Original Article

Multiple achromatic plumage ornaments signal to multiple receivers

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We investigated whether achromatic plumage traits can act as multiple ornaments in an Arctic-breeding passerine, the snow bunting (*Plectrophenax nivalis*). Specifically, we examine whether multiple ornaments are providing multiple differing messages, are redundant, are unreliable signals of male quality, or are aimed at different receivers. We measured plumage reflectance and pigmentation patterns made conspicuous during male inter- and intrasexual displays that advertise different plumage regions. Our results indicate that although several aspects of male plumage may have redundant messages, different body regions appear aimed at different receivers. The wings of males—displayed primarily toward females during courtship—appear to indicate a pair's future reproductive performance. Conversely, melanin-based plumage reflectance displayed during intrasexual threat displays provides information on territory features and a male's capacity to defend it (i.e., territory size, territory quality, testosterone levels). Taken together, we suggest that snow buntings have multiple ornaments that provide information of differential importance in inter- versus intrasexual communication. This study demonstrates that achromatic plumage traits can serve in complex communication. *Key words:* achromatic plumage, individual quality, multiple ornaments, multiple receivers, Plectrophenax nivalis. *[Behav Ecol]*

INTRODUCTION

Males often display elaborate ornaments that are honest indicators of individual quality, where ornament production or maintenance comes at a cost to the bearer (Zahavi 1975; Andersson 1994a). These ornaments can be used in inter- and intrasexual signaling: in the former, females can use male ornamentation to assess and choose potential mates (Hill 1991; Parker et al. 2003), whereas in the latter, conspecific males can use ornamentation to select territory neighbors (Greene et al. 2000), or assess the dominance rank of potential opponents (Mennill et al. 2003; reviewed in Santos et al. 2011).

The evolution of multiple ornaments in numerous species appears inconsistent with the theory of honest signaling. Theoretical models have suggested that females should simply favor the most honest and detectable signal, ignoring any others (Schluter and Price 1993; also see Johnstone 1996); it would therefore seem suboptimal for males to produce multiple costly ornaments if females do not assess them. Three hypotheses have been suggested to explain why multiple signals evolve (Møller and Pomiankowski 1993) and are supported by theoretical models (Johnstone 1995; under certain conditions: Johnstone 1996). The *multiple message hypothesis* states that different signals are indicative of different aspects of male condition; the *redundant signal hypothesis* predicts that multiple signals will indicate similar aspects of condition, decreasing the likelihood that individual quality

will be improperly assessed; and the *unreliable signal hypothesis* suggests that multiple ornaments do not actually indicate current male condition—these may have evolved through runaway selection due to female preference (Fisher 1915) but over time have become uncorrelated to individual condition (described in Møller and Pomiankowsky 1993). Andersson et al. (2002) also proposed that inter- and intrasexual selection may simultaneously contribute to the maintenance of multiple ornaments: as such, the *multiple receiver hypothesis* suggests that multiple ornaments may be evaluated by inter- and intrasexual conspecifics concurrently, with males and females selecting for the use of different ornaments.

All 4 hypotheses have been examined in several avian systems, all of which display complex ornaments (Hebets and Papaj 2005): different pigmentation types (i.e., carotenoid and melanin; Jawor and Breitwisch 2004; Freeman-Gallant et al. 2010), intrinsic versus extrinsic signals (i.e., plumage and territory or bower quality; Marchetti 1998; Doucet and Montgomerie 2003), plumage color versus length (i.e., badge color and tail length; Andersson et al. 2002), or even plumage versus wattle length (Papeschi and Dessi-Fulgheri 2003). To date, fewer studies have examined whether black, grey, and white patterns (termed achromatic plumage) act as multiple ornaments (although see Pärt and Qvarnström 1997; Mennill et al. 2003; Török et al. 2003; Doucet et al. 2005), despite the apparent use of black and white plumage patterns in visual behavioral displays (see Galván 2008) and its common occurrence across avian species. Achromatic species provide a useful system for the study of multiple ornaments because these plumage traits depend on a single mechanism of production (i.e., the degree of melanin pigmentation). Nonetheless, achromatic plumage remains a strong candidate for an efficient mode of visual communication due to the highly conspicuous contrast between black and white body

regions (Endler 1992; Andersson 2000). Moreover, although much of the attention focused on achromatic plumage has revolved around its function as a status signal (reviewed in Santos et al. 2011), recent evidence has demonstrated that achromatic plumage may also act as a condition-dependent signal (McGlothlin et al. 2007; Gladbach et al. 2011).

We investigated the potential for signaling using multiple ornaments in an Arctic-breeding, purely achromatic species. Breeding male snow buntings (*Plectrophenax nivalis*) are primarily white throughout their head, breast, and wings with black on their mantle, primaries, and inner rectrices (tail feathers; Figure 1a). Furthermore, males have alternating black and white areas of plumage within the wing that are conspicuously visible when they are displayed during mate-attraction advertisements (Tinbergen 1939)—males hold out their wings and turn to face away from females. Specifically, males have white wings with black primary tips, a black alula (set of 2 black feathers on the leading edge of the wing) and some have black spots within the white area of the wing (Figure 1b). Consequently, plumage has the potential to act as an achromatic signal of male quality in this species and serve in intersexual attraction (Tinbergen 1939; see Andersson 2000). Males also defend territories solely for access to nesting sites and perform visual intrasexual threat displays advertising different aspects of their plumage: their breast, mantle, and rectrices (Tinbergen 1939). As such, we hypothesized that males might use multiple achromatic visual signals (wings vs. body) to advertise different and complex sets of information to different receivers. Accordingly, we investigated the potential information content of inter- and intrasexual signals in the context of the *multiple message, redundant signal, unreliable signal*, and *multiple receiver hypotheses* (Table 1). We explored the relationship between achromatic plumage traits and male quality using a novel variable selection technique to identify important plumage predictors of male quality. Finally, we validated integrative measures of individual condition and territoriality that have fitness-related consequences as proxies of male quality.

