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Signal architecture: temporal variability and individual consistency of multiple sexually selected signals

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Summary

1. Multiple signals should be favoured when the benefit of additional signals outweigh their costs. Despite increased attention on multiple-signalling systems, few studies have focused on signal architecture to understand the potential information content of multiple signals.

2. To understand the patterns of signal plasticity and consistency over the lifetime of individuals we conducted a longitudinal study of multiple signals known to be under sexual selection in male lark buntings, *Calamospiza melanocorys*.

3. Within years, we found extensive among-individual variation in all four plumage ornaments we measured. Surprisingly, there were few correlations among these signals, suggesting that individuals contain a mosaic of signals. Signals were only moderately repeatable across years, which indicates some signal plasticity or age related change. In some years, the direction of change in particular signals relative to the previous year was consistent for most individuals in the population, suggesting that broad scale ecological factors affected the ornament phenotype. Different ornaments were affected by different ecological or social factors because the population-wide shift in a given signal was independent of change in other signals.

4. Our combined results suggest that different signals—including different components of the same color patch in some cases—provide diverse and independent information about the individual to signal receivers in the context of sexual selection.

Key-words: condition-dependence, lark bunting, longitudinal study, multiple ornaments, repeatability, sexual selection

Introduction

It is now clear that complex signals, including multiple sexual ornaments, are widespread and play an important role in sexual selection (Burley 1981; reviewed in Candolin 2003). For example, organisms may have multiple color patches (e.g. black and red spots on guppies, *Poecilia reticulata*) or produce signals in multiple sensory modalities (e.g. song and color patches in many birds). A key question about complex signalling traits is what trait or combination of traits defines an individual signal (Hebets & Papaj 2005)? In some cases the putative multiple signalling traits clearly involve different parts of the body or different sensory modalities. If expression of these distinct traits is highly correlated, then what appear to be multiple signals may in fact serve as one signal (Badyaev 2004; Hebets & Papaj 2005). Likewise, a feature that might seem to be a single signal can have multiple components (e.g. size and color of a color patch) and even here it can be challenging to distinguish which parts integrate and function as one signal, and which comprise separate signals (Hebets & Papaj 2005).

Two different but complementary approaches have been used to determine whether a focal trait or set of traits constitutes a 'distinct signal' that is independent from other signals (Hebets & Papaj 2005). The most widely adopted method is to observe the behavioural responses of individuals—signal receivers—to natural or experimental variation in putative signal traits determined a priori by the researcher (e.g. Jennions & Petrie 1997; Calkins & Burley 2003; Chaine *et al.* 2013). If receivers respond differently to the different traits (Bókony, Lendvai & Liker 2006; Chaine *et al.* 2011), or if the traits elicit responses in different classes of receivers (Andersson *et al.* 2002), then they are assumed to function as independent signals. A second, less common approach is to examine the phenotypic architecture of the signal traits—namely, the correlations among traits within and across years—as a means of revealing the degree to which signals and signal components are linked vs. independent, and hence their potential to provide receivers with independent information (Hebets

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& Papaj 2005). Here, we take this second signal architecture approach to understand multiple signals in male lark buntings (*Calamospiza melanocorys*). This study builds on previous work showing that both males (Chaine & Lyon 2008b) and females (Chaine & Lyon 2008a) respond to variation in multiple plumage signals in male lark buntings.

Determining the strength of phenotypic correlations among traits is a key step in establishing the potential for each trait to contain different information for receivers (Hebets & Papaj 2005). Signals that are very tightly linked with each other will be unlikely to provide independent information to a receiver (Candolin 2003; Badyaev 2004; Hebets & Papaj 2005). From a receiver's perspective, two tightly linked traits could in fact be a single signal with multiple components (Hebets & Papaj 2005). In contrast, traits that show low phenotypic correlations with each other have the potential to provide receivers with different information about the bearer (Candolin 2003) regardless of the underlying genetic relationship between these traits (Roff & Fairbairn 2007). For example, positive correlations could reveal high quality individuals when making two good signals is difficult (e.g. in challenging environments), whereas negative correlations could indicate that trade-offs exist among signals. It remains to be determined how often different signalling traits are correlated and the directionality of these relationships.

Signals that are static over medium time frames (e.g. plumage) but that change over the lifetime of an organism can tell us a lot about signal architecture and the potential information content available to receivers. For example, birds grow new plumage through molt so that in each subsequent breeding season, different feathers make up a given plumage signal. In most birds plumage signals change little between molts. Change in the physical attributes of a plumage signals across molts—and especially how similar change is among individuals in a population—can tell us about the link between a signal and the environment, or condition dependence (Rowe & Houle 1996; Cotton, Fowler & Pomiankowski 2004). If all individuals in a population change signals in a similar way (e.g. all get bigger), then broad scale environmental factors influence signal expression (Garant, Sheldon & Gustafsson 2004; Hegyi *et al*. 2007, 2008). In contrast, if individuals change in different ways (i.e. the signal becomes enhanced in some individuals, reduced in others), then local factors such as individual condition or social environment more likely influence signal expression (Gustafsson, Qvarnstrom & Sheldon 1995; Przybylo, Sheldon & Merilä 2000; Gonzalez *et al*. 2002).

When individuals display multiple signals, the relationships between these signals can also change over time, with implications for our interpretation of the types of information available to the signal receivers. To our knowledge, such patterns have not yet been investigated. For example, two signals might be highly correlated in one breeding season, but be unrelated in other breeding seasons. Observing strong correlations between signals in 1 year might lead to the conclusion that the signals are redundant or not independent. However, if this association is transient and disappears in other years, then the two signals have the potential to reveal different aspects of condition independently in different environments. From a receiver's perspective, the value of information contained in two signals will depend on how tightly associated they are in a given year with the consequence that two signals do not provide added information in years where they are highly correlated. However, a lack of correlation in some years helps us as observers to determine that two signals can provide some independent information in certain environments. Longitudinal analyses of signal traits help us understand the independence of information provided in multiple signals and are key to understanding temporal variation in selection which increasingly appears to be widespread (Chaine & Lyon 2008a; Siepielski, DiBattista & Carlson 2009; Bro-Jørgensen 2010; Cornwallis & Uller 2010).

