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Multiple achromatic plumage signals of male quality in the snow bunting (*Plectrophenax nivalis*)

Sarah Guindre-Parker

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**MULTIPLE ACHROMATIC PLUMAGE SIGNALS OF MALE QUALITY IN THE SNOW
BUNTING (*PLECTROPHENAX NIVALIS*)**

by

SARAH GUINDRE-PARKER

A Thesis

Submitted to the Faculty of Graduate Studies
through Biological Sciences
in Partial Fulfillment of the Requirements for
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Windsor, Ontario, Canada

2012

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(*Plectrophenax nivalis*)

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DECLARATION OF CO-AUTHORSHIP

I hereby declare that this thesis incorporates material that is the result of joint research. My data chapter is co-authored with my supervisor, Dr. Oliver Love, as well as our collaborators Dr. Grant Gilchrist, Dr. Stéphanie Doucet and Ms. Sarah Baldo. While the primary contributions to this chapter have been by the author, my supervisor and our collaborators all provided important feedback in designing the project and statistical analyses. Dr. Love provided valuable input during the writing of this manuscript. Additionally, Drs. Gilchrist and Doucet also contributed through provision of logistics and equipment needed to complete this project, while Ms. Baldo assisted in collecting and processing data. Chapter 2 is prepared as a manuscript to be submitted to *Behavioural Ecology*. I am the sole author of Chapters 1 and 3, thus they are written in first person.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis, and have obtained written permission from each of the co-authors to include the above materials in my thesis. I certify that, with the above qualification, this thesis, and the research to which it refers, is the product of my own work, completed during my registration as a M.Sc. candidate at the University of Windsor.

I declare that, to the best of my knowledge, my thesis does not infringe upon anyone's copyright nor violate any proprietary rights and that any ideas, techniques, quotations, or any other material from the work of other people included in my thesis, published or otherwise, are fully acknowledged in accordance with the standard referencing practices. Furthermore, to the extent that I have included copyrighted material that surpasses the bounds of fair dealing within the meaning of the Canada Copyright Act, I certify that I have obtained a written permission from the copyright owners to include such materials in my thesis.

I declare that this is a true copy of my thesis, including any final revisions, as approved by my thesis committee and the Graduate Studies office, and that this thesis has not been submitted for a higher degree to any other University or Institution.

ABSTRACT

Although males can produce many ornaments, the evolution of multiple ornaments is not well understood. We investigated achromatic plumage traits in the context of multiple ornaments in Arctic-breeding snow buntings (*Plectrophenax nivalis*). We examined whether multiple ornaments: are providing multiple messages, are redundant, are unreliable signals or are aimed at different receivers. We measured plumage reflectance and pigmentation patterns that are differentially, but conspicuously advertised during male inter- and intra-sexual displays. Our results indicate that although several signals are redundant, different body regions appear aimed at different receivers. The wings of males—displayed during courtship—indicate male expected reproductive performance. Conversely, melanin reflectance displayed during intra-sexual threat displays signals territoriality. Different information provided by distinctive aspects of plumage may have differential importance in inter- versus intra-sexual communication. This study demonstrates that even relatively simple plumage traits can serve in complex communication.

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CHAPTER 1—GENERAL INTRODUCTION

EVOLUTION OF ORNAMENTS

The theory of sexual selection serves to propose how secondary sexual traits—such as elaborate ornamentation—can evolve (Darwin 1871). Several hypotheses aim to explain how elaborate ornaments may be maintained evolutionarily. *Fisher's hypothesis* (or *runaway selection*) proposes that elaborate ornaments may exist simply due to female preference for their attractiveness (Fisher 1915). The initial cause of preference for a trait is not important (i.e. a sensory bias, an honest signal, increased probability of detection, etc.), but over evolutionary time and through assortative mating, the genes for the elaborate ornament and for the preference of this ornament have become linked through positive feedback. Essentially, it is adaptive to possess the trait to gain mating opportunities, but it is also adaptive to possess the preference for this trait because these females will produce attractive offspring, which will also gain mating opportunities. This hypothesis suggests that inter-sexual selective pressures are driving the evolution of ornamentation. Conversely, the *handicap principle* suggests that elaborate ornaments have evolved to be honest signals of individual quality. To signal individual quality honestly, the production of these ornaments must come at a cost or the ornaments must be a handicap (Zahavi 1975). Females can assess individual quality through male-produced ornaments that inform mate choice decisions (Hill 1991). This inter-sexual signalling is particularly likely to evolve if females gain fitness benefits from mating with high-quality males (Fisher 1930). Conversely, intra-sexually selected ornaments can serve as signals of status or dominance: conspecific males can assess the competitive abilities of their opponents through ornaments (reviewed in Santos et al. 2011). However, the role of inter-versus intra-sexual selective pressures in shaping ornamentation is largely under-studied, as they can be difficult to tease apart and few signalling studies consider the possibility of both occurring simultaneously (discussed in Berglund et al. 1996; although see Jones and Hunter 1999, Andersson et al. 2002).

INDIVIDUAL VARIATION IN QUALITY AND CONDITION

There is great interest in the relationship between phenotypic (i.e. individual) variation and plumage ornamentation; the concept of ‘individual quality’ is frequently invoked to indicate what ornamentation can signal, yet is rarely defined (Lambrechts and Dhondt 1986; Hill 1991). Wilson and Nussey (2009) reviewed the subject and proposed the following definition of individual quality: “the axis of phenotypic variation that best explains variance in individual fitness”. There are many downfalls to this definition (Lailvaux and Kasumovic 2010), including the difficulty of quantifying both fitness and this proposed axis of phenotypic variation. Hill (2011) proposed an alternative definition: “the capacity to withstand environmental challenges”. For this thesis, the operational definition of individual quality combines the two above ideas as follows: *the ability to maintain homeostasis through changing environments or life-history stages, and the fitness-related consequences of this ability*. As Hill (2011) further suggests, individual quality combines genotype, somatic state and epigenetic state.

Similarly, the meaning of ‘individual condition’ is rarely defined explicitly, despite being a commonly used term in ecological studies (Jakob et al. 1996; Evans 1997). When it is defined, this tends to be done vaguely: a recent publication suggests that condition may represent “some kind of physiological state” (Garrett and Brooks 2012). Furthermore, the terms ‘quality’ and ‘condition’ are often used interchangeably (Jones and Montgomerie 1992, Hill 2011). Here, I refer to quality and condition as separate attributes (as in Andersson et al. 2002)— the term ‘condition’ refers to an individual’s current state (physiological or not) that can vary dynamically with environmental change. Individuals facing favourable environments are expected to be in higher condition than when facing harsh environments.

Individual quality is repeatable (“the proportion of variance in a character [occurring] among rather than within individuals ”; Lessells and Boag 1987) and consists of multiple aspects of condition. In this sense, we can use multiple measures of individual condition that have fitness-related consequences as proxies for individual quality (Simmons 1995, Andersson et al. 2002). It follows that condition-dependent ornaments depend on individual condition at the time of production. Therefore, for the purposes of

this thesis, I predict that high quality individuals are better able to maintain high-functioning processes and good condition—even when faced with intrinsic or extrinsic stressors—and thus produce relatively better ornaments than lower quality individuals.

MULTIPLE ORNAMENTS

Previous ornamentation research has largely focused on a single ornament, yet many species possess multiple potential ornaments (see Møller and Pomiankowski 1993; Johnstone 1996). Multiple ornaments appear inconsistent with the widely accepted *handicap hypothesis*—many theoretical models have suggested that female preference for multiple ornaments is not evolutionarily stable (Schluter and Price 1993; also see Johnstone 1996). It seems paradoxical for a species to evolve several handicapping ornaments if a receiver is not assessing all of them. However, while multiple handicapping ornaments are often believed to be evolutionarily unstable (Iwasa and Pomiankowski 1994), Møller and Pomiankowski (1993) have proposed three hypotheses to explain their evolution:

1. Multiple message hypothesis

The *multiple message hypothesis* suggests that multiple ornaments may be maintained simultaneously when each ornament is indicative of a different aspect of condition. Different ornaments could indicate differing aspects of condition that no single ornament can reflect simultaneously, or represent condition-dependent traits on different timescales. Multiple messages would evolve in species where assessing multiple aspects of condition are important for selecting high quality mates and maximizing reproductive success.

