component values (i.e. hue, chroma and brightness) were calculated from the spectral reflectance curves of each bill sample (309–700 nm) and analysed by RDA. In the resulting biplot (Fig. 3), brightness and chroma were positively associated with axis 1 and hue negatively associated. Forward selection and Monte Carlo permutation tests of the significance of body/condition variables (Table 2) show that culmen length explained the largest proportion of the variability in bill colour ($P = 0.04$). After addition of culmen length to the ordination, the subsequent additions of cloaca size and percentage of ectoparasites did not make significant contributions ($P \geq 0.41$) to explaining the additional variation in bill colour data. Culmen length was negatively associated with axis 1 and positively

Table 2
Results of forward selection and Monte Carlo permutation tests from RDA on male blackbird bill sample hue, chroma and brightness values derived from reflectance spectra and body/condition variables

	Lambda-1	Lambda-A	*P*	*F*
Culmen length	0.15	0.15	0.04	4.96
Cloaca size	0.03	0.02	0.41	0.68
Percentage of ectoparasites	0.00	Not calculated	Not calculated	Not calculated

The lambda-1 column lists the body/condition variables in order of the variance they explained singly (i.e. when that particular variable was used as the only body/condition variable). The variance was in addition to the variance explained by covariables. The lambda-A column lists the body/condition variables in order of their inclusion in the model, together with the additional variance each variable explains at the time it was included and, the significance of the variable at that time (*P* value) together with its test statistic (*F* value). Eigen values: axis 1 = 0.169; axis 2 = 0.00.

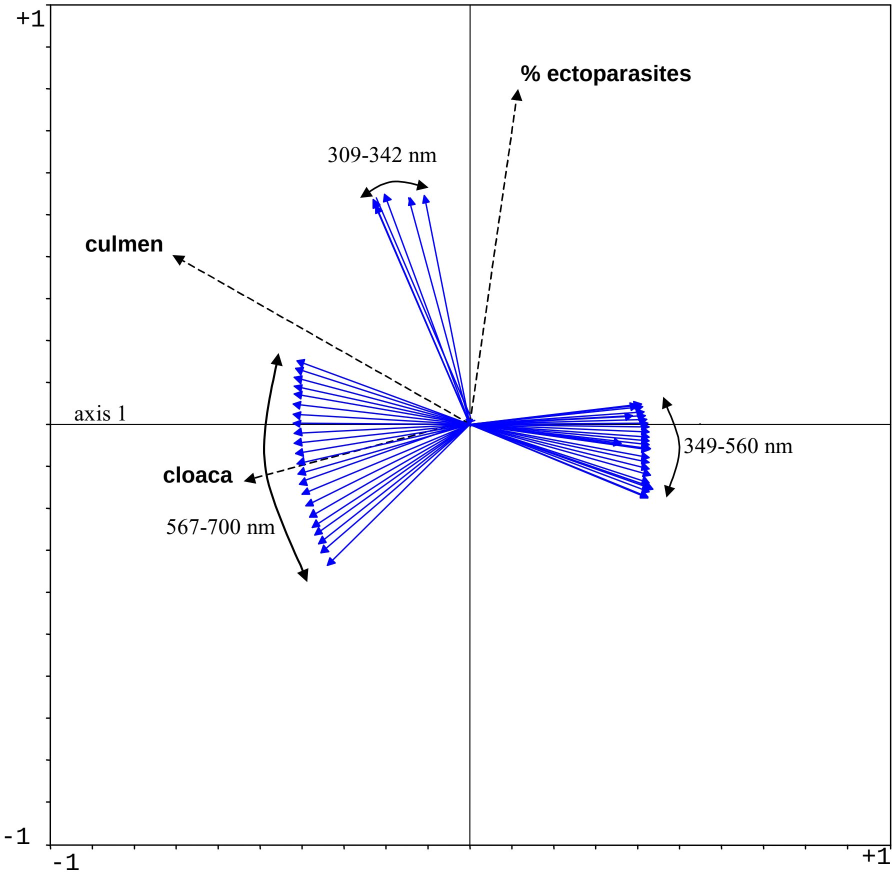

Fig. 2. RDA biplot of spectral reflectance curve values from bill samples of male blackbirds and body/condition variables. Solid arrows represent spectral reflectance values. Dashed arrows represent body/condition variables.

related to bill sample hue. The relationships between body/condition measurements and bill colour data in Figs. 2 and 3 were very similar. Longer culmen length was positively associated with higher hue values and negatively associated with a lower brightness/chroma value (i.e. more orange bills).