We investigated the patterns of trait variation and architecture in several signalling ornaments in male lark buntings, including both variation among individual males within years and the degree to which males were consistent or varied in signal expression across their lifetimes. Lark buntings display a number of plumage ornaments, whose color suggests that they depend on different physiological and developmental mechanisms (McGraw & Hill 2000; Griffith, Parker & Olson 2006). Signals with different underlying mechanisms should function independently of each other because they would show different relationships with environmental and social factors. For example the white wing patch feathers of lark buntings are likely generated by feather microstructure (Prum 2006), whereas the black breeding plumage of males results from melanin deposition during feather growth (Jawor & Breitwisch 2003). Previous studies confirm that these ornaments are the targets of sexual selection in lark buntings, and function as multiple signals in two basic sexual contexts (Chaine & Lyon 2008a,b). Female buntings show strong preference for particular male signals when choosing a social mate in a given year, but the signals favoured by females vary across years, and in some cases, females switch the direction of their preference for a given signal across years (Chaine & Lyon 2008a). Many of these same signals are also used in agonistic interactions among males, and different signals appear to be used in different aggressive signalling contexts (Chaine & Lyon 2008b).

Here, we build on our previous behavioural work and examine phenotypic correlations among traits to determine the degree to which the different signals could contain independent information. We examine the same traits previously shown to function as multiple signals in both female mate choice (Chaine & Lyon 2008a) and male–male competition (Chaine & Lyon 2008b): the area and color of dark body feathers and light wing patch feathers (see methods below), two measures of body size and residual mass (Fig. 1 and Fig. S1 in Chaine & Lyon 2008a). We

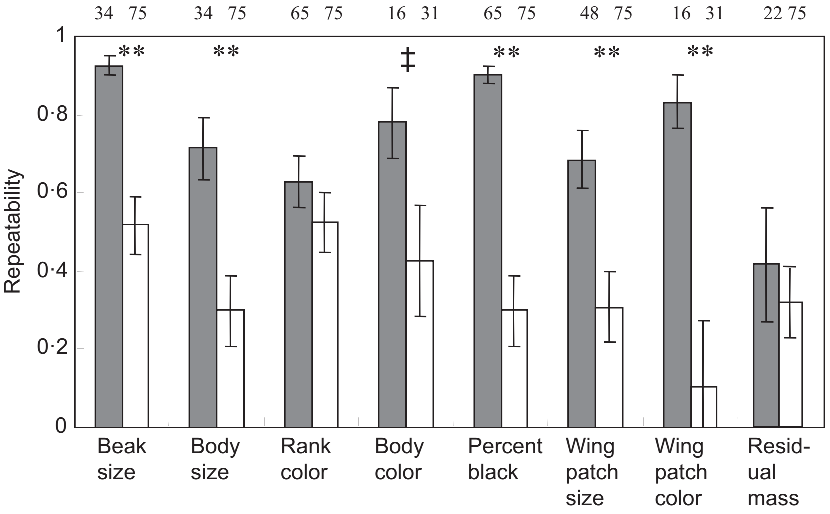

Fig. 1. Repeatability of male signals ± 1 SE. Filled bars represent estimates of within year repeatability (roughly measurement error) and white bars represent estimates of male repeatability across years. Numbers in each sample are reported above the bar. All individual repeatabilities are significant at $P < 0{\cdot}01$, except 'Wing Patch Color' across years where $P > 0{\cdot}05$. Comparison of within and across year repeatabilities denoted above bars by $^{‡}P < 0{\cdot}1$, $^{**}P < 0{\cdot}01$.

use population-wide and longitudinal data to address three questions about signal integration and variation in sexually selected signals in lark buntings: (i) to what degree are different signals correlated within individuals in a given year, (ii) to what degree are ornaments consistent or variable within individuals across time, and (iii) do the relationships between different signals remain similar over time.

Materials and methods

STUDY ANIMAL, STUDY SITE AND BASIC METHODS

Lark buntings are migratory songbirds that breed throughout the high plains of central North America (Shane 2000). Males defend display territories; some fail to attract a social mate, most males are socially monogamous, but low levels of polygyny occur (A. Chaine and B. Lyon unpubl. data). Both males and females incubate (Barna 2004), feed nestlings and fledglings (Shane 2000; Yackel Adams, Skagen & Adams 2001).

We studied breeding lark buntings from May to July on an 80 ha study plot on the Pawnee National Grassland, Colorado USA from 1999 to 2003. We trapped birds with Potter traps at fixed feeding stations throughout the season. Each captured bird was banded with a numbered aluminium band (USFWS) and a unique color band combination for individual identification.

To quantify body size, we measured mass and several standard morphological traits: exposed culmen, length of the beak from tip to nares, wing chord and tarsus length. We categorized males as hatch year (i.e. breeding in their first summer) or older based on the color of primary and secondary flight feathers (brown in yearling males, black in older males; Shane 2000). None of the 346 chicks banded in the first 2 years of this study were recaptured or resighted as an adult, limiting our ability to determine the exact age of individuals or measure heritability of signals.

PATCH SIZE MEASUREMENTS

For wing patches and body feather patches we quantified both the size of the patch and the color of the patch (see below) since size and color of a patch could vary independently. Male plumage is generally black, but individuals vary tremendously in the proportion of brown feathers mixed among the black feathers. We assessed the proportion of black vs. brown feathers to estimate 'patch area' of black body feathers (Fig. S1; Chaine & Lyon 2008a,b). We estimated the proportion of black feathers on each of four body regions (head, nape, back and rump) and ranked white spotting on the birds' bellies (1–4) and subsequently combined these into one overall measure of percent black feathers (see below).