2. Redundant signal hypothesis

The *redundant signal hypothesis* (or *back-up signal hypothesis*; Johnstone 1996) predicts that multiple ornaments can converge to represent the same or similar aspects of condition. For the receiver, using multiple ornaments could be more informative in assessing individual condition than relying on a single ornament. Redundant signals

would evolve in species where selecting a mate based on more than one signal improves the accuracy or reduces the costs of assessing potential mates (Candolin 2003).

3. Unreliable signal hypothesis

The *unreliable signal hypothesis* proposes that multiple ornaments may not currently reflect individual condition. Many traits could have initially been preferred by females due to their attractiveness, honest signalling or sensory biases, but are now simply maintained by female preference for a trait that no longer reflects individual condition (as in *runaway selection*). Unreliable signals would evolve in species where producing such ornaments is not particularly costly and where variation in mating success continues to be linked to ornaments through preference alone. However, the degree to which females rely on these ornaments in choosing mates is predicted to decrease slowly over evolutionary time (Møller and Pomiankowsky 1993).

MULTIPLE RECEIVERS

The three hypotheses proposed by Møller and Pomiankowsky (1993) assume that a single receiver has shaped male ornamentation (traditionally assumed to be the female; Møller and Pomiankowsky 1993). The above hypotheses are not exclusive to inter-sexual selection, however, and intra-sexual selection may also play an important role in the evolution and maintenance of secondary sexual traits (Smith 1972; also see Berglund et al. 1996). Andersson et al. (2002) proposed and found empirical support for a fourth hypothesis to explain the evolution and function of multiple ornaments. The *multiple receiver hypothesis* suggests that different ornaments may be selected and maintained by separate receivers: that is, both inter- and intra-sexual selection pressures can shape multiple ornaments. This hypothesis has been examined in some systems (Andersson et al. 2002; Loyau et al. 2005), but largely in relation to relatively highly exaggerated ornaments (although see Marchetti 1998).

ACHROMATIC PLUMAGE

Achromatic species are ones with no colour in their plumage (i.e. black, white or grey) and are common within and across avian families (Table 1). However, studies of achromatic plumage signalling are scarce relative to chromatic signals—perhaps because this type of plumage is the ancestral state of plumage colouration (compared to carotenoid-based or structural colours; Stoddard and Prum 2011). 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). Achromatic signals have been studied previously in regards to status signalling, relating signals to dominance rank (reviewed in Santos et al. 2011). However, recent evidence suggests that achromatic plumage may also act as a condition-dependent signal (McGlothlin et al. 2007, Gladbach et al. 2011). Consequently, achromatic plumage signals have the potential to provide information relevant to both inter- and intra-sexual receivers.

SNOW BUNTINGS

Snow buntings (*Plectrophenax nivalis*) are an Arctic-breeding passerine whose range extends throughout circumpolar regions. This achromatic species is sexually dimorphic in size and plumage—males tend to be heavier and have significantly longer wings (males: mass = 40g, wing chord = 110mm; females = 37g, wing chord = 104mm; Montgomerie and Lyon 2011). Males also have contrasting black and white plumage, while females are largely grey and white. North American populations of this long-distance migrant can breed in the low to high Arctic and winter between southern Canada and the northern United States. Males arrive to the breeding grounds between March and May, preceding female arrival by several weeks (varies geographically; Montgomerie and Lyon 2011).

Snow Bunting Reproduction

Snow buntings are socially monogamous during the breeding season: females build the nest, males feed their incubating mate, and bi-parental feeding is necessary to rear young successfully (both quantity and quality of offspring; Lyon et al. 1987). In my focal

breeding population at East Bay Island (64°02'N, 81°47'W), the average lay date is June 19th±3 days (mean±S.E.M. from 2007-2011) and females lay a clutch of 5.6±0.5 eggs (O. Love, unpubl. data). Nestlings hatch asynchronously and remain in the nest for a period of approximately 11 days (range 9-13; Montgomerie and Lyon 2011). Pairs at my study site typically successfully fledge 3.8±0.5 offspring (2007-2011; OPL, unpubl. data), where brood reduction occurs due to hatching asynchrony and starvation rather than nest predation (Hussell 1985; SGP, personal observation). Although East Bay Island is small (0.25 km²), it accommodates a relatively high density of 17±4 breeding pairs annually, equivalent to approximately 70 pairs/km² (2007-2011; OPL, unpubl. data).

Both incubation feeding as well as chick provisioning by the male are necessary to increase reproductive success: males that do not feed their incubating mate lost approximately 2 reproductive units due to poor egg development (as a result of poor incubation; Lyon and Montgomerie 1985) while a male removal experiment revealed that males that could not feed their chicks produced half as many nestlings as ones which were allowed to contribute to nestling provisioning (Lyon et al. 1987). Generally, females appear to provision nestlings at a faster rate, but have shorter foraging distances than males (Falconer et al. 2008). Additionally, both parents tend to increase their feeding rate both when a pair has a larger brood, and as nestling age (Falconer et al. 2008). Abiotic factors, such as the ambient temperature, can also influence parental feeding rates—perhaps through altering the thermoregulatory demands of chicks or the development of insects (Hoset et al. 2004).

Male Plumage

Snow buntings undergo a complete molt once per year, beginning concurrently with provisioning their young at the end of the breeding season (Tinbergen 1939; Montgomerie and Lyon 2011). The definitive basic plumage that males produce at this time consists of black primaries, inner rectrices and alula. The remainder of the tail and wings are white, along with the undertail coverts. The head, breast, belly and flanks are also white, tipped in brown. Similarly, the nape, mantle, rump and scapulars are black, with whitish-brown feather tips. In the spring, on route to the breeding grounds or after their arrival, males will actively wear away the brown-tipped body regions to reveal their

striking black and white breeding plumage (though some males can retain very faint brown feather-tips; Montgomerie and Lyon 2011). Consequently, breeding males are entirely white, except for a black mantle and rump (wings and tail remain unchanged; Figure 1).

Intra-sexual interactions

This species is considered nest-site limited since it nests in cavities created by rock assemblages (Montgomerie and Lyon 2011). As such, males defend territories—usually established before the arrival of females—which exist solely to provide sufficient possible nest site choices for females (a single territory may contain many potential nesting sites; Tinbergen 1939). Breeding birds forage non-competitively at communal feeding ponds.

Males defend territories from neighbours or intruders with threat displays: when a male intruder is observed, the territory owner will turn to face the intruder and lower his head, exposing his back (Tinbergen 1939). Males continue to dip their heads up and down, as well as lifting their tail. If the intrusion persists, the interaction between the territory owner and the intruding male can intensify to a physical fight. During flight, fighting males will try to get the other to the ground using their feet and bills (Tinbergen 1939). On occasion, males will grab each other's feet and fall to the ground together. Male-male fighting generally ends with one male fleeing. Male attacks are always intra-specific and are restricted to defending territories or social mates from conspecifics (Tinbergen 1939). Territory boundaries are defended throughout the breeding season, until chick provisioning begins (Tinbergen 1939; although see Romero et al. 1998).

Inter-sexual interactions

Females arrive to the breeding grounds once most males have already established territories and will wander solitarily from feeding flocks to visit occupied territories (Tinbergen 1939). Males repeatedly engage in visual displays directed at these visiting females: males spread their wings back and down, turning to face away from the female (thus displaying the pigmentation patterns on their wings). Males also display this same posture after copulating with their social mate. Tinbergen (1939) noted that the courtship

display appears to serve in demonstrating “the conspicuous color patterns of the plumage”, implying that male snow buntings may advertise their plumage and communicate using these behavioural displays.