4. Discussion

Carotenoid-based plumage colouration is a condition-dependent trait in birds (see review by Hill, 1999). Comparatively little is known about carotenoid-dependent, bill colouration (versus plumage colour) as a condition-dependent trait. In this study, we correlated male blackbird bill colour (a likely carotenoid-dependent, sexually selected trait) with body/condition variables that may reflect male quality. We measured bill colour using photometric techniques, ensuring objectivity in colour quantification. The data were analysed using the multivariate statistical techniques of canonical ordination, which, unlike univariate statistical techniques, produced visual and statistical information on the relationships between bill colour and male quality variables.

4.1. Reflectance spectra and colour quantification

Because carotenoids reflect primarily in the visible wavelengths (Goodwin, 1984), exclusion of the UV waveband when quantifying carotenoid-dependent plumage or integument pigmentation has not been perceived to be a major problem (Hill, 1998). However, in this study, maximum reflectance from blackbird

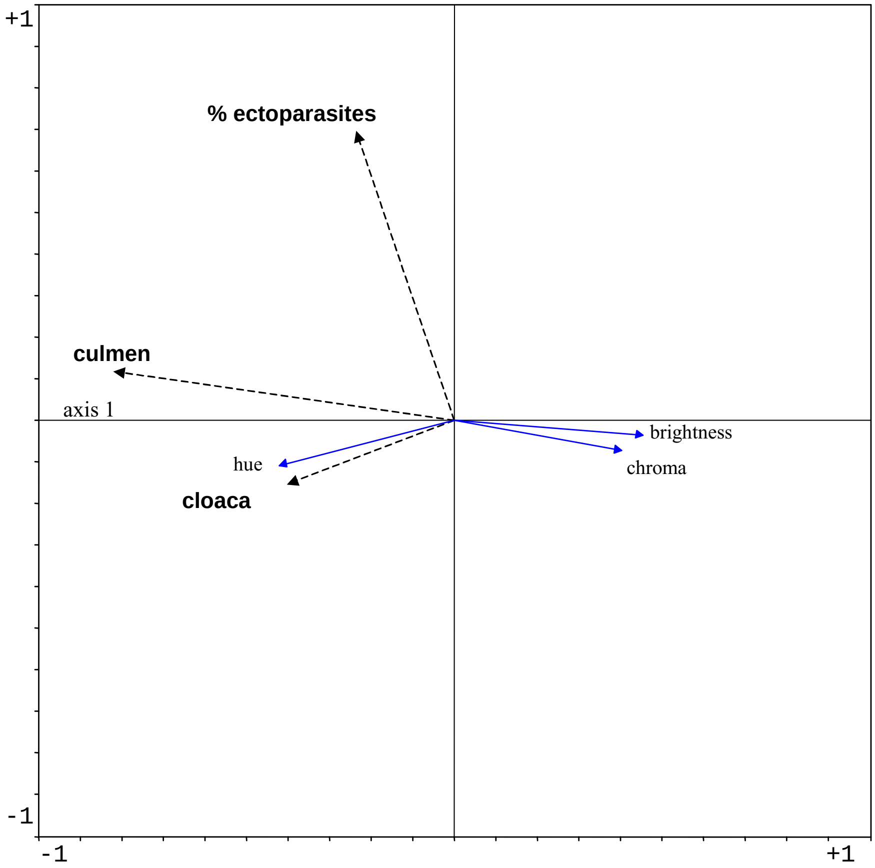

Fig. 3. RDA biplot of hue, chroma and brightness from spectral reflectance curves of male blackbird bill samples and body/condition variables. Solid arrows represent hue, chroma and brightness values. Dashed arrows represent body/condition variables.

bill samples was at 309–350 nm *and* at 500–600 nm, although we did not find any association between the maximum reflectance of blackbird bill samples in the UV waveband and any of the body/condition variables measured. The fact that a species' plumage or integument reflects in the UV does not guarantee a role for UV signalling (Cuthill et al., 2000; Hunt et al., 2001; but see Hausmann et al., 2003). However, altering UV reflection can influence hue perception at longer wavelengths (Pearn et al., 2001) and we should always be aware of the possible contribution of the UV waveband when investigating avian colouration regardless of whether a signalling role is suspected or not.

Analyses based on reflectance spectra of male blackbird bill samples and colour components derived from the reflectance spectra were very similar (compare Figs. 2 and 3). Analysing the entire reflectance spectra of blackbird bill samples with RDA allowed examination of individual wavelengths and their associations with the body/condition variables (Fig. 2). However, hue, chroma and brightness values are very useful tools for explaining colour variation, and the two approaches may be complementary.