We measured white wing patch size on fully extended wings using two different methods (Fig. S1). In 1999 and 2000, we measured wing patch size as a rectangle, using length from the first to last white feather and height at the widest point. To increase accuracy, in 2001 we began measuring actual wing patch area from digital photographs taken perpendicular to the wing. Measurements were obtained using Adobe Photoshop 5.5: the white wing patch feathers were isolated from the rest of the photograph using the 'magic wand' tool, we then counted the number of pixels comprising the selected area, and then converted pixel number into area (mm^2) based on calibration with a ruler included in all photos. Values for the left and right wings were averaged to obtain a single measure for each male and to minimize error introduced through variation in feather arrangement within the wing patch. To compare measures obtained using the two different methods, we standardized each of the two measurement types to mean of zero and standard deviation of one.

COLOR MEASUREMENTS

We assessed the color of body feathers and wing patches as in past studies (Chaine & Lyon 2008a,b). Body feather coloration was assessed for black feathers only and was measured in two ways: as a rank index of body feather color, with four shade categories of black based on reference photographs of male lark buntings that spanned the observed range of male colors, and measurements of the precise color of body feathers using a spectrometer (2001–2003). The spectrometer yielded an objective measure of color that also included variation beyond the human visual range (300–700 nm, Cuthill *et al.* 1999). The same four body regions were assessed by the two color measurement methods: head, nape, back and rump. To distinguish between the two measures in the text, we refer to visual ranked estimates as 'rank color' and the spectrometer measures as 'body color'. We also measured the brightness of white wing patch feathers using spectrometry.

We measured color using an Ocean Optics USB2000 spectrometer and a PX-2 pulsed xenon light source connected with a fibre-optic probe (Ocean Optics, Dunedin, FL, USA). The probe was fitted with a black solid plastic tip to block incident light, restrict measurement to an area 2 mm in diameter, standardize the distance from the fibre-optic tip to the feather (6 mm), and standardize the measurement angle (45°; Andersson & Prager 2006). Data were collected using Ocean Optics' OOIbase software. The spectrometer was calibrated between each measurement using a spectralon white standard (Labsphere, Inc, North Sutton, NH) and a flat black standard to ensure accuracy of measurements on black feathers. We obtained three color measures for each of the four body regions and for wing patches.

We calculated relevant color measures from standard equations for tristimulus color systems (hue, chroma/saturation, brightness) using ColoR1.7 software (software link and review of methods in Montgomerie 2006). For wing patches we calculated overall brightness as well as brightness and saturation in the UV range (320–400 nm) since the amount of light reflected in this range is where the biggest difference among individuals lies (Siitari & Huhta 2002; Chaine *et al.* 2011). For body feather patches we focused on overall brightness since there was little variation among individuals in hue or saturation. Higher brightness values of body feathers indicates greyer coloration, while lower brightness values indicate blacker coloration. This is counter-intuitive with respect to the quality of the signal and opposite the pattern for rank color, so we reversed the sign of the resulting principal component related to body color brightness so that darker males have higher values for body color. This transformation has no effect on the statistics themselves.

REPEATABILITY OF MEASURES

Some banded males returned to the study site in two or more years, allowing us to estimate the consistency of male signals across time as measured by repeatability of male signals (Becker 1985; Lessells & Boag 1987). Lack of repeatability across years could be due to actual change in male signals or to measurement error. To determine the magnitude of measurement error, we measured some birds on different days in the same year. Repeated measures of body color and spectrometry within years were combined with repeated measurement of museum specimens to reduce the effects of natural feather wear that occurs within the breeding season (e.g. McGraw & Hill 2004; Delhey *et al.* 2006) on measurement error estimation. In contrast with birds in the wild, the color of museum specimens would not change between measures taken 1 month apart; lack of repeatability would be due entirely to measurement or sampling error. To parallel methods used in the field, data on body color for both live birds and museum specimens were collected by multiple observers, We determined repeatability of wing patch size by measuring a second wing patch photo of a given bird taken on a different day (Chaine & Lyon 2008b).

STATISTICS

All statistical analyses were completed in SYSTAT 10.2 or in spreadsheet software using two-tailed probabilities. All variables were normally distributed (skewness and kurtosis < 1·5 for all traits and Durbin Watson's $D < 2{\cdot}3$ for all residuals) so we use parametric statistics throughout. We combined measures of the different body parts with principal components analysis (PCA) to obtain an overall value for each signal trait (e.g. overall color of body feathers). PCA is preferable to other summary methods since it makes no assumptions about differences in the sizes of parts or the units of measures such as brightness and saturation of wing patch color. We ran separate PCAs on the following *a priori* 'signal traits' rather than one analysis of all measures together because the orthogonal selection of more than one component would preclude subsequent examination of correlations among signals: (i) body size, (ii) rank color, (iii) body color, (iv) percent black body feathers and (v) wing patch color (brightness). We retained all components with an eigenvalue larger than one, and present information on raw traits, eigenvalues and factor loadings in Table S1. We calculated residual mass (Brown 1996) as the residuals of mass regressed on the composite body size measure from the principal components analysis. Residual mass did not change significantly within a season (Repeated Measures ANOVA, $n = 23$, $F = 1{\cdot}68$, $P = 0{\cdot}21$), so we did not include capture date as a covariate in any analyses. We conduct multiple comparisons when examining correlations among signals, which could increase the risk of Type I errors, yet table-wide correction could also decrease the chance of detecting true correlations. We therefore provide both uncorrected and corrected significance tests (along with correlation coefficients) to allow readers to evaluate the results independently.