In addition to the threat and courtship displays described above, males will occasionally engage in flight song displays characterized by flying upwards, then slowly fluttering down while singing. This display has the potential to accentuate both the pattern of pigmentation within the wings and the body plumage, although when males are moving or high in the sky these plumage traits may be hard to assess. It is unclear who the intended receiver of this display may be (Tinbergen 1939), as it is performed when both males and females are present (SGP, personal observation).

THESIS GOAL

The objective of this thesis is to determine whether multiple ornaments may exist in an achromatic species. Specifically, I will examine whether black and white plumage signals in breeding male snow buntings are correlated to individual quality proxies, and whether their plumage may act as multiple signals, redundant signals, unreliable signals or may serve in communication with multiple receivers.

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Table 1: The proportion of North American avian species where males exhibit purely achromatic plumage during the breeding season (excluding iridescent achromatic plumage) by major avian groups defined in National Geographic’s *Field guide to the birds of North America* (2002, 4th edition¹).

Avian Group	# Achromatic Species	# Total Species	% Achromatic Species
Loons	3	4	75
Grebes	2	7	29
Albatrosses	2	6	33
Shearwaters & Petrels	15	24	63
Storm-Petrels	9	9	100
Frigatebirds & Tropicbirds	2	3	67
Boobies and Gannets	1	6	17
Pelicans	1	2	50
Aningas & Cormorants	1	7	14
Herons, Bitterns & Egrets	4	13	31
Storks & Flamingos	0	3	0
Ibises & Spoonbills	0	4	0
Ducks, Geese & Swans	10	58	17
Hawks, Kites & Eagles	4	29	13
Caracaras & Falcons	0	9	0
Partridges, Grouse & Turkeys	0	17	0
New World Quails	0	6	0
Rails, Gallinules & Coots	0	11	0
Cranes	0	3	0
Lapwings & Plovers	0	15	0
Oystercatchers, Stilts & Avocets	2	5	40
Sandpipers & Phalaropes	1	62	02
Skuas, Gulls, Terns & Skimmers	45	52	87
Auks, Murres & Puffins	12	21	57
Pigeons & Doves	0	16	0
Parakeets & Parrots	0	16	0
Cuckoos, Roadrunners & Anis	2	8	25
Owls	1	19	5
Nightjars	0	8	0
Swifts	0	8	0
Hummingbirds	0	21	0
Trogons	0	2	0
Kingfishers	0	3	0
Woodpeckers	0	23	0
Tyrant Flycatchers	3	42	7
Shrikes	2	3	67
Vireos	1	15	7

Avian Group	# Achromatic Species	# Total Species	% Achromatic Species
Crows, Jays & Magpies	2	20	10
Larks	0	2	0
Swallows	0	10	0
Chickadees & Titmice	1	12	8
Verdins & Bushtits	0	2	0
Creepers & Nuthatches	0	5	0
Wrens	0	9	0
Dippers	0	1	0
Kinglets & Old World Warblers	1	10	10
Old World Flycatchers	0	5	0
Thrushes & Robins	0	25	0
Mockingbirds & Thrashers	0	11	0
Bulbuls & Starlings	0	5	0
Wagtails & Pipits	2	10	20
Waxwings & Silky-flycatchers	0	3	0
Wood-warblers	1	57	2
Olive Warblers	0	1	0
Tanagers	0	6	0
Towhees, Sparrows & <i>Emberiza</i>	3	58	5
Buntings			
Cardinals, Grosbeaks & <i>Passerina</i> Buntings	0	12	0
Blackbirds & Orioles	0	24	0
Finches	0	22	0
Old World Sparrows & Weavers	0	4	0
Total	133	874	15

¹ Dunn, J.L. et al. 2002. Field guide to the birds of North America (Fourth edition).

National Geographic Society, Washington.

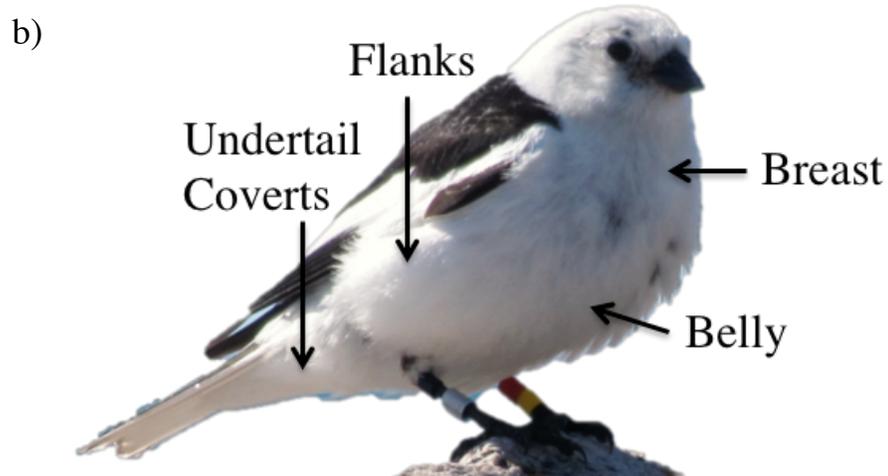
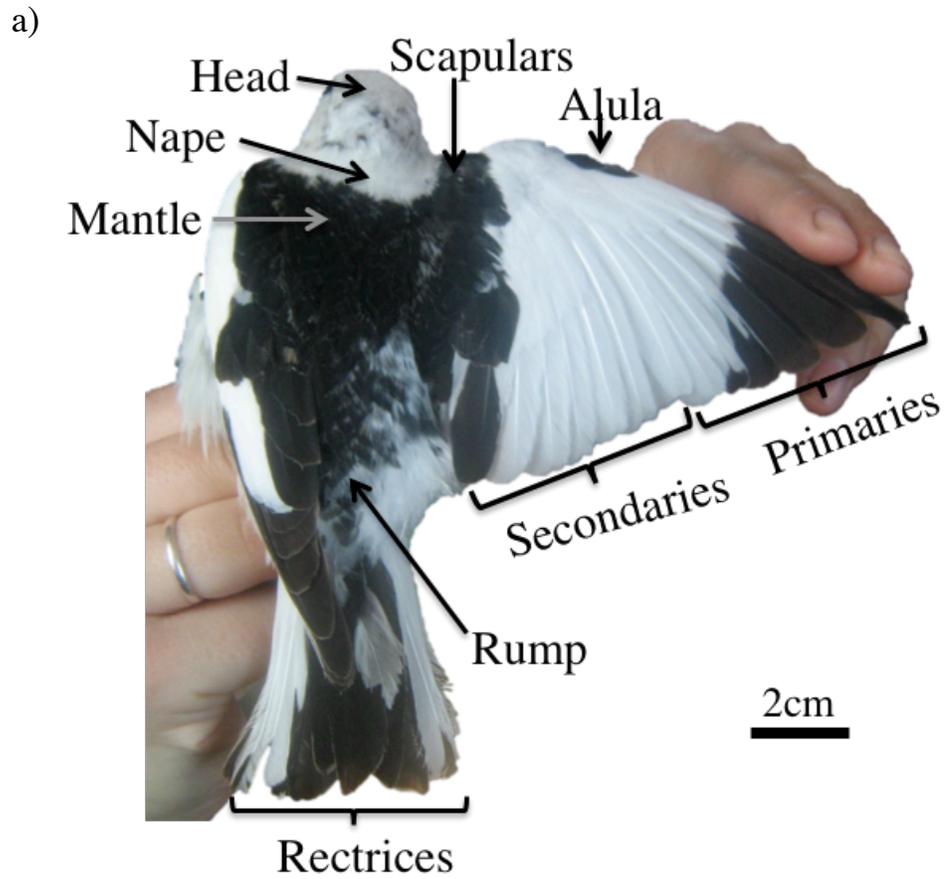


Figure 1: Male snow bunting breeding plumage regions a) from the back, and b) from the side.