METHODS

Study species and sampling

We studied breeding pairs of snow buntings from late May to August of 2010 ($N = 17$) and 2011 ($N = 13$) at East Bay Island, Nunavut, Canada (64°02′N, 81°47′W). High breeding densities at this location (approximately 70 pairs/km^2; Love OP, unpublished data) likely result from an abundance of granite rock assemblages, ideal nesting habitat for this crevice-nesting species (Montgomerie and Lyon 2011). Snow buntings are socially monogamous during the seasonally constrained breeding period: males defend territories, females build the nest, males feed their incubating mate, and biparental feeding is necessary to successfully rear young (Lyon et al. 1987). Pairs at our study site attempt a single brood each breeding season (Love OP, unpublished data). The majority of males arrive to the island
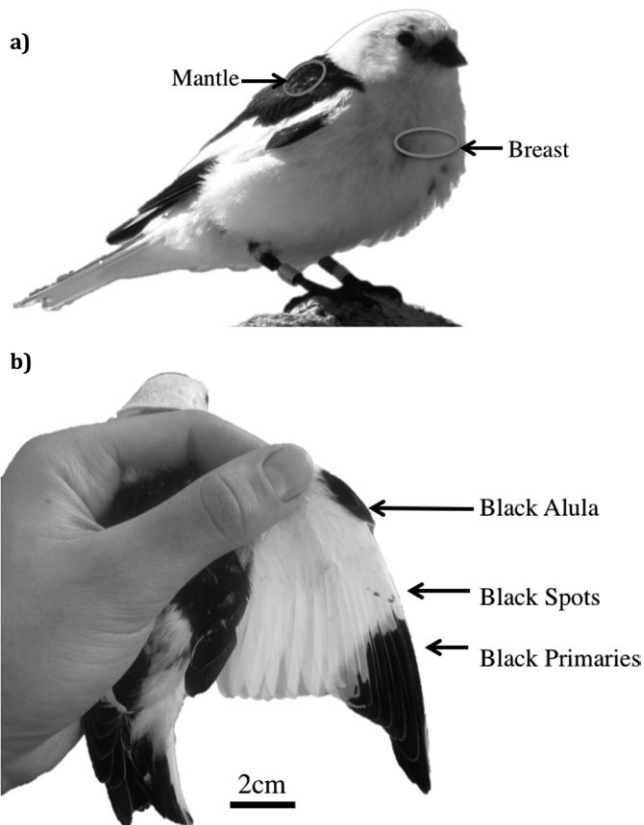
Figure 1
Male snow bunting breeding plumage traits measured (a) body regions from which feather samples and reflectance measurements were taken and (b) wing pigmentation pattern variables assessed using wing photographs and ImageJ. This image does not represent the actual photograph used in the analyses and is for illustrative purposes only. Photographs by S.G.-P.

Table 1

Hypotheses for the evolution and maintenance of multiple ornaments (as described in Møller and Pomiankowski 1993; Andersson et al. 2002), evidence that would support each hypothesis, and examples within our study that support each hypothesis

Hypothesis	Evidence	Support?	Example in snow buntings
Multiple message	Different quality-related traits predicted by different plumage ornaments or ornament types	✔	Breast UV-chroma predicts IgY levels, whereas rectrix UV-chroma predicts testosterone
Redundant signal	Quality-related traits predicted by many plumage ornaments	✔	Primaries, alula, spots, mantle brightness, and rectrix brightness can all predict territory quality
Unreliable signal	Some plumage ornaments unrelated to quality-related traits yet preferred by females	✗	N/A
Multiple receiver	Different plumage ornaments related to quality-related traits that are differentially useful for inter- and intrasexual signaling	✔	Melanized plumage predicts territoriality versus wing patterns predict future reproductive performance

N/A, not applicable.

before females (80%), and have territories set up before they form a social pair (mean Julian arrival date ± standard errors; 2010 males: 153 ± 1.3; 2010 females: 160 ± 1.5; 2011 males: 156 ± 0.6; 2011 females: 164 ± 0.6). We trapped males and subsequently females after their arrival in late May with seed-baited Potter and walk-in traps, and applied a unique metal and color-band combination to all individuals. We aged birds as either second year (inexperienced breeders) or after second year (experienced breeders) according to a protocol described previously (Smith 1992). At this time, we also collected a small blood sample from the brachial vein for hormonal and immunological analyses. Whole blood was centrifuged for 10 min at 12 000 rpm within an hour of sampling, after which plasma was isolated and frozen at –20 °C. Males were retrapped during their mate's egg-laying period at which point we took a second blood sample as well as feather samples: we took a small feather sample (approximately 6–10) from the center of the white breast and black mantle in addition to the left and right third rectrices (outermost tail feather that is primarily black). We also took photographs of the left wing, outstretched at a perpendicular angle from the body (similar to Hanssen et al. 2009). Wing photographs were all taken by a single person (S.G.-P.) to reduce variation in wing positioning.