Results

SIGNAL VARIATION AMONG MALES

Principal components analysis of body size morphology yielded two components representing 'beak size' and 'body size' that accounted for 67·2% of the variation in male size morphology. Each component displayed low variation in the population (Table S1; CV beak size = 5·6%, CV body size = 2·9%). Principal components summary of ranked body feather color (i.e. shade of black, with larger values representing darker plumage) produced a single component that captured 65·6% of the variation among males, and the measure varied considerably among males (Table S1; CV = 23·8%). The proportion of the body covered by black feathers yielded one component accounting for 49·8% of the variation in component traits and showed moderate variation among males (Table S1; CV = 13·3%). Wing patch size also varied considerably among males (CV = 13·2%). All of these measures were highly repeatable within years (Fig. 1).

PCA summary of black body color measured with the spectrometer yielded a single component, body color, representing 57·0% of the overall variation in black body feather coloration (Table S1). Body color varied considerably among males (CV = 43·5%), with larger values corresponding to blacker males after sign reversal of the component. The analysis of wing patch color created a single component associated with overall and UV brightness and UV saturation, representing 75·5% of the variation in those measures, and showed moderate variation among males (Table S1; CV = 18·8%). Higher values of this principal component indicate brighter and more UV saturated wing patch feathers. Both measures were significantly repeatable within years (Fig. 1).

CORRELATIONS BETWEEN SIGNALS

We first compare correlations with data from all 5 years pooled, and below we analyse the same correlations for each year separately. Most pair-wise comparisons of signal traits within individuals showed weak or no correlation, but a few comparisons yielded moderate correlations that were highly significant (Table 1). Not surprisingly, two measures of the same signal, rank color and body color,

Table 1. Population level Pearson's correlation coefficients among signal traits. Sample sizes are $N = 624$ (all measures except spectrometry), $n = 337$ (spectrometry)

Trait	Beak size	Body size	Rank color	Body color	Percent black	Wing patch size	Wing patch color
Body size	–						
Rank color	0·08*	0·08*					
Body color	−0·02	−0·01	0·60**,†				
Percent black	0·04	0·11**	0·25**,†	0·27**,†			
Wing patch size	0·01	0·13**	0·16**,†	0	0·10*		
Wing patch color	−0·07	0·07	−0·01	−0·17**,†	0·06	0·12*	
Residual mass	–	–	−0·05	−0·18**,†	0·01	0·01	−0·06

Significance at *$P < 0·05$, **$P < 0·01$.
†If significant after sequential Bonferroni correction.

showed the strongest correlation. All other significant correlations were considerably weaker, with significant coefficients ranging from 0·27 to 0·08 (Table 1). Overall, 11 of the 24 correlations between signals (excluding the correlation between the two measures of body color) showed a significant relationship. Five of 24 correlations remained significant (Table 1) with adjustment of alpha levels for table wide error rates.

Correlations between signals that convey redundant information should show similar strengths of association in different years if sample sizes are reasonably similar. To investigate this, we examined correlations as above, but also did so separately for each year of the 5-year study and then compared the strength of associations among years for each given signal trait. Overall, 23 of 114 correlations showed a significant relationship, and 5 of 114 correlations remained significant after sequential Bonferroni adjustment—three of which are correlations between the two measures of body feather color (Table 2). Sample sizes ranged from 80 to 162 depending on the year, so it is unlikely that any meaningful relationships between two signals would have been missed. For a given set of correlations between the same two signals, few coefficients maintained the same sign or strength. Notable exceptions are for pairs of signals that also showed significant correlations when we pooled data from all years. For example, darker individuals always had more black feathers (both measures of color vs. percent black), larger wing patches (rank color vs. wing patch size), duller wing patches (body color vs. wing patch color) and a lower residual mass (body color vs. residual mass). However, despite the consistency of these correlations, their strength remained weak—generally $< r = 0·30$—as was true for most correlations between signals in all years.

SIGNAL CONSISTENCY AND VARIATION ACROSS YEARS

Repeatability of signals across years

We compared the plumage characteristics of adult males (i.e. excluding yearling males due to age-dependent change; see below) across years to determine the degree of consistency within individuals across time. Of 624 banded males, 74 individuals returned in subsequent years, some in multiple years, for a total of 176 recaptures. All signals, with the exception of wing patch color, were significantly repeatable for males across years (Fig. 1). However, since repeatability values were considerably less than one for all signals, individual males clearly change somewhat in traits across years. To determine the degree to which non-repeatable variation in each signal represents true trait change vs. measurement error, we compared the across-year repeatability values with those obtained by within-year repeated measurements (an estimate of measurement error). Repeatability values within years were significantly higher than the across-year values (Fig. 1) with the exception of rank color, indicating that the lower repeatability measures across years reflects actual trait change, and not simply measurement error. We therefore examined the degree to which year-to-year plumage change showed patterns consistent with the effects of age, residual mass or annual variation of ecological conditions.

Age-dependent signal change

Yearling males in many songbirds are often duller than older males (Rohwer, Fretwell & Niles 1980) so we compared plumage coloration of first year males with older birds to see if lark bunting plumage changes with age. This analysis excludes the color of primary and secondary flight feathers because they are completely diagnostic of age (and were used to age birds). First year birds differed from older birds by being somewhat smaller in body size, having smaller wing patches, and by having lighter plumage with a lower proportion of black body feathers (Fig. 2). Discriminant function analysis indicates that first year and older adult birds can be distinguished using a combination of the measured signal traits ($F_{8,608} = 18·6$, $P < 0·001$), but the discrimination is imperfect with only 71% of males correctly assigned.