CHAPTER 2—COMPLEX SIGNALING WITH SIMPLE PLUMAGE: MULTIPLE ORNAMENTS IN AN ACHROMATIC SPECIES¹

ABSTRACT

Although males can display multiple elaborate ornaments indicative of quality, the evolution of multiple ornaments is not well understood. Furthermore, studies of multiple ornaments have focused primarily on species with exaggerated, multi-modal traits. We investigated whether simple achromatic plumage traits can act as multiple ornaments in an Arctic-breeding passerine, the snow bunting (*Plectrophenax nivalis*). Specifically, we used a breeding population in Nunavut, Canada, to 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 intra-sexual 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 towards females during courtship—appear to indicate male expected reproductive performance. Conversely, melanin-based plumage reflectance displayed during intra-sexual 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 an achromatic species can have multiple ornaments that provide information of differential importance in inter- versus intra-sexual communication. This study demonstrates that even relatively simple plumage traits can serve in complex communication.

KEYWORDS: achromatic plumage, multiple ornaments, multiple receivers, individual quality, *Plectrophenax nivalis*

¹This chapter is the outcome of joint research with my adviser, Dr. Oliver Love, and our collaborators Dr. Stéphanie Doucet, Dr. Grant Gilchrist and Ms. Sarah Baldo.

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 intra-sexual signalling: in the former, females can use male ornamentation to assess and choose potential mates (Hill 1991; Parker et al. 2003) while in the latter, conspecific males can use ornamentation to select territory neighbours (Greene et al. 2000), or assess the dominance rank of potential opponents (Mennill et al. 2003; reviewed in Santos et al. 2011).

However, the evolution of multiple ornaments in numerous species appears inconsistent with honest signalling theory. Theoretical models have suggested that females should simply favour the most honest and detectable signal, ignoring any others (Schluter and Price 1993; also see Johnstone 1996); it would 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 misassessed; and the *unreliable signal hypothesis* suggests that multiple ornaments do not actually indicate current male condition. However, Andersson et al. (2002) also proposed that intra-sexual selection may contribute to the maintenance of multiple ornaments: as such, the *multiple receiver hypothesis* suggests that multiple ornaments may be evaluated by inter- and intra-sexual conspecifics simultaneously, with males and females selecting for the use of different ornaments.

All four hypotheses have been examined in several avian systems, all of which display multimodal ornaments: different pigmentation types (i.e. carotenoid and melanin; Jawor and Breitwisch 2004; Freeman-Gallant et al. 2010), intrinsic vs. extrinsic signals (i.e. plumage and territory or bower quality; Marchetti 1998; Doucet and Montgomerie 2003), plumage colour vs. length (i.e. badge colour and tail length; Andersson et al. 2002), or even plumage vs. wattle length (Papeschi and Dessi-Fulgheri 2003). To date, no research has examined whether simple black, grey or white patterns (termed achromatic

plumage) act as multiple ornaments, despite the apparent use of black and white plumage patterns in complex visual behavioural displays (see Galván 2008) and its common occurrence within and across avian families. 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 signalling 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). Specifically, males have white wings with black primary tips, a black alula (set of two 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 inter-sexual attraction (Tinbergen 1939; see Anderson 2000). Males also defend territories solely for access to nesting sites and perform visual intra-sexual threat displays advertising different aspects of their plumage: their breast, mantle and rectrices (Tinbergen 1939). As such, we considered that males might use multiple achromatic visual signals (wings versus body) to advertise different and complex sets of information to different receivers. Accordingly, we investigated the potential information content of inter- and intra-sexual 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 ($64^{\circ}02'N$, $81^{\circ}47'W$). High breeding densities at this location (approximately 70 pairs/km²; OPL, unpubl. 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 bi-parental feeding is necessary to successfully rear young (Lyon et al. 1987). Pairs at our study site attempt a single brood each breeding season (OPL, unpubl. data). We trapped males and females following arrival in late May with seed-baited potter and walk-in traps, and applied a unique metal and colour-band combination to all individuals. We aged birds as either second year (SY; inexperienced breeders) or after-second year (ASY; 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 minutes at 12 000rpm within an hour of sampling, after which plasma was isolated and frozen at $-20^{\circ}C$. Males were re-trapped 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 3rd rectrices (outermost tail feather that is primarily black; Figure 2a). 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 (SGP) to reduce variation in wing positioning.

Plumage Analyses

Body Reflectance

We quantified the reflectance of three 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, Florida, USA). We taped six breast or mantle feathers to a matte, black piece of cardboard 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 (Figure 2b). 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, Dunedin, Florida, USA), where reflectance measures represent the percent 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 300nm to 700nm (Figure 3)—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 480nm and 486nm. We averaged the 5 measurements for each body region and using CLRV1.05 (Montgomerie 2008), extracted brightness (mean reflectance from 300-700nm) and UV-Chroma (proportion of reflectance from 300-400nm) variables for the breast, mantle and rectrices (average of left and right rectrices).

Wing Pigmentation Patterns

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. We then used a standardized colour-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 four 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 is based on a combination of 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 expected reproductive performance and plumage traits (ignoring any possible intermediate effects). 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 inter-sexual communication, intra-sexual 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 a 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; OPL, unpubl. 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, quantified as levels of circulating Immunoglobulin Y (IgY) serum proteins, as a measure of current condition. 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 and Raclot 2006; Bourgeon et al. 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 percent change) using an in-house enzyme-linked immunosorbent assay (ELISA) that utilizes commercial anti-chicken antibody (Martinez et al. 2003; Bourgeon and Raclot 2006; Bourgeon et al. 2006). This method has been validated in 6 avian species and we optimized it for snow buntings: we diluted our samples at 1:32000, 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 (Martinez et al. 2003; Bourgeon and Raclot 2006; Bourgeon et al. 2006) and read absorbance at 405nm—the change in colour measured is proportional to the IgY content of the sample and levels are expressed in arbitrary absorbance units. The mean intra- and inter-assay coefficients of variation were 3.0% and 8.9%, respectively.

Ptilochronology, the study of feather growth rates, is a useful index of past condition (i.e., at the time of feather production; Grubb 1989). Males with wider growth bars, or 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 (since growth bars are difficult to view at the extremities), using a modified protocol by Grubb (1989). Growth rates are expressed in bars/mm 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 co-vary, see Andersson 1994b). In snow buntings, feather growth rates are indicative of male post-breeding 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 pre-breeding 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 intra-sexual 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 behaviour (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, Michigan, USA) and followed a standard extraction step. Plasma samples were diluted in 1mL deionized water and homogenized with 5mL 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: 50 μ L of diluted samples were run in triplicate with 50 μ L of testosterone tracer and 50 μ L of antiserum, incubated for two hours at 26°C and shaken at 300rpm. The wells were rinsed five times with a wash buffer, and incubated as before for one hour with 200 μ L of Ellman's reagent (containing substrate to Acetyl Cholinesterase tracer, causing colour change). The absorbance was read at 412nm, where the change in colour 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%, with mean intra- and inter-assay 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 behaviours between neighbours (described in Tinbergen 1939)—we focused on how close neighbours 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 three 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 5m radius of the nest. We chose the first two variables given the importance of nest microclimate in the Arctic (more sheltered eggs get colder if not incubated properly, area of roof keeps eggs free from wind and precipitation; Lyon and Montgomerie 1987), while the third is an approximation of the potential number of available nest sites within the territory. These three measures, along with territory area, were combined in a principal component analysis to summarize territory characteristics with multivariate scores: two principal component scores had eigenvalues greater than one and explained 41.8% and 31.7% of the variation in territories, respectively. After varimax rotation, the first principal component score included the three metrics of territory quality (rotated eigenvectors: distance to nest, 0.72; roof area, 0.78; rock cover within 5m 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 Predicted Reproductive Performance

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 the most preferred males (as predicted by Kokko et al. 2006). 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 (OPL, unpubl. 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 predicted reproductive performance. While extra-pair copulations have been reported previously for this species (in 1/5 nests; see Hofstad et al. 2002) within-pair reproductive success may remain a good estimate of a male's predicted reproductive performance due to the importance of bi-parental care.