4.2. Body/condition variables

There is evidence to suggest that bill colour in male blackbirds may be correlated with male health/quality (Faivre et al., 2003). Male blackbirds with orange bills are heavier and tend to be mated to females in better condition that make more breeding attempts per season than females mated to males with yellow bills (Faivre et al., 2001). Males with orange bills, also have fewer blood parasites than yellow-billed males (Hatchwell et al., 2001). In this study, we did not find any significant relationships between percentage feather ectoparasites or cloaca size of male blackbirds and bill colour. Proctopyhllodid feather mites feed on waxes and fatty acids from the feathers (Walter and Proctor, 1999). In some species, proctopyhllodid mites are known to affect host condition (Thompson et al., 1997; Harper, 1999); however, other studies have shown the same mites to be commensal and possibly mutualistic (Blanco et al., 1999, 2001). It is possible that proctophyllodid feather mite abundance does not negatively affect blackbird health and condition and therefore does not have any influence on carotenoid-dependent bill pigmentation. By contrast, haematozoan parasites may affect the ability of male blackbirds to accumulate and produce carotenoid pigments to a larger extent than ectoparasites. Alternatively, because correlational studies often fail to detect costs of parasitism, experimental manipulations of parasite load may be required to test for potential effects of parasites, especially indirect effects such as energetic costs (Booth et al., 1993; Figuerola et al., 2003).

Extra-pair paternity is common within broods of blackbird populations (cited in Creighton, 2001) although extra-pair copulations are rarely observed (Snow, 1958; Birkhead et al., 1993). Inter-specific variation in cloacal protuberance dimensions reflects variation in levels of sperm competition among species (Birkhead et al., 1993); males that copulate frequently have large cloacal protuberances to avoid sperm depletion. A similar correlation has been observed between individuals within a species (Kempenaers et al., 1999). However, cloacal protuberance dimensions have related to few morphological characteristics that might indicate male quality or condition (Kempenaers et al., 1999; Lombardo, 2001). We found no correlation between bill colour and cloacal dimensions of blackbirds. Behavioural cues may be more important when assessing relative male quality for extra-pair partners.

Culmen length was positively associated with more reflectance at longer wavelengths and a higher hue value (i.e. more orange-pigmented bills). Similarly, Faivre et al. (2001) did not find any correlation between male blackbird bill colour and body condition, although there was a positive relationship between bill colour and body weight. Foraging success (number of prey captured) is not influenced by size in blackbirds (Desrochers, 1992) although larger birds may be better at catching particular prey that are rich in carotenoids. Larger males may also be more effective at defending territories during male–male interactions (Rohwer, 1982) ensuring access to carotenoid-rich food sources (Endler, 1980; Hill, 1991); they may also be capable of defending larger territories. Recent studies on blackbirds by Bright and Waas (2002) and Préault et al. (2002) found no evidence of female preference for a particular male bill colouration. There was, however, evidence that bill colour plays a role in determining the outcome of male–male interactions (Bright and Waas, 2002; but see Préault et al., 2002). Behavioural rather than (or as well as) morphological cues may be more important for females when assessing relative male quality, particularly in a species such as the blackbird, where males contribute significantly to parental care of the offspring and females are dependent on the male for food provisioning during nesting (Snow, 1958). During male–male interactions, colour cues may be more important for quickly assessing the competitive ability of territory residents and intruders (Bright and Waas, 2002).

In conclusion, the only male quality variable we measured that was positively correlated with bill colour in blackbirds was culmen length. Larger males may be better at defending territories during male–male interactions and/or may defend larger territories, ensuring access to plentiful food and carotenoids that influence bill colour. It is possible that other male attributes may be correlated with male blackbird bill colour and reveal more information about individual quality than the morphological measures taken in this study. Future studies should consider the relationship between bill colour and behavioural measures such as aggressiveness, territory size, song rate and nest attendance.

Acknowledgements

We are grateful to members of the Waikato Ornithological Society, Hugh Clifford, Bev Galloway and Clinton Care, for providing mist-netting training, equipment and expertise. D. Duganzich at AgResearch, Hamilton, I. Duggan, J. Green and C. Pilditch at the University of Waikato provided advice on the statistical analyses. We thank Paul Martinsen and Andrew McGlone at HortResearch, Hamilton for the use of, and assistance with photometric equipment and data and D. Bishop, AgResearch, Wallaceville for identifying feather mites. Thanks to G. Reynolds, K. Ayers, D. Taylor, S. Nakagawa, M. Miyazaki, C. Loomb, R. Bolstad and I. Castro for practical assistance and valuable advice. J. Briskie, G. Hill, C. Pilditch and J. Green and two anonymous referees commented on earlier drafts of this manuscript. This study was carried out with approval from the University of Waikato Animal Ethics Committee (Protocol Numbers 406 and 430).

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