We also examined if age-dependent plumage change continued in males after their second year by determining if change in signal traits was directional for males that returned repeatedly after their second breeding season. Because repeated measures ANOVA is extremely sensitive to

Table 2. Pearson's correlation coefficients among signal traits for each year separately. Sample sizes (spectrometry) 1999 = 80; 2000 = 155; 2001 = 145 (130); 2002 = 82 (59); 2003 = 162 (148)

Trait	Year	Beak size	Body size	Rank color	Body color	Percent black	Wing patch size	Wing patch color
Body size	1999	−0·09	–					
	2000	0·12	–					
	2001	−0·17*	–					
	2002	−0·01	–					
	2003	−0·01	–					
Rank color	1999	−0·09	0·14	–				
	2000	0·12	0·19*	–				
	2001	0·07	0·10	–				
	2002	0·05	−0·03	–				
	2003	0·11	−0·01	–				
Body color	2001	−0·02	−0·02	**0·49**, †**	–			
	2002	−0·12	−0·01	**0·67**, †**	–			
	2003	−0·06	−0·05	**0·66**, †**	–			
Percent black	1999	0·04	0·17	**0·23***	–	–		
	2000	0·03	0·17	**0·32**, †**	–	–		
	2001	0·14	0·02	**0·28****	**0·34**, †**	–		
	2002	0·06	0·12	**0·36****	**0·15**	–		
	2003	0·02	−0·07	**0·21****	**0·25****	–		
Wing patch size	1999	−0·08	0·07	**0·16**	–	0·19	–	
	2000	0·11	0·23**	**0·24****	–	0·12	–	
	2001	0·02	0·16	**0·19****	0·06	0·12	–	
	2002	−0·06	−0·11	**0·11**	0·10	−0·03	–	
	2003	−0·03	0·17**	**0·10**	−0·04	0·06	–	
Wing patch color	2001	−0·12*	0·22	0·01	**−0·15**	0·002	−0·07	–
	2002	−0·01	0·09	0·10	**−0·02**	0·22	0·02	–
	2003	−0·04	−0·01	−0·05	**−0·22****	−0·02	0·21**	–
Residual mass	1999	0·25*	0·31**	0·16	–	0·28*	0·11	–
	2000	−0·08	−0·11	−0·02	–	0·11	−0·01	–
	2001	0·17*	0·02	−0·10	**−0·09**	−0·03	0·13	−0·08
	2002	0·12	0·11	−0·09	**−0·14**	−0·09	−0·02	−0·10
	2003	−0·02	−0·05	−0·09	**−0·14**	−0·13	−0·10	−0·06

*$P < 0{\cdot}05$, **$P < 0{\cdot}01$.

†Significant after sequential Bonferroni correction; bold values are traits that were significant after sequential Bonferroni correction in analyses with all years combined shown in Table 1.

differences in the number of replicates, we ran separate analyses for males caught in 2, 3 and 4 years (two and three for spectrometer data) of the study, respectively, to maximize use of the available data. None of the signals changed directionally with time—these signals are not age-dependent once a male is past his first year of life (repeated measures ANOVA; all signal traits except spectrometry: 2 years, $n = 62$; 3 years, $n = 18$; 4 years, $n = 6$; spectrometry traits: 2 years $n = 27$; 3 years $n = 6$; all $P > 0{\cdot}05$, except beak size and body color for 2 years where $P = 0{\cdot}02$ and 0·05, respectively; Fig. 3).

Environmentally mediated signal trait change

Since signal change was independent of age for males 2 years or older, we investigated whether any signal traits changed across years in a coordinated way. Such coordinated change could indicate that large scale environmental influences affect changes in male signals—if the entire population experiences the same large-scale environmental factors that vary across time, then any of their signal traits that are directly sensitive to environmental conditions will show similar changes across time. Several of the signals showed these types of coordinated year effects, as evidenced by mean change that differed significantly from zero for analyses only involving males that returned across years (Fig. 4; significance assessed by paired *t*-tests). For example, beak size decreased in 2 years while wing patch size and residual mass increased in 1 year and decreased in another (Fig. 4). Body color also increased significantly from 2002 to 2003 (Fig. 4). Finally, the change across years in proportion of body feathers that were black showed a striking oscillating pattern, repeatedly increasing and decreasing from 2000 to 2003 (Fig. 4). Although most signal traits showed evidence of directional change in at least 1 year of the study, no single year affected most or all signal traits at the same time.

Correlated change in signal traits across years

Since some of the signals we measured were correlated with each other within years (Table 1), we examined if the degree of change across years in one signal for an individual was correlated with the degree of change in a second signal across the same years. Such correlated changes between signals could suggest strong integration of different

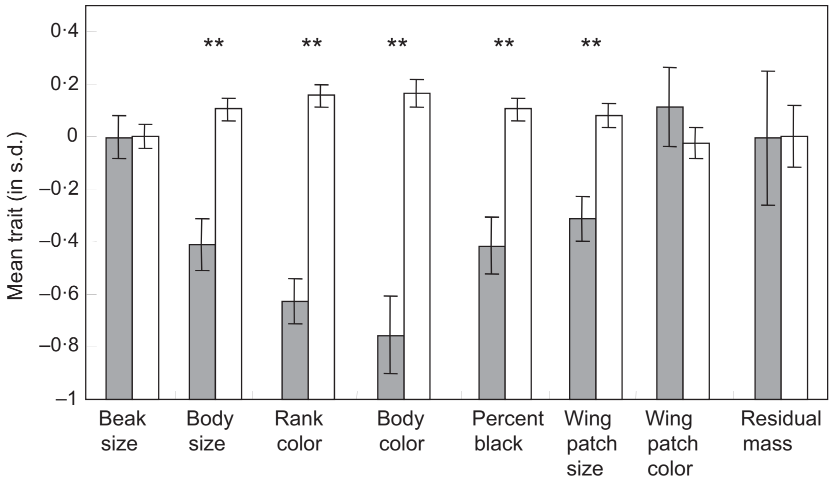

Fig. 2. Comparison of signal traits between hatch year (1 year old) and birds older than 1 year in the population. Bars show mean and standard error with all signal traits standardized to mean = 0 and standard deviation = 1. All analyses had 498 adults and 126 hatch year birds, except spectrometry traits with 277 adults and 60 hatch year birds. White bars represent birds older than 1 year and filled bars represent hatch year birds. $^{**}P < 0{\cdot}01$.

signal components. Increases in wing patch size across years were correlated with darkening rank body color and increases in body size (Table 3). Also, as wing patch size increased, the color of the wing patch tended to get duller. There was no relationship between changes in male body feather color (either measure) and changes in the proportion of black feathers, but there was a negative association between changes in body color and changes in wing patch color.