Plumage analyses

We quantified the reflectance of 3 body regions accentuated by the threat display—the breast, mantle, and rectrices—with an Ocean Optics USB4000 Spectrometer and PX-2 Xenon Pulsed Lamp (Ocean Optics, Dunedin, FL, USA). We taped 6 breast or mantle feathers to a matte, black piece of cardboard staggered by only a few millimeters to replicate the overlap of feathers on live birds. Rectrices were taped to the cardboard as single feathers and reflectance was measured at the widest part of the feather. Holding the bifurcated fiber-optic probe at a perpendicular angle to the feathers, we took 5 subsequent measures of the same region, lifting the probe and repositioning at each measure. Spectrometer operating software recorded data (OOIBase 32, Ocean Optics), where reflectance measures represent the percentage of light reflected in relation to a white Spectralon standard (near perfect reflectance, as in Mennill et al. 2003). Analyses of reflectance were restricted between 300 and 700 nm—the visual spectrum of most birds (reviewed in Bennett et al. 1994)—and we smoothed a small blip in the curve caused by the light source by averaging the endpoints between 480 and 486 nm. We averaged the 5 measurements for each body region and using CLRv1.05 (Montgomerie 2008). We extracted the following measurements for the breast, mantle, and rectrices (average of left and right rectrices) from spectral curves: brightness (mean reflectance from 300 to 700 nm) and UV-chroma (proportion of reflectance from 300 to 400 nm).

To characterize melanized plumage patterns displayed during courtship, we measured the area of multiple pigmented regions on the wing of males using a digital tablet to manually trace the total area of the wing (which could not be automated because the white areas of the wings resembled the light-colored background too closely). We then used a standardized color-threshold procedure to measure areas of black versus white plumage in ImageJ (v1.45 National Institute of Health, USA). The output provided both the total wing area, as well as the area of all separate black regions (Figure 1b). In total, we defined 4 measures that characterized patterns of black and white pigmentation within wings: the area of the black primaries, the average area of each spot within the white area of the wing, the total area of all spots, and the area of the alula patch. Each variable was expressed as a proportion of the total wing area.

Male quality

Our operational definition of individual quality combines ideas proposed by Hill (2011) and Wilson and Nussey (2009) as follows: *the ability to maintain homeostasis through changing environments or life-history stages, and the fitness-related consequences of this ability.* In an attempt to capture individual variation in male quality as holistically as possible, we measured multiple aspects of male condition and territoriality that may be important in snow buntings including individual arrival date, the change in immunoglobulin levels from arrival to breeding, the growth rates of feathers, testosterone levels at territory establishment, territory size, and territory quality. We also examined female preference for plumage traits, as well as the direct relationship between future reproductive performance and plumage traits (ignoring any possible intermediate effects given the already complex direct relationships). See below for an explanation of the inclusion of each of these variables. We further separate these traits as providing information that is valuable for intersexual communication, intrasexual communication, or both (Table 2) to assess whether different plumage traits could provide information to different receivers.

Male condition

Individual variation in the arrival date to the breeding grounds can be indicative of variation in individual quality in Arctic birds (Bêty et al. 2004) and earlier arrival dates may be advantageous in seasonal breeders where reproduction is time constrained. Early males may acquire higher quality territories and breed earlier (Smith and Moore 2005), as has been suggested for snow buntings (Montgomerie and Lyon 2011). We began trapping males in late May with seed-baited Potter and walk-in traps. Due to our high trapping effort, we used the day of first capture as an approximation of the arrival date of individuals. Data from a Geolocation-based migratory study in this population confirm that the date of first capture represents male arrival date to the breeding grounds, although more accurately for later arriving than earlier arriving males (2010–2011; Love OP, unpublished data). The latest arriving males overlapped temporally with the earliest arriving females, such that these males likely had not yet established a territory once early females had begun assessing potential mates.

We used an index of humoral immunity as a measure of current condition, quantified as levels of circulating immunoglobulin Y (IgY) serum proteins. IgY levels integrate both genotypic and phenotypic effects (Apanius and Nisbet 2006), thus they may be a reliable and useful proxy of individual quality. Notably, increases in plasma IgY levels are symptomatic of mounting an immune response (Roitt et al. 1998), and IgY levels are highly dependent on changes in body condition and parasite loads (Bourgeon et al. 2006; Bourgeon and Raclot 2006; Tomás et al. 2007; Bourgeon et al. 2010). As such, positive increases in IgY levels in snow buntings are indicative of mounting an immune response, or having an infection, and would be interpreted as being in lower current condition. We measured changes in IgY from arrival to breeding (as a percentage of change) using an in-house enzyme-linked immunosorbent assay (ELISA) that utilizes commercial antichicken antibody (Martínez et al. 2003; Bourgeon et al. 2006; Bourgeon and Raclot 2006). This method has been validated in 6 avian species and we optimized it for snow buntings: we diluted our samples at 1:32 000, which falls within the linear range of a sigmoidal curve in a serial dilution cascade (as outlined in Bourgeon et al. 2006). We used a previously described protocol (Martínez et al. 2003; Bourgeon et al. 2006; Bourgeon and

Table 2

Information content for quality proxies used in this study and justification for the classification of each as intersexual, intrasexual, or mixed information

Trait	Justification	References
Intersexual information		
Female preference	Earlier arriving females should prefer to mate with higher quality males first	Kokko et al. (2006)
Immune response	Females should pair preferentially with a male that is currently in good condition; that is, combating an immune challenge may impair his ability to provide paternal care	Råberg et al. (2000)
Feather growth rates	Females should pair with a male that was in good condition during the previous breeding season; that is, at the time of feather growth	Takaki et al. (2001)
Future fledglings	Females should preferentially pair with males that have high future reproductive performance	Hill (1991)
Mixed information		
Male arrival date	Females should pair with a male that has already established a territory and is ready to breed. Male arrival date may impact the ability to acquire a higher quality territory (although some males have been displaced on the later arrival of a higher quality male)	Alataro et al. (1984) and Smith and Moore (2005)
Territory quality	Females should pair with a male able to defend the minimum number of suitable nesting sites. Males should fight preferentially over higher quality areas	Tinbergen (1939) and Lanyon and Thompson (1986)
Intrasexual information		
Testosterone levels	Males should forgo fighting with a higher quality male in order not to be injured or to save time and energy once a social hierarchy has been established	Rohwer (1975)
Territory size	Males that defend a larger territory may have to spend more time confronting territory intruders or working harder to defend a larger area	Ewald et al. (1980)

Raclot 2006) and read absorbance at 405 nm—the change in color measured is proportional to the IgY content of the sample and levels are expressed in arbitrary absorbance units. The mean intra- and interassay coefficients of variation were 3.0% and 8.9%, respectively.