Statistical Analyses

We used least-angle regression models (LARS; Efron et al. 2004) with a least absolute shrinkage and selection operator modification (LASSO; Tibshirani 1996)—a newly emerging and highly relevant statistical technique for complex ecological data (Murray and Connor 2009; Oppel et al. 2009)—to select important plumage predictors of male quality (see Appendix 1 for details). We conducted a separate LARS-LASSO model for every dependent variable (i.e. male quality proxies), including the ten plumage traits assessed, 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 two model selection criteria: Mallows' C_p and the mean squared prediction error (MSPE) (Mallow 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. Three males returned from 2010 to 2011 and were resampled. We treated these as independent observations since 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 (sample sizes are indicated in Tables 4 and 5). All analyses were run in R 2.14.2 (R Development Core Team, 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 (Table 3, 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 signs of 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 expected 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 favourable 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 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 4). Although 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), our study is the first to explicitly consider these in the context of multiple ornament hypotheses. Specifically, we found evidence for three of the four 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 different types of information in snow buntings. However, we found strong support for the *multiple receiver hypothesis*, which is consistent with the inter- versus intra-sexual displays of our study species: the mantle and rectrices advertised to males during threat displays convey information about

potential aggression and territoriality, while 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 signalled 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 bi-parental care is necessary (Hill 1991). Perhaps signal content for a male's expected 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 one plumage ornament could predict most quality-related traits. Territory quality was predicted by five 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 intra-sexual importance. Breast brightness was the most inter-individually 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 may rely on this trait to gather information about conspecifics.

Snow Bunting Quality

Our measures of male condition and territoriality appear to collectively represent male quality, since 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; SGP, 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 in our population 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) 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 (since 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 versus during breeding season, respectively), and yet both represent 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 amongst one another (pair-wise 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

While 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 eventual reproductive performance). However, our measure of female preference is an indirect one, and mate choice trials may provide

an alternative means to 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 inter-annually (Chain and Lyon 2008), and therefore more than two 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 inter-annually 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 our finding that female mate choice alone does not correlate to a particular plumage trait. While we were unable to control for female quality in our current analyses, variation in inter-female quality may be an important consideration for future studies of snow bunting mate selection.

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) while 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 hyemalis*) can be used in signalling both status (Balph et al. 1979) and condition (McGlothlin et al. 2007). The latter example, along with our study (i.e. breast reflectance), are the only documented cases 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 signalling. However, if this phenomenon is indeed rare, it may be because common mechanisms driving plumage production, dominance, and condition simultaneously are rare—drivers of social interactions and individual condition may differ too greatly to influence the production of a single plumage signal.

The Evolution of Multiple Ornaments

Our finding that redundant signalling may be common in snow buntings could occur because producing black and white feathers may be more mechanistically similar than producing multi-modal ornaments (i.e. bower versus 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 pigment-less 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 while 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 two physiological measures—immunoglobulin levels and testosterone—can only be signalled through differing plumage traits. Similarly, multiple receivers may select different signals of male quality relevant to intra- versus inter-sexual interactions. In this sense, the *multiple receiver hypothesis* is really an extension of the *multiple message hypothesis* to include more than one receiver. Different ornaments

predicting different aspects of quality may have evolved because males and females require information about a signaller that is unrelated (or trade-off). Pre-breeding 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 Anderson 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 inter-sexual displays (see Galván 2008). Although all plumage traits examined in snow buntings are produced approximately synchronously (i.e., post-breeding molt), the differing mechanisms by which black feather reflectance and wing patterns are produced could explain the difference between the information content of these signals. While both the reflectance of mantle feathers and the pigment patterns of the wings are melanin-based, the localized deposition of some melanin in different wing feathers may rely on melanocyte control (Ito 2003), while the quality of reflectance of mantle feathers may depend on concentrations of pigments in these feathers, or the ratio of two melanin pigments within the feathers (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 while melanin patch sizes do (Meunier et al. 2011). Our findings are similar, where the area of spots predicts expected fledging success whereas mantle and rectrix reflectance do not.

Conclusion

In summary, we find that an achromatic species that is relatively simple in appearance can use plumage reflectance and pigmentation patterns to signal complex information. We provide the first 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 inter-sexual selective pressures. We provide new 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, 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 colours while some remain entirely achromatic.

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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
<i>Multiple Message</i>	Different quality-related traits predicted by different plumage ornaments or ornament types	✓	Breast UV-chroma predicts IgY levels while rectrix UV-chroma predicts testosterone
<i>Redundant Signal</i>	Quality-related traits predicted by many plumage ornaments	✓	Primaries, alula, spots, mantle brightness and rectrix brightness can all predict territory quality
<i>Unreliable Signal</i>	Some plumage ornaments unrelated to quality-related traits yet preferred by females	✗	N/A
<i>Multiple Receiver</i>	Different plumage ornaments relate to quality-related traits that are differentially useful for inter- and intra-sexual signaling ¹	✓	Melanized plumage predicts territoriality vs. wing patterns predict expected reproductive performance

¹See Table 2 for a description of which quality proxies may provide inter- versus intra-sexual information

Table 2: Information content for quality proxies used in this study and justification for the classification of each as inter-sexual, intra-sexual or mixed information.

	Trait	Justification	References
<i>Inter-sexual Information</i>	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; i.e. 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; i.e. at the time of feather growth	Takaki et al. 2001
	Expected Fledglings	Females should preferentially pair with males that have high expected reproductive performance	Hill 1991
<i>Mixed Information</i>	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 upon the later arrival of a higher quality male)	Alataro et al. 1984; Smith and Moore 2005
	Territory Quality	Females should pair with a male able to defend the minimum number of possible nesting sites to find one that is suitable Males should fight preferentially over higher quality areas	Tinbergen 1939; Lanyon and Thompson 1986
<i>Intra-sexual Information</i>	Testosterone Titers	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

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. 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).

Predictor Variables	Dependent Variables							
	Arrival Date	Growth Bars	Change in IgY	Arrival Testosterone	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)		

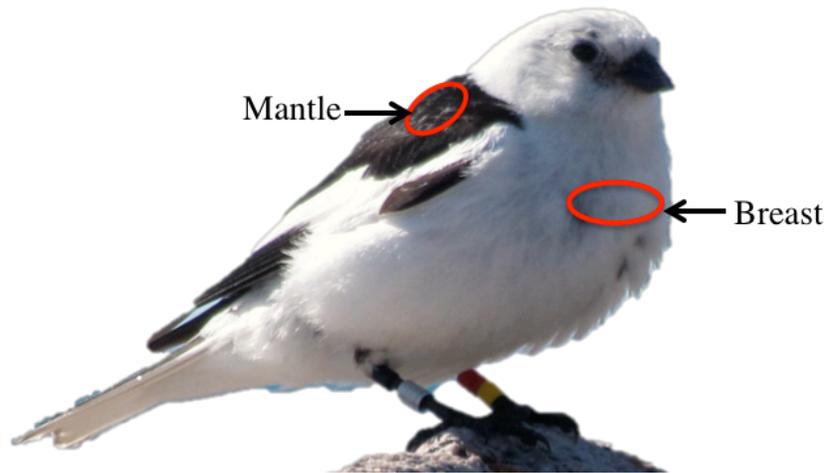
Table 4: Model summary and selection criteria for variables outlined in Table 3; Mallows' C_p values and cross-validation results for the LARS-LASSO model selected for each dependent variable examined. Model consistency refers to the proportion of N-fold cross-validation test groups that were parsimonious with the top model.

	Dependent Variables							
	Arrival Date	Growth Bars	Change in IgY	Arrival Testosterone	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 (\pm S.E.)	1.00 \pm 0.26	1.03 \pm 0.21	1.04 \pm 0.64	1.10 \pm 0.34	1.12 \pm 0.42	1.01 \pm 0.31	0.92 \pm 0.23	1.04 \pm 0.50

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. 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.