Correlated changes associated with one trait in particular, residual mass, are of special interest because it is a potential index of body condition. However, no other signals changed with changes in residual mass, except that males that increased residual mass tended to get lighter with respect to body color (Table 3). We also examined the association between a male's residual mass in a given year (not change in residual mass) and changes in his signal traits from that year to the next. In no case was residual mass associated with the degree of change in a male's signal traits (all $P > 0{\cdot}1$, $n = 85$ except for signals measured by spectrometry where $n = 29$).

Discussion

Despite intense interest in multiple and multi-component signals, surprisingly few studies have sought to determine if the different traits measured are indeed separate signals or components of one signal trait (Hebets & Papaj 2005). For example, a high correlation between patch size and color in red shouldered widowbirds (*Euplectes axillaris*;

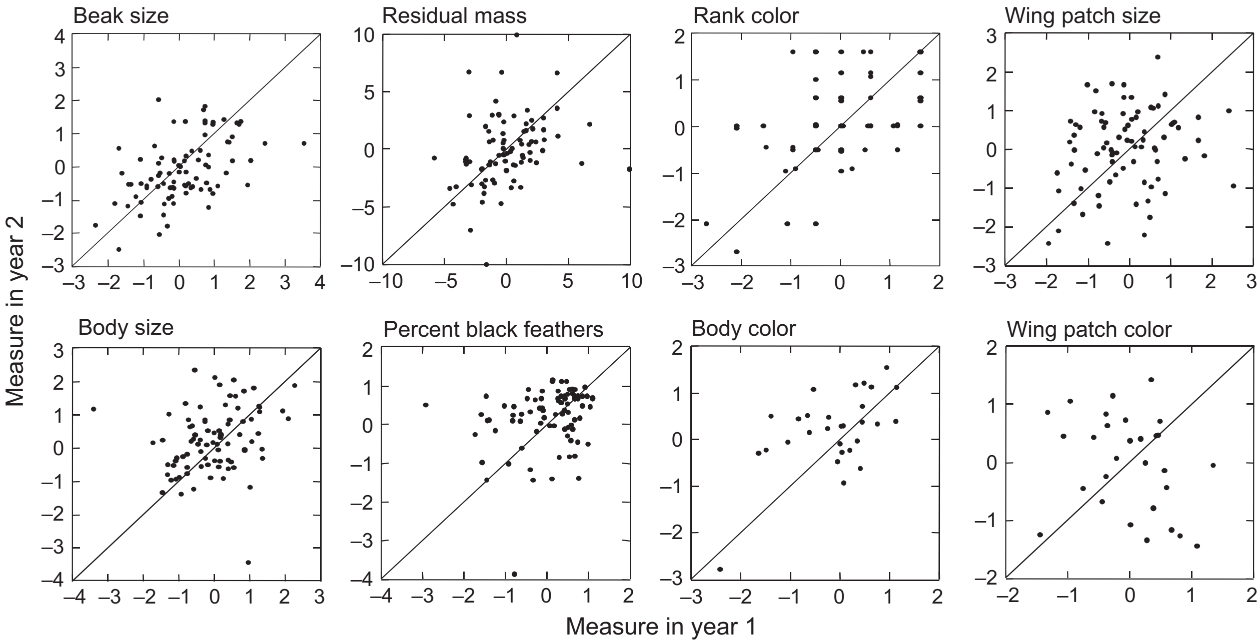

Fig. 3. Age related change in male signals from second year and older (i.e. yearling males excluded from analysis) depicted as measurement of a male's signal trait in the first year captured compared to measurement in the following year (e.g. only two sequential years are plotted). All points would fall above or below the 1:1 line if signal trait change was age related whereas equal scatter around it reflects age-independent change. Sample sizes are $N = 85$ except for spectrometry where $N = 29$.

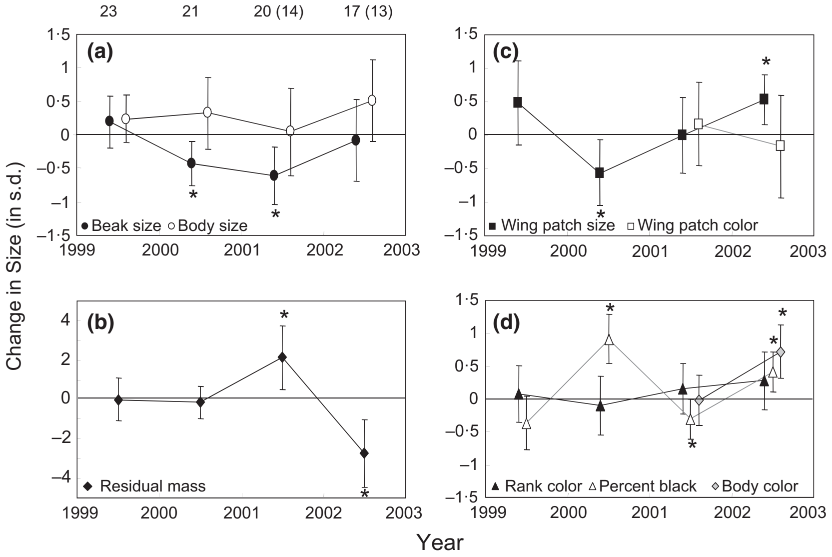

Fig. 4. Changes in male signal traits (mean = 0, SD = 1) for individuals returning in consecutive years. Points show the average change in male signals calculated as the differences in signals (year 2 – year 1) for each individual caught in both years. Error bars are 95% confidence intervals. Sample sizes presented above panel a are the same for all signal traits except spectrometry samples which are presented in parentheses. (a) body size, (b) residual mass, (c) wing patches and (d) body feather color. Significance from a paired *t*-test denoted by *$P < 0{\cdot}05$.