Ptilochronology, the study of feather growth rates, is a useful index of condition at the time of feather production (Grubb 1989). Males with wider growth bars (i.e., faster growth rates) have greater survival and this relationship is repeatable within individuals (Takaki et al. 2001), suggesting that growth rates are influenced by both genetic and environmental factors and may relate to individual quality. Additionally, growth rates can be linked to the quality of feather structure and pigmentation (Hill and Montgomerie 1994). We measured feather growth rates as the width of one set of alternating dark and light bars in the middle two-thirds of the rectrices (because growth bars are difficult to view at the extremities), using a modified protocol by Grubb (1989). Growth rates are expressed in bars per millimeters and are averaged within a feather and between left and right rectrices. We took the residual of growth rates on total tail feather length, to control for the length of the feather grown (as tail length and growth rate can covary, see Andersson 1994b). In snow buntings, feather growth rates are indicative of male postbreeding condition of the previous year (at the time of molt; Montgomerie and Lyon 2011): males that grew their feathers faster were in better condition at this time.

Male territoriality

In snow buntings, testosterone levels peak prebreeding when males are establishing territories and females begin arriving to the breeding grounds (Romero et al. 1998). This sex steroid is an important driver of intrasexual aggression and territoriality in many bird species (reviewed in Wingfield et al. 1987). We therefore quantified arrival testosterone titers as a measure of territoriality and a proxy of male–male aggressive behavior

(as suggested by the challenge hypothesis; Wingfield et al. 1990). Male snow buntings that have higher arrival plasma testosterone concentrations are expected to be more aggressive. We used a commercial ELISA (Cayman Chemical Company, Ann Arbor, MI, USA) and followed a standard extraction step. Plasma samples were diluted in 1 mL deionized water and homogenized with 5 mL of dichloromethane after which the lower steroid-containing dichloromethane layer was removed and the dichloromethane was evaporated overnight. The assay was optimized for snow buntings and extracted samples were reconstituted with assay buffer at a 1:20 dilution. We followed the manufacturer's protocol as in previous studies (i.e., Naguib et al. 2004). The absorbance was read at 412 nm, where the change in color measured is inversely proportional to free testosterone initially found in the sample. Testosterone concentrations (ng/mL) were calculated in reference to a standard curve run on each plate. Our average extraction recovery efficiency was 71% ($N = 16$), with mean intra- and interassay coefficients of variation of 7.7% and 10.6%, respectively.

We also assessed territory size and quality for each male. We mapped out territory boundaries by observing male–male territorial behaviors between neighbors (described in Tinbergen 1939)—we focused on how close neighbors could approach each other before chasing and fighting one another, determining this point to be a territory boundary. We digitized a map of territory boundaries and measured territory area using a tablet and the ImageJ tracing tool. In addition, we measured 3 metrics of potential territory quality with the knowledge that the sole function of territories in this species is to provide an adequate number of suitable nest sites for females (Tinbergen 1939; Montgomerie and Lyon 2011): the distance from the nearest crevice opening to the closest edge of the nest cup, the approximate cover area of the rock directly above the nest, and the proportion of rock cover within a 5 m radius of the nest. We chose the first 2 variables given the importance of nest microclimate in the Arctic; more sheltered eggs, deeper into a crevice get

colder if not incubated properly such that nests under larger rocks and with a greater distance from the nearest opening are colder, lower quality sites (Lyon and Montgomerie 1987). The third is an approximation of the potential number of available nest sites within the territory, where territories that have high rock cover have more potential crevices for birds to nest. These 3 measures, along with territory area, were combined in a principal component analysis to summarize territory characteristics with multivariate scores: 2 principal component scores had eigenvalues greater than 1 and explained 41.8% and 31.7% of the variation in territories, respectively. After varimax rotation, the first principal component score included the 3 metrics of territory quality (rotated eigenvectors: distance to nest, 0.72; roof area, 0.78; rock cover within 5 m radius, –0.72) and the second represented territory area (rotated eigenvector, 0.91). Raw territory area and quality variables were significantly, linearly related to the principal component score on which they loaded most heavily (R^2 range: 0.52–0.84; $P < 0.0001$ for all), thus we took the principal component scores to represent territory quality and size, respectively, and used these in all subsequent analyses. A negative territory quality score is associated with a better territory, where the nest microhabitat is less prone to heat loss and where the territory contains greater access to nesting sites. A positive territory size score is associated with a larger territory.

Female preference and future reproductive performance
Because there is selection to initiate reproduction early in Arctic-breeding species—where breeding is time constrained (Sandercock et al. 1999; Lepage et al. 2000)—we expected that early arriving females would pair quickly and begin laying their clutch as soon as they could (Perrins 1970). Thus, we used female arrival date as a proxy for pairing date (Gil and Slater 2000) and female mate preference, assuming that females arriving to the breeding grounds earlier had their first choice of mate and would pair with preferred males (as predicted by Kokko et al. 2006). Briefly, earlier females can chose their breeding partner from all available males on the island (presumable preferred males are chosen as mates first, when available); as females arrive later, however, there are fewer unpaired males to choose from. We began trapping snow bunting females in late May with seed-baited Potter and walk-in traps, prior to female arrival and used the day of first capture as an approximation of the arrival date of individuals. Geolocation-based migratory data at our study site show that the date of first capture is a very reliable measure of female arrival date to the breeding grounds (Love OP, unpublished data). Males who were paired to earlier arriving females would be the preferred social mates.