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)		
Arrival Testosterone		-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 (±S.E.)	0.98±0.34	1.22±0.34	0.63±0.22

a)



b)

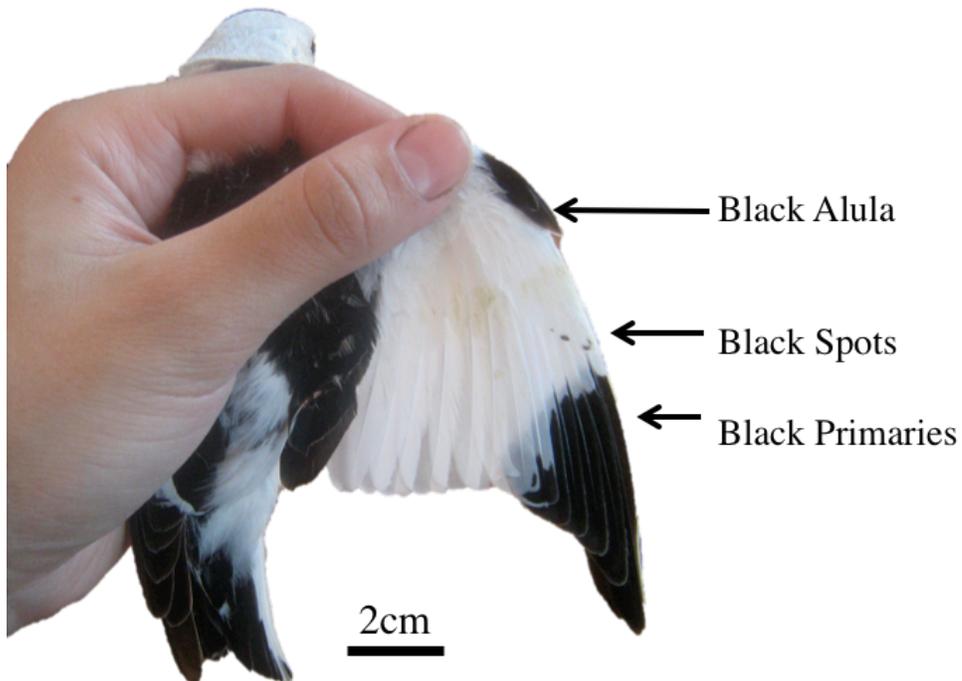
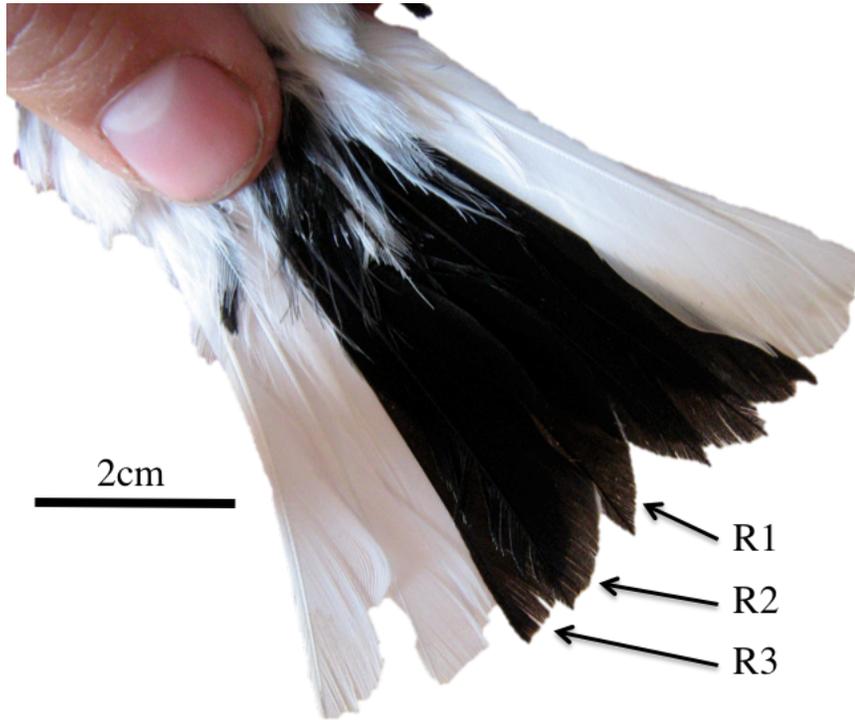


Figure 1: Male snow bunting breeding plumage traits measured: a) body regions from which feather samples and reflectance measurements were taken and b) wing pigmentation pattern variables assessed using wing photographs and ImageJ.

a)



b)



Figure 2: Male snow bunting a) rectrix pigmentation patterns and the b) area of the third rectrix (R3) used for spectral analyses. The shaded circle represents the positioning of the light probe and the smaller center circle represents the area of the feather where reflectance is measured.

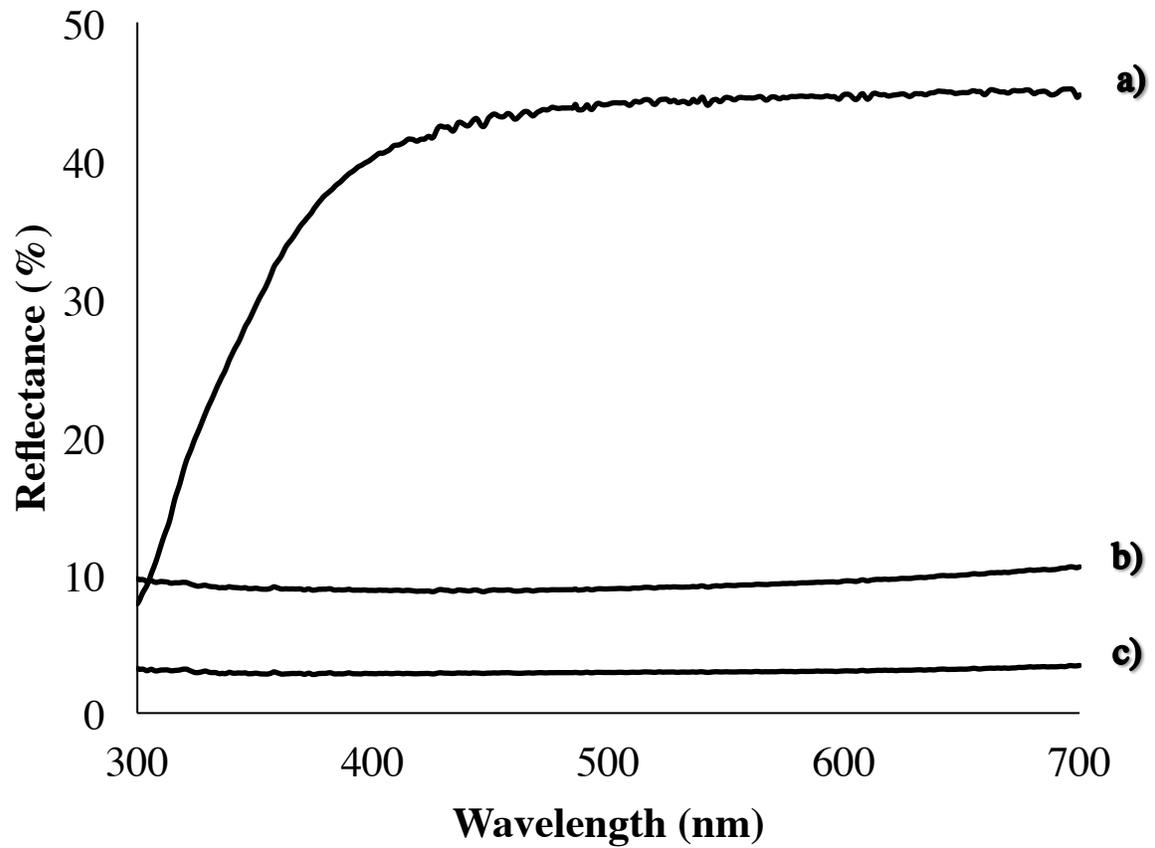


Figure 3: Mean snow bunting plumage reflectance spectra over the visual range of birds (300-700nm) for the a) white breast, b) black mantle and c) black rectrices (all $N=29$). Brightness is calculated over the entire range of the spectrum (300-700nm) while UV-chroma is calculated over the UV range of the spectrum (300-400nm).