Pryke & Andersson 2003) suggests that these two components each carry little independent information and likely function as a single signal. Badyaev & Young (2004) analysed links among components of color patches in three species. In the house sparrow (*Passer domesticus*), the components were linked developmentally and would thus likely provide similar information. In contrast, in house finches (*Carpodacus mexicanus*) and common redpolls (*Carduelis flammea*), the trait components were weakly correlated, which Badyaev & Young (2004) interpreted as developmental independence and with the potential for each trait component to signal independent information. The relationships among signal traits help us understand the potential independence of information content of signal components (Hebets & Papaj 2005), but single-year snapshots can be misleading as the relationship between condition-dependent traits can change. Our goal here was to use longitudinal data to better understand signal architecture and the potential information content of multiple sexual signals.

LINKAGE AMONG SIGNALS

Examination of signal architecture—correlations among signal traits within and among years—can tell us if traits can provide independent information, as well as the temporal consistency of this independence. A few of the traits we measured in lark buntings were correlated with each other within years (11 of 24 correlations significant or 5 of 24 after controlling for multiple comparisons for all years combined). However, even these correlations were not very strong with one trait explaining only 7% of the variance in the second trait. This suggests that most traits we measured could be multiple signals that convey independent information. Moreover, examining the correlations separately for each year of the study revealed that very few pairs of traits showed consistent significant correlations in each of the 5 years (Table 2). A number of authors have pointed out that genetic correlations can be masked when good environmental conditions influences phenotypes such that the usual correlation breaks down (van Noordwijk & de Jong 1986; Houle 1991; Roff & Fairbairn 2007), so weak correlations simply provide evidence that two traits can provide some different information to receivers regardless of their underlying genetic relationship. It is difficult to compare the patterns we observed with those of other species because no other study has examined the stability of correlational structure in multiple signal traits across time. Our analysis in lark buntings emphasizes the point that correlations based on single year studies can be misleading

Table 3. Correlated change between pairs of signals across consecutive years for individual males who were present in 2 years

Trait	Beak size	Body size	Rank color	Body color	Percent black	Wing patch size	Wing patch color
Body size	0·01						
Rank color	0·045	−0·15					
Body color	0·04	0·12	−0·10				
Percent black	0·14	0·17	0·09	0·22			
Wing patch size	0·01	0·28*	0·30*	0·11	−0·05		
Wing patch color	−0·15	0·01	−0·18	−0·38*	0·15	−0·34	
Residual mass	−0·09	−0·30**	0·04	−0·35	−0·17	−0·18	0·14

Shown are Pearson's correlation coefficients. Sample sizes are $N = 85$ (all measures except spectrometry), $N = 29$ (spectrometry).
*$P < 0{\cdot}05$, **$P < 0{\cdot}01$, none are significant after sequential Bonferroni correction.

because they reflect short-term effects of a common environment (van Noordwijk & de Jong 1986; Zera, Potts & Kobus 1998).

The strength of the correlation between two traits can indicate the potential for the traits to contain independent information for receivers. We found only weak relationships between the size and color components of the two different plumage patches (i.e. black and white) in data from all years combined. For example, wing patch color and wing patch size were only weakly correlated (r = 0·12) and both rank and body color were only moderately correlated with the proportion of black feathers (r = 0·27 and 0·25, respectively). These correlations are considerably weaker than those reported for other species, where size and color have been interpreted as composites of the same signal (house finch: r = 0·48 Badyaev *et al.* 2001; red-shouldered widowbird shoulder patch: r = 0·59 Pryke & Andersson 2003; red-collared widowbird *Euplectes ardens* collar patch: r = 0·76 Pryke, Lawes & Andersson 2001). Although the weak correlations we found between patch size and color suggest that each trait could signal independent information, whether they actually serve as multiple signals depends on how receivers use the information. Our previous work on the responses of receivers to these traits —both potential mates and rivals—suggests that the different traits we have measured are treated as separate signals by receivers (Chaine & Lyon 2008a,b). Manipulative experiments to test the independent effect of each signal are still necessary to determine if such traits are independent signals, yet few studies have undertaken the complex experimental designs required (reviewed in Rowe 1999) and none have been conducted in species where selection fluctuates over time as it does in lark buntings (Chaine & Lyon 2008a).

Further indication that signal traits in lark buntings provide independent information comes from the lack of coordinated change in pairs of traits across years. Traits that are not independent traits due to production by the same physiological or genetic mechanism should change in unison across years. However, only 2 of the 12 pairs of traits (0/12 after correction; Table 3) that were correlated within years in lark buntings showed a correlation in the degree of change across years. Furthermore, the few instances of coordinated change we did observe involved traits that have very different developmental origins (e.g. non-pigmented wing patches and melanin colored body feathers), not traits that share a developmental pathway (e.g. melanin body feather color and percent coverage of black feathers). A longitudinal examination of trait associations helps avoid incorrect conclusions about the underlying nature of trait associations seen in 1 year.

POTENTIAL INFORMATION PROVIDED BY SIGNAL TRAITS

Signal architecture (trait correlations) and the pattern of change in trait expression in individuals across years can provide insight into the types of information that signal traits could convey to receivers. In the following sections, we show how longitudinal patterns of trait change and changes in the correlations among traits can be used to evaluate what types of information could be conveyed by signal traits in lark buntings.