We also tracked the reproductive output of breeding pairs by locating nests and visiting them biweekly to determine laying date. As in other Arctic species, earlier breeding is expected to provide an advantage in seasonal environments (Lepage et al. 2000). We visited nests regularly and used the number of nestlings present at 8 days of age—the day prior to the earliest fledging date possible (Montgomerie and Lyon 2011)—as our estimate of the number of fledglings and male future reproductive performance.

Statistical analyses

Commonly used variable selection techniques are flawed and rarely suitable for ecological analyses (Whittingham et al. 2006; Mundry and Nunn 2009). Thus, we used a newly emerging and highly relevant statistical technique for complex ecological data (Murray and Conner 2009; Oppel et al. 2009) to select important plumage predictors of male quality (see Supplementary Material for details): this technique is called least angle regression (LARS; Efron et al. 2004) with a least absolute shrinkage and selection operator modification (LASSO; Tibshirani 1996). We conducted a separate LARS-LASSO model for each dependent variable (i.e., male quality proxies), including the 10 assessed plumage traits male age and year as our independent variables. We then built models to validate our choice of male quality measures, using all male condition and territoriality traits, male age and year as our independent variables to predict female preference, laying date, and reproductive performance (dependent variables). All variables were standardized prior to analyses (mean = 0, standard deviation = 1), and we selected important predictors using the parsimonious results of 2 model selection criteria: Mallows' C_p and the mean squared prediction error (MSPE) (Mallows 1973; Efron et al. 2004). We performed *N*-fold cross-validation to obtain the MSPE, where *N* is the number of observations used in the model—sometimes called "leave-one-out cross-validation." This technique produces unbiased results, does not depend on random subgroup selection, and provides a clear indication of the influence of individual observations on variable selection. Only the output from the best supported parsimonious model for each dependent variable is presented (Tables 3–5); the standardized model coefficients represent the slope and strength of the relationship between each predictor and the dependent variable and are comparable across models because all variables are standardized. The sample sizes in these tables represent the number of male birds used in each analysis. Three males returned from 2010 to 2011 and were resampled. We treated these as independent observations because all returning males paired with a new female, had a new territory and had molted a new set of feathers—removing returning males did not alter our findings. Sample sizes vary for each model as a result of missing data for some snow bunting pairs. All analyses were run in R 2.14.2 (R Development Core Team 2012, Vienna, Austria), using the LARS package (authors: Efron and Hastie; available at http://cran.r-project.org/web/packages/lars/).

RESULTS

Plumage and quality

Male snow bunting plumage traits predicted many proxies of quality (Tables 3 and 4). We found that breast brightness along with wing spotting were important predictors of male arrival date, along with male age. Specifically, birds with brighter, whiter breasts and less wing spotting arrived to the breeding grounds earlier. Male breast UV-chroma could also predict whether males had an immune response over the breeding season, where individuals with lower UV reflectance in their breasts showed no sign of mounting an immunological response. All plumage traits studied were unrelated to feather growth rates, which could only be predicted by year. Similarly, earlier arriving females appeared to have no distinct preference for a particular plumage trait— none of the predictor variables were related to female arrival date. The main predictors of increased future reproductive performance were reduced spotting on the wing and lower breast UV-chroma. Conversely, many male plumage traits predicted territory quality including the proportion of black primaries within the wing, alula size, wing spotting, as well as mantle and rectrix brightness. Males had more nesting sites within their territory and a potentially favorable nest microclimate when they had a greater proportion of black primaries on their wing, a smaller alula, decreased spotting as well as darker rectrices, but a lighter mantle. Rectrix brightness, as well as breast and rectrix UV-chroma could also predict territory size; males defending a larger

Table 3

Variation in male plumage traits is related to quality; standardized parameter coefficients of LARS-LASSO models that used year, male age, and all plumage measures as predictor variables

Predictor variables	Dependent variables							
	Arrival date	Growth bars	Change in IgY	Testosterone levels	Territory quality	Territory size	Female preference	Chicks fledged
Year		0.914 (1)						
Male age	−0.414 (2)							
Black primary					−0.116 (4)			
Alula size					0.090 (5)			
Average spot					0.516 (1)			−0.254(2)
Total spotting	0.195 (1)							−0.522 (1)
Breast brightness	−0.181 (3)							
Breast UV-chroma			0.400 (1)			−0.201 (3)		−0.153 (3)
Mantle brightness					−0.150 (2)			
Mantle UV-chroma								
Rectrix brightness					0.137 (3)	−0.199 (1)		
Rectrix UV-chroma				−0.272 (1)		0.249 (2)		

All blank cells represent a coefficient of zero. In parentheses, we indicate the step at which each predictor variable is added (although this is not a strong indicator of variable importance).

territory tended to have lower UV reflectance of the breast but higher UV-chroma in their rectrices along with darker rectrices. Lastly, male rectrix UV reflectance was selected as an important predictor of testosterone levels such that males with lower UV-chroma had higher arrival testosterone titers.