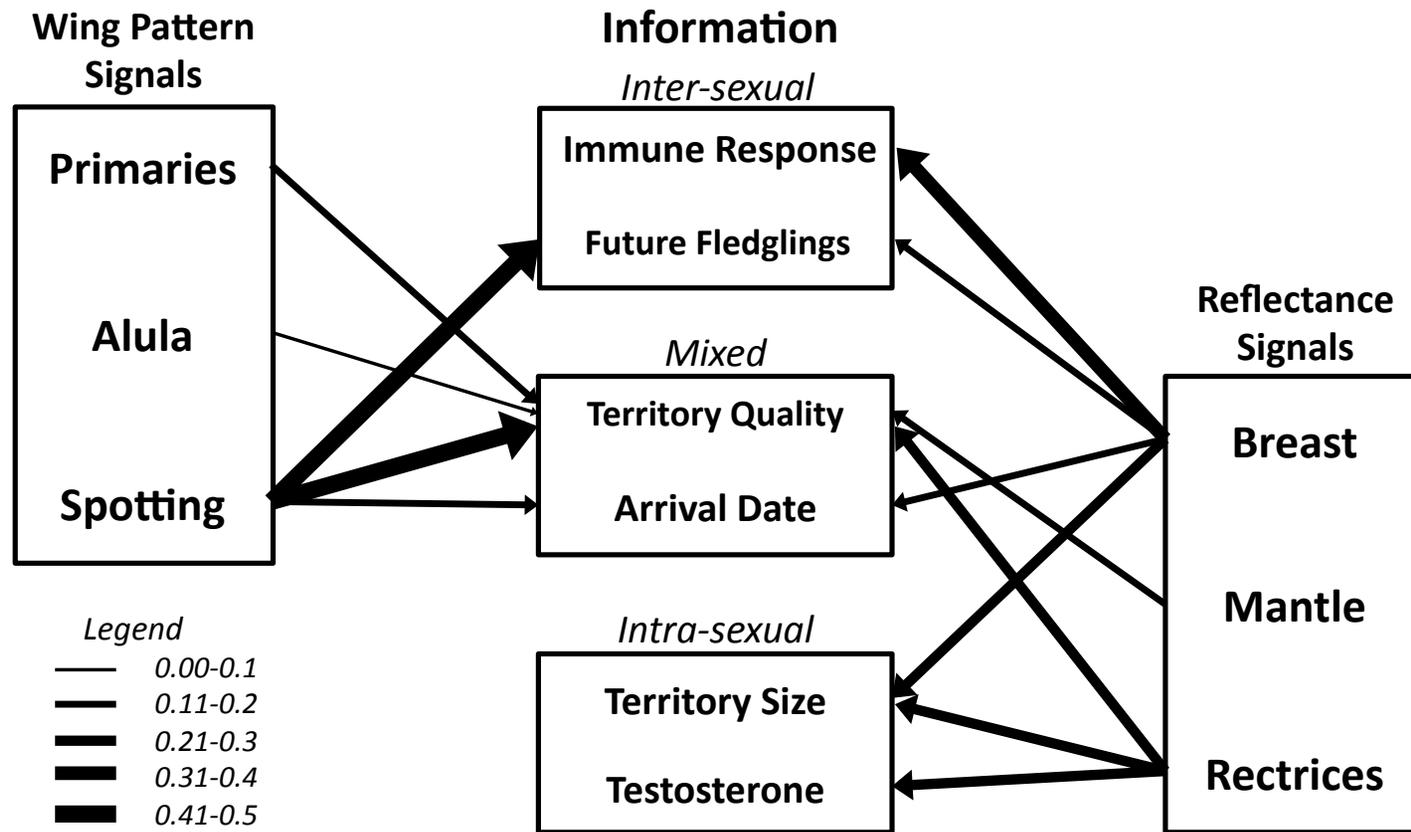


Figure 4: Male snow bunting plumage traits can act as multiple ornaments. Arrows arbitrarily point to the dependent variable and represent correlations with plumage predictor variables identified by the LARS-LASSO models. Dependent variables for which no predictor was selected are not shown (see table 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.

APPENDIX 1

LEAST ANGLE REGRESSION AND THE LASSO MODIFICATION

Variable Selection Techniques

Variable-selection techniques commonly used in ecological studies are inadequate for the type of variable selection we required: stepwise variable selection is biased and inconsistent (Whittingham et al. 2006; Mundry and Nunn 2009) while information criterion model selection procedures (i.e., BIC or AIC) rely on strong a priori predictions and are not designed for data exploration (Anderson and Burnham 2002). Alternatively, building a single model to include all plumage variables does provide unbiased parameters yet may not be the optimal model and is likely to include many extraneous variables. As an alternative, bio-statisticians have recently urged ecologists to consider the use of algorithmic models to select important predictor variables (Murray and Conner 2009; Oppel et al. 2009). Presented here are several currently accepted options, and our justification for selecting the least angle regression algorithm with a least absolute shrinkage and selection operator modification to identify important plumage predictors of individual quality.

Ridge Regression

Ridge regression is a type of penalized regression that may be used to circumvent the problems of multicollinearity (Hoerl and Kennard 1970)—where many predictor variables are correlated amongst one another, leading to decreased accuracy in estimating coefficients or excluding important predictors from the final model (i.e. when both correlated independent variable are equally important predictors of the dependent variable yet only one is identified to be so; Blalock 1963). Essentially, ridge regression modifies the residual sum of squares used in traditional ordinary least square regression with a constant (K , the ridge parameter) that penalizes large parameter estimates (ones with high variance). This introduces a bias in calculating the parameter estimates (since estimates are multiplied by a constant; Hoerl and Kennard 1970), but reduces the variance of estimates—known as the bias-variance trade-off. Ridge regression alone does not act in

variable selection, however, and an additional modification is necessary for this to be accomplished.

Least Absolute Shrinkage and Selection Operator—LASSO

Least Absolute Shrinkage and Selection Operator (LASSO) is also a form of penalized regression where weak predictors of the dependent variable have their coefficients shrunk to reduce variance (although increase bias). LASSO differs from ridge regression, however, as it can shrink parameters to zero and act in selecting important variables (ones with non-zero parameters; Tibshirani 1996). This is achieved through minimizing the L_1 -norm (the rectilinear distance) rather than the L_2 -norm (i.e. as in ordinary least squares regression and ridge regression; the Euclidean distance). The primary difference between minimizing the L_1 - versus L_2 -norm stems from the geometry that each uses: rectilinear distances, also called taxicab distances, work on a predetermined grid where you can only move on up-and-down or side-to-side axes, whereas Euclidean distances are the shortest distances between two points or as the crow flies. Formally, rectilinear distances are the absolute sum of their coordinates (Krause 1987), whereas Euclidean distances are calculated by Pythagoras' theorem as the shortest distance between two coordinates (Coxeter 1961). Constraining parameter estimates by a constant in rectilinear distances has the tendency to drive many of the parameter estimates to zero. Unfortunately, LASSO regression alone has several limitations including being computationally expensive, difficult to optimize (i.e. select the shrinkage coefficient) and having limited means to evaluate the model selected (Efron et al. 2004).

Forward Stagewise Regression

Alternatively, forward stagewise regression can select variables in a manner similar to forward selection. Forward selection acts by adding the predictor most correlated to the dependent variable into the model. It then identifies the next predictor that, when added to the model, will ameliorate the model by minimizing the sum-squared-error. This process continues until no additional predictor can be added to improve the model. Forward selection is problematic because once a variable is added to the model it cannot be dropped. It is important to realize that as new predictor variables are added to the model,

the estimated parameters (β) of previous predictors are modified—they can even decrease substantially such that the parameter of the first variable added to the model, the one most correlated to the dependent variable, can end up with the lowest parameter estimate. Consequently, parameter estimates may be unreliable in identifying the most important predictors or important predictors may even be excluded, and largely as an artefact of trying to compute the full ordinary least squares estimate.