Signal consistency and possible genetic/ developmental information

Adult male lark buntings showed moderate repeatability of plumage traits across years, which could be indicative of either genetic or early developmental effects on plumage. All traits, except wing patch color, were significantly repeatable across years despite large environmental variation among years on the breeding grounds, where lark buntings undergo most of their yearly complete molt (Shane 2000; range of average temperature during nesting across years: 12–20 °C, cumulative winter rainfall across years: 87–322 mm; SGS LTER data base). Repeatability estimates give an upper estimate to heritability of a trait (Falconer 1981) and often provide a reasonable indication of heritable variation (e.g. forehead patch size in collared flycatchers (*Ficedula albicollis*): repeatability r = 0·74, heritability h^2 = 0·58, Hegyi, Török & Toth 2002) even when controlling for the effects of early developmental conditions (Garant, Sheldon & Gustafsson 2004). Thus, similar to other species (reviewed in Mundy 2006), lark bunting plumage traits may be heritable and function as signals of genetic quality.

Age

Many species have plumage that changes with age (Rohwer, Fretwell & Niles 1980; Lyon & Montgomerie 1986) and such age-dependent traits can be important in female choice (e.g. Simmons & Zuk 1992). Plumage of yearling male buntings was consistently duller than that of older males, but for most traits (except primary feather color) there was considerable overlap so that plumage is not a reliable indicator of age. Moreover, yearling males comprise a small fraction of the breeding male population (16% of resident males, A. Chaine and B. Lyon, unpublished data). Thus, most of the variation in sexually selected traits in lark buntings is independent of age, a pattern reported in several other studies (Slagsvold & Lifjeld 1992; Hegyi, Török & Toth 2002; Badyaev & Duckworth 2003; Hill 2003; Wolf *et al.* 2004).

Plasticity in signals and condition dependent signalling

In a number of species, signal traits provide condition-dependent information (Gustafsson, Qvarnstrom & Sheldon 1995; Candolin 2003; Cotton, Fowler & Pomiankowski 2004). Most male lark bunting plumage and body size traits do change somewhat across years and thus could reflect condition-dependent information. Some studies have tracked trait changes for individuals across years (e.g. Kruuk *et al*. 2002; Gustafsson, Qvarnstrom & Sheldon 1995; Griffith & Sheldon 2001; Hegyi, Török & Toth 2002), but very few have tracked temporal patterns for multiple traits (Badyaev & Duckworth 2003; Garant, Sheldon & Gustafsson 2004; Hegyi *et al*. 2007).

Examining population wide consistency in the direction of change in plastic traits provides insight into the scale of environmental influences that cause phenotypic variation. Most lark bunting traits showed synchronous directional change across one or more years of the study—a pattern expected for traits whose expression depends on large-scale environmental drivers—but a few also showed some years of asynchronous change among males, potentially indicating more local influences. These patterns indicate that phenotypic plasticity of male sexual signals is influenced by both broad and local scale factors, and that the relative influence of broad vs. local factors varies across years.

The traits we studied here have all been shown to be under female choice in some years, although the specific traits preferred by females vary from year to year (Chaine & Lyon 2008a). Condition-dependent traits could signal current male condition and, consequently, predict direct fitness benefits to a female. Furthermore, if environmental factors vary among years in a way that affects multiple condition-dependent signals in different ways or are influenced by different aspects of the environment, females may enhance direct fitness benefits by attending to different traits in different years (Reid & Weatherhead 1990; Zuk, Ligon & Thornhill 1992; Chaine & Lyon 2008a). Indeed, female lark buntings gain direct fitness benefits not only by choosing males with specific plumage traits, but by changing their preferred traits across years (Chaine & Lyon 2008a). Such a pattern would provide a strong selective force for the evolution and maintenance of multiple sexual ornaments.

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Data accessibility

Plumage and body size trait data from male lark buntings caught between 1999 and 2003, repeated measurements of plumage spectrometry, and plumage trait data of museum specimens are deposited in the Dryad Digital Repository (doi: 10.5061/dryad.n15m7) (Chaine & Lyon 2015).

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Fig. S1. Photograph of a male lark bunting illustrating plumage color measures.

Table S1. Factor loadings for PCA analyses of body size and plumage characters (percent black, rank color, body color, wing patch color).

Supplementary information for “Signal architecture: temporal variability and individual consistency of multiple sexually selected signals” by Alexis S. Chaine and Bruce E. Lyon.

Appendix S1 comprises Figure S1 and Table S1.

Figure S1: Male lark bunting in a flight display illustrates plumage patches we measured. Note the brown colored feathers on the rump and a few small brown feathers on the head which were quantified as part of the ‘percent black’ measurement (percent brown vs. black feathers on each body region). White wing patch size was measured from photographs of wings extended much like that of this bird in flight. Photograph by Bruce Lyon.

Table S1: Eigenvalues and component loadings for each signal trait in the principal components analysis.

Body Size PCA

Eigenvalue	1.488	1.198
Factor Loadings		
	Beak Size	Body Size
wing chord	-0.007	0.78
tarsus	0.071	0.764
nostril	0.858	0.077
culmen	0.865	-0.005

Rank Body Color

Eigenvalue	2.625
Factor Loadings	
	Rank Color
Head color	0.662
Nape color	0.871
Back color	0.883
Rump color	0.806

Spec Body Color

Eigenvalue	2.277
Factor Loadings	

	Spec Color
Head brightness	0.632
Nape brightness	0.731
Back brightness	0.822
Rump brightness	0.818

Percent Black

Eigenvalue 2.491

Factor Loadings

	Percent Black
Head Percent	0.711
Nape Percent	0.806
Back Percent	0.722
Rump Percent	0.688
Belly Rank	0.586

Wing Patch Color

Eigenvalue 2.265

Factor Loadings

	Wing Brightness
Total Brightness	0.848
UV brightness	0.997
UV chroma	0.742