Male quality

When validating our choice of proxies for male quality, we found that most of the condition and territoriality traits investigated related to female preference or reproductive performance (Table 5). Females appeared to prefer to pair with males in higher condition: earlier arriving females paired with males that arrived earlier to the breeding grounds and did not mount an immune response over the breeding season (as indicated by changes in their IgY levels), although these males also had slower feather growth rates. Three aspects of male quality were also important predictors of female laying date, with physiological measures having the greatest predictive ability. Females initiated reproduction earlier when their mate had an earlier arrival date, lower arrival testosterone levels, and a decrease in IgY levels from arrival to breeding. Lastly, male current condition—as approximated by the

change in IgY levels—was the only significant predictors of within-pair annual reproductive performance where males that did not mount an immune response fledged a greater number of young.

DISCUSSION

Multiple achromatic ornaments

Our findings support the occurrence of multiple ornaments in an achromatic species—all measured plumage traits were predictors of at least some of the quality-related measures that we considered (Figure 2). Similarly, previous work implies that a purely achromatic species can have multiple achromatic plumage signals of quality (i.e., Pärt and Qvarnström 1997; Török et al. 2003). Specifically, we found evidence for 3 of the 4 hypotheses that explain the evolution of multiple ornaments: the *multiple message*, *redundant signal*, and *multiple receiver hypotheses* (Table 1).

We found limited evidence of multiple messages in snow buntings, where breast UV-chroma was the only plumage trait able to predict the change in IgY levels and rectrix reflectance was the only trait able to predict testosterone levels. These findings suggest that different plumage traits may provide

Table 4

Model summary and selection criteria for variables outlined in Table 3; Mallows' C_p values and cross-validation results for the LARS-LASSO model selected for each dependent variable examined.

	Dependent variables							
	Arrival date	Growth bars	Change in IgY	Testosterone levels	Territory quality	Territory size	Female preference	Chicks fledged
Selected model summary								
Residual sum of squares	19.3	17.9	15.1	26.4	15.8	18.5	28.0	15.7
Mallows' C_p	2.25	−5.49	−2.83	−0.0369	3.59	−0.146	−2.42	5.37
df	4	2	2	2	6	4	1	4
N	29	29	24	24	29	29	29	26
N-fold cross-validation								
Model consistency	0.897	1.00	1.00	0.917	0.862	0.966	N/A	0.808
Mean squared prediction error (±SE)	1.00 ± 0.26	1.03 ± 0.21	1.04 ± 0.64	1.10 ± 0.34	1.12 ± 0.42	1.01 ± 0.31	0.92 ± 0.23	1.04 ± 0.50

df, degrees of freedom; SE, standard error; N/A, not applicable. Model consistency refers to the proportion of N-fold cross-validation test groups that were parsimonious with the top model.

Table 5

Variation in male quality-related traits is related to female preference and reproductive performance; results of LARS-LASSO models that used year, male age, and all proxy measures of quality as predictor variables

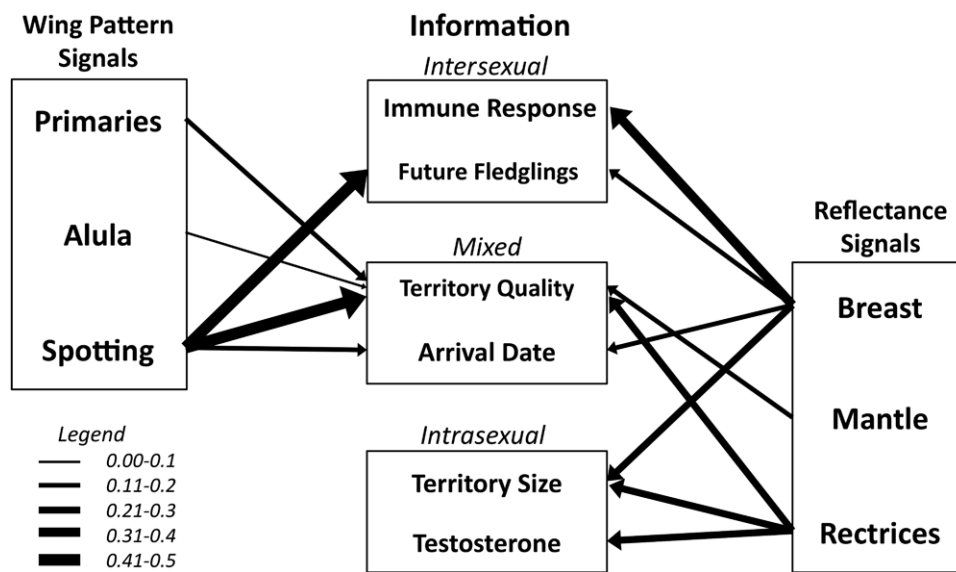| Predictor variables	Dependent variables		
	Female preference	Laying date	Chicks fledged
Standardized model coefficients			
Year			
Male age			
Change in IgY	0.290 (3)	0.048 (1)	−0.305 (1)
Arrival date	0.564(1)	0.075 (3)	
Growth bars	−0.321 (2)		
Testosterone levels		−0.142 (2)	
Territory quality			
Territory size			
Selected model summary			
Residual sum of squares	12.5	13.9	12.2
Mallows' C_p	−0.67	11.5	3.19
df	4	4	2
N	24	21	21
N-fold cross-validation			
Model consistency	1.00	0.801	0.952
Mean squared prediction error (±SE)	0.98 ± 0.34	1.22 ± 0.34	0.63 ± 0.22

df, degrees of freedom; SE, standard error. Standardized parameter coefficients are presented for all the important predictors identified (not indicated are all other parameters with a value of 0). In parentheses, we indicate the step at which each predictor variable is added. Model summary and cross-validation results are included. Model consistency refers to the proportion of N-fold cross-validation trials that were parsimonious with the top model.

different types of information in snow buntings. However, we found strong support for the *multiple receiver hypothesis*, which is consistent with the inter- versus intrasexual displays of our study species: the mantle and rectrices advertised to males during threat displays convey information about potential aggression and territoriality, whereas the wing patterns presented solely to females during courtship indicate a male's potential within-pair reproductive performance. Information that may be of value to both males and females, such as territory quality and arrival date, was signaled through both wing patterns and body reflectance. Male and female snow buntings may focus on different signals, specifically targeting ones that communicate information relevant to their sex-specific interactions during breeding. We were surprised to find that male condition was largely unrelated to wing pattern variables, as paternal condition at the time of pairing is often thought to be important in socially monogamous species where biparental care is necessary (Hill 1991). Perhaps signal content for a male's future reproductive performance is more important to females than an indirect assessment of potential parental abilities through his current condition.

Finally, we also found strong support for the *redundant signal hypothesis* as more than 1 plumage ornament could predict most quality-related traits. Territory quality was predicted by 5 plumage traits, including both wing patterns and body reflectance. Similarly, most ornaments examined were correlated to multiple proxies of quality; the plumage trait able to predict the greatest variety of quality-related information was breast reflectance, where this body region was an important predictor of multiple measures of both inter- and intrasexual importance. Breast brightness was the most interindividually variable plumage trait measured (range: 29–50% reflectance), and the breast is the most visible plumage trait to receivers facing a male. Breast variability and visibility may explain why both males and females could rely on this trait to gather information about conspecifics.

We found surprisingly little correlation between multiple plumage traits (only 20%, or 9 of 45 pairwise correlations were significant at the $P < 0.05$ level). Correlated measures included average spot size and total spotting; breast brightness and total spotting; mantle UV-chroma was correlated to both total spotting breast UV-chroma; and rectrix UV-chroma was correlated to average spot size, total spotting, breast

Figure 2
Male snow bunting plumage traits can act as multiple ornaments. Arrows arbitrarily point to the dependent variable and represent correlations with plumage predictor variables identified by the LARS-LASSO models. Dependent variables for which no predictor was selected are not shown (see Table 3). Arrows are relatively proportional to the absolute value of standardized parameter coefficients (β), and thus can be compared across models (see legend for magnitude). Table 3 should be consulted for the direction of these relationships and the Methods section should be consulted for their biological significance.

UV-chroma, mantle UV-chroma, and rectrix brightness. Most correlated traits were selected as predictors of the same quality proxies, with the exception of the rectrix UV-chroma, which was the primary predictor of territory traits. Future studies should examine how correlations between these traits arise and how this influences visual communication in snow buntings.

Snow bunting quality

Our measures of male condition and territoriality appear to collectively represent male quality because almost all selected traits were related to reproduction—as per our operational definition of "quality"—and many related to female preference. The only traits unrelated to reproductive performance were territory quality and size, which may not be limited in a population such as the one at East Bay Island (nest sites are seemingly abundant; Guindre-Parker, S, personal observation). Similarly, snow buntings defend territories solely to access potential nesting sites, such that defending a territory with a certain threshold of nesting sites may be all that is required to secure a mate (providing little additional fitness-related benefits). However, we believe territory quality and size could still relate to territoriality and male quality given that very large territories, or higher quality territories, can require greater time and energy to defend (Ewald et al. 1980). Again, further examination of the use of territories and potential costs of defending these (i.e., intermediate effects) at our study site, along with populations at lower density sites, may be necessary to understand how or if snow bunting territoriality can influence reproduction.

Although support for the *redundant signal hypothesis* could result from the inability to measure quality effectively (because by measuring multiple proxies of quality, we may be measuring multiple redundant traits), we would argue that the quality-related measures chosen in our study differ in the aspects of quality they represent. For example, feather growth rates and current immunoglobulin level changes differed temporally (at time of feather growth vs. during breeding season, respectively), and yet both are good representations of individual condition (Grubb 1989; Bourgeon et al. 2010). Similarly, additional quality-related traits differed in their information content, such as testosterone as a measure of aggression versus male arrival date, which may relate to migratory decisions (Petersen 2009). Lastly, quality proxies measured were uncorrelated among one another (pairwise correlations, $P > 0.05$). This suggests that the quality-related traits we chose represent independent aspects of condition and territoriality, and that only by examining them together can we gain a better understanding of what represents a high quality male snow bunting.

Female preference

Although females appeared to show a preference for condition-dependent traits (male arrival date, changes in immunoglobulin levels, feather growth rates), earlier arriving females did not appear to choose males with particular plumage traits. This finding is surprising given that we expected to see a relationship between plumage traits and female preference, particularly if females use plumage in assessing male quality (as suggested by our finding that plumage traits can predict future reproductive performance). However, our measure of female preference is an indirect one, and mate choice trials may provide an improved means of determining whether females show direct preferences for certain plumage characteristics.

Recent evidence has suggested that female preference for a given plumage trait may vary adaptively interannually (Chaine and Lyon 2008), and therefore more than 2 years of data may be necessary to understand social mate selection in snow buntings. Although females can show consistent preferences for male quality-related traits, they may use different specific plumage traits interannually for mate selection, particularly if signals tend to be redundant (i.e., Marchetti 1998). This possibility could explain why we did not find a clear female preference for any particular plumage trait. Alternatively, male mate choice may occur simultaneously (Jones et al. 2001)—ignoring the possibility of mutual mate selection could explain why female mate choice alone does not correlate to a particular plumage trait. Although we were unable to control for female quality in our current analyses, variation in interfemale quality may be an important consideration for future studies of snow bunting mate selection.

Alternatively, perhaps even across the multiple traits we measured as potential ornaments, we did not assess the specific trait used in mate choice. Display quality may also contribute to effective signaling and may be an important consideration for mate choice (Chargé et al. 2010; Cornuau et al. 2012)—unfortunately, we were not able to quantify male behavioral displays because of logistical constraints. There is also evidence that plumage neatness, and not reflectance or patch area itself is a female-preferred trait (Ferns and Hinsley 2004). Further studies are necessary to explore this possibility.

Condition-dependent achromatic signals

Previous studies of melanin- and carotenoid-based signals have suggested that melanin-based plumage is not condition-dependent (Hill and Brawner 1998; Badyaev and Hill 2000). Contrary to this conclusion, our findings support those of recent studies indicating that achromatic plumage may serve as a condition-dependent signal (also Török et al. 2003; McGlothlin et al. 2007). The primary difference between previous studies and ours stems from our choice of a purely achromatic species rather than one that exhibits both melanin- and carotenoid-based ornaments. In a species that only has black and white plumage available to use as a signal, the evolution of condition-dependent achromatic plumage may be more likely than one with additional carotenoid-based signals.

We also show that achromatic plumage can signal both condition and territoriality, something that few studies of achromatic plumage consider simultaneously—consequently, it is difficult to say whether this finding is common among other species. In collared flycatchers (*Ficedula albicollis*), the white wing patch size is a signal of condition (Török et al. 2003), whereas the size of the forehead patch is a badge of status (Pärt and Qvarnström 1997). Likewise, the proportion of white within the tail of dark-eyed juncos (*Junco hyemails*) can be used in signaling both status (Balph et al. 1979) and condition (McGlothlin et al. 2007). The latter example, along with our study (i.e., breast reflectance), is the only documented case of the same achromatic plumage trait being indicative of both condition and territoriality. This occurrence may simply be rarely observed because researchers only choose to consider condition or dominance in their studies of achromatic plumage signaling; more studies exploring this possibility are needed.

The evolution of multiple ornaments

Our finding that redundant signaling may be common in snow buntings could occur because producing black and white feathers may be more mechanistically similar than producing multimodal ornaments (i.e., bower vs. plumage

reflectance; Doucet and Montgomerie 2003). Signals that are relatively inexpensive to produce, although less informative, may remain honest (Zahavi 1993)—achromatic plumage signals may be redundant as a result of the low relative cost of producing pigmentless or melanin-based feathers (Hill and Brawner 1998). This can result from a selective trade-off for signal efficacy versus content (Andersson 2000), where signals that emphasize content should be more costly, yet may be less conspicuous, whereas signals that emphasize detection efficacy should be more conspicuous but potentially less costly. Redundant ornaments may also result from common upstream cellular processes, influencing male quality (and thus condition or territoriality traits) and the production of multiple plumage traits (*shared pathway hypothesis*; Hill 2011).

Multiple messages should evolve when distinctions between multiple aspects of quality are important for the receiver (Møller and Pomiankowsky 1993). In snow buntings, it appears that 2 physiological measures—immunoglobulin levels and testosterone—can only be signaled through differing plumage traits. Similarly, multiple receivers may select different signals of male quality relevant to intra- versus intersexual interactions. In this sense, the *multiple receiver hypothesis* is really an extension of the *multiple message hypothesis* to include more than 1 receiver. Different ornaments predicting different aspects of quality may have evolved because males and females use signals that are unrelated (or trade-off). For example, prebreeding territoriality may be unrelated to, or even trade-off with, eventual reproductive output such that males and females have evolved preferences for different ornaments (see Andersson et al. 2002). A potential trade-off may be the immunosuppressive effects of elevated testosterone, where males with high testosterone may better defend territories (Wingfield 1985), but have suppressed immune responses (although this trade-off may be complex; see Peters 2000).

Alternatively, multiple ornaments may result when the mechanism of ornament production differs between the ornaments visible during ritualized intra- and intersexual displays (see Galván 2008). Although all plumage traits examined in snow buntings are produced approximately synchronously (i.e., postbreeding molt the year before), the differing mechanisms by which black feather reflectance and wing patterns are produced could explain the difference between the information content of these signals. Although both the reflectance of mantle feathers and the area of pigment patterns of the wings are driven by melanization, the localized deposition of some melanin in different wing feathers that result in wing patterns may rely on melanocyte control (Ito 2003), whereas the quality of reflectance of mantle feathers may depend on concentrations of pigments in these feathers (e.g., ratio of eumelanin and pheomelanin; McGraw et al. 2005). This suggestion is consistent with a recent meta-analysis showing that eumelanin-based plumage reflectance may not relate to reproduction, whereas melanin patch sizes do (Meunier et al. 2011). Our findings are similar, where the area of spots predicts future fledging success, whereas mantle and rectrix reflectance do not.

Lastly, we point out that additional factors are important in the evolution of multiple ornaments: future work should investigate the potential role of receiver sensory biases, signal–environment interactions, intersignal interactions, and flexible female preferences in studies of multiple ornaments (Candolin 2003; Hebets and Papaj 2005; Chaine and Lyon 2008).

CONCLUSION

In summary, we find that an achromatic species can use plumage reflectance and pigmentation patterns to signal complex information. We provide evidence that purely black, grey, and white birds can exhibit multiple ornaments, and we suggest that the evolution of these ornaments may largely depend on the mechanisms of plumage production, as well as differing intra- and intersexual selective pressures. We also provide novel evidence that achromatic plumage can signal condition-dependent information, and that breast plumage can signal condition and territoriality simultaneously. We urge researchers to consider achromatic plumage as a potentially complex form of visual communication and to investigate the production costs, genetic basis, as well as fitness consequences of this type of plumage signal. These studies will contribute significantly to elucidating why some species have evolved alternative plumage colors, whereas some remain entirely achromatic.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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