Forward stagewise regression overcomes these problems by only adding part of a variable, or as much of a variable as needed, to the model at a given time (Hastie et al. 2001). Forward stagewise regression begins as in forward selection by selecting the predictor variable most correlated with the dependent variable. However, rather than adding the entire variable to the model, stagewise regression only adds as much of a variable as needed until the residuals of this regression are as correlated with a second predictor as the first predictor is to the dependent variable. At this point, the second predictor is added until a third variable is as related to the residuals and so on. Again, this process will continue until no additional variable can explain the remaining residuals, or until a stopping rule is reached. The only disadvantage of using forward stagewise regression is that in order to add only as much of a variable as needed, it proceeds in tiny incremental steps—this can be computationally cumbersome (Hastie et al. 2001).

Least Angle Regression (LARS)

Least Angle Regression (LARS) is an efficient algorithm that is computationally as straightforward as stepwise methods yet less ‘greedy’ (Efron et al. 2004). LARS, like forward stagewise selection, will add only as much of a predictor variable as necessary. Unmodified, LARS will continue on for s steps, where s is the number of predictors included in the model; in other words LARS can act to select all predictor variables in order of importance.

The LARS algorithm can be modified to provide solutions for LASSO and forward stagewise regression, but has the advantage of eliminating the computational limitations of both techniques. The performance of the LARS algorithm with a LASSO modification or with a forward stagewise modification are highly comparable (Hastie et al. 2001), but we chose to use LARS with a LASSO modification simply because this

technique is not restricted to linear relationships (due to rectilinear geometry). In addition, LARS-LASSO allows variable selection to move both forwards and backwards (as opposed to forward only): if the parameter of a predictor drops to 0 in LARS-LASSO models, then the predictor is dropped from the model. In other words, with the LASSO modification, LARS allows parameters to enter and drop from the model instead of simply adding parameters until s is reached.

Selecting a model using the LARS-LASSO procedure can be done in one of two ways (similar performances, Madigan and Ridgeway 2004; although see Ishwaran 2004): through minimizing Mallows' C_p (Mallow 1973) or minimizing the mean squared prediction error (MSPE) with cross-validation (Efron et al. 2004). The C_p is an unbiased estimate of the sum of squared errors at each step, penalized for the number of predictors included in the model. In essence, minimizing C_p is almost identical to minimizing the AIC parameter during information criterion analyses. Conversely, k -fold cross-validation divides the data into k equal groups, where each group is used in succession as the test group, while all others are used to build the model. For each of the k -folds, the model is calculated and used to predict the dependent variables of the test group. The MSPE is calculated as the average difference between the observed and predicted values (using the test group). Like C_p , MSPE is a measure capturing both the variance and bias of the model (analogous to precision and accuracy, respectively).

In summary, we chose to use the LARS algorithm with a LASSO modification to identify important plumage predictors of quality for many reasons: it is more conservative than stepwise selection, robust to multicollinearity, did not make distributional assumptions about variables, and allowed for selection of predictor variables in forward and backward directions.

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CHAPTER 3—GENERAL DISCUSSION

OVERVIEW AND IMPLICATION OF RESULTS

In Chapter 2, we provide the first empirical evidence that an achromatic species possesses plumage traits that can act as multiple ornaments indicative of male quality. Specifically, in male snow buntings (*Plectrophenax nivalis*), we find evidence to support the *multiple receiver hypothesis* since melanin-based mantle and rectrix reflectance are predictors of territoriality, while wing pigmentation patterns are indicators of expected reproductive performance. We suggest that this finding, along with the knowledge of previously described inter- and intra-sexual displays (Tinbergen 1939), indicates that male and female snow buntings may both act as receivers and may use different plumage signals that relate to sex-specific signal content. We also found support for the *multiple message* and *redundant signal hypotheses*, where a number of measures of male quality are signalled by a single plumage trait, whereas others by more than one plumage traits.

Our results have important implications for the study of animal communication since we demonstrate that a relatively simple type of non-coloured plumage can be used in complex communication. This possibility has often been ignored, or overlooked, in the past given that the current appreciation of how achromatic signalling functions is limited compared to our understanding of chromatic colour signalling. The results from Chapter 2 are a perfect example that even systems that are assumed to be relatively simple may be more complex than previously thought, and that exploring this complexity can lead to furthering our understanding of basic biological concepts.

To date, only eight empirical studies (including this thesis) have focused on visual communication in purely black, white or grey species. Our study provides new insight into the evolutionary role of achromatic plumage signalling, and provides potential clarification to areas of research that are currently disputed. For example, researchers have debated whether achromatic plumage acts as a condition-dependent signal for over a decade (Hill and Brawner 1998; Badyaev and Hill 2000). Unfortunately, support against

the condition-dependence of achromatic signals has relied on data from species exhibiting both melanin- and carotenoid-based plumage ornaments. As such, current findings may be specific to species that have both carotenoid- and melanin-based signals. In a species that is entirely achromatic, black and white ornaments may indeed serve an entirely different purpose (i.e. may act in a condition-dependent manner). In fact, if we consider that five of the six current studies assessing the condition-dependence of black and white plumage in achromatic species have supported this long-refuted concept (including our own; see Table 1), we would draw a very different conclusion about the use of achromatic plumage in condition-related signalling. Furthermore, it is even less well understood how achromatic species may signal territoriality and condition simultaneously, either through different ornaments, or through the same plumage trait. Researchers have only considered the possibility that achromatic species can signal both dominance and condition in three species (including our own; Table 1). Again, our study supplements the single previous study that has demonstrated that a single achromatic plumage trait may both signal territoriality and condition.

I hope that our results will inspire the design of future research projects to consider both dominance and condition as the potential information content of achromatic signals. Many currently published projects on plumage signalling in achromatic species remain inconclusive as to whether or not achromatic plumage can act to simultaneously signal condition and dominance (Table 1). In many of these cases, the authors may already have additional data on condition (i.e. body condition, fat scores, parasite loads) and could easily assess the relationship between plumage and these condition-related measures without any additional data collection. Revisiting these studies within a new paradigm—that achromatic plumage may be an efficient simultaneous signal of dominance and condition—would greatly contribute to our understanding of visual communication and the evolution of plumage colouration as a whole.

LIMITATIONS OF THE STUDY AND FUTURE DIRECTIONS

Correlative Study

The primary limitation of our study, as in the majority of previous studies that have examined multiple ornaments, is its correlative nature (although see Andersson et al. 2002). It is difficult to perform an experimental manipulation in a wild population without a prior understanding of naturally occurring relationships; this is even truer in a system where we are examining multiple plumage traits simultaneously. Consequently, this study should be considered as the first part of many in understanding the role of plumage signalling in driving territorial interactions, mate choice and fitness in snow buntings. To address this drawback, I suggest that mate choice experiments be performed over several years (due to potential inter-annual variation in mate preferences; Chain and Lyon 2008b). Similarly, plumage ornament manipulations (i.e. manipulating plumage area size on the wing with paint or bleach; altering the UV-reflectance of plumage with UV-blocking chemicals; see Vedder et al. 2008) should be performed at different times (i.e. before males begin setting up territories or once territories are established but before female arrival to the island) to explore both the intra- and inter-sexual consequences of variation in plumage traits.

Plumage Measurements

One weakness of our choice of plumage traits was that we measured the area of some plumage traits (i.e. wing patterns), and the reflectance of others (i.e. body regions) without considering the reverse—the reflectance of wing pattern areas and the area of the black mantle or white breast may also serve as visual signals (as in Mennill et al. 2003; Gladbach et al. 2011). This limitation is an artefact of logistical constraints, as we did not feel confident in reliably measuring these alternative characteristics of wing and body plumage. The pigmentation within the wing areas can be highly variable—which specific region within the primaries or the alula do we measure to capture reflectance holistically? Furthermore, some were too small to measure or non-existent in some males (i.e. wing spots). Similarly, measuring the area of body feather regions would be very difficult both in positioning the birds consistently and in standardizing the way we arrange these highly flexible feathers. The body of the bird—unlike the wing—could not be held in a 2D

plane, which would add uncertainty to our measurements of mantle or breast area. Nevertheless, receivers might use these added plumage characteristics to evaluate individual quality; only measuring wing pattern areas and body reflectance may add to the uncertainty in our data and limit our understanding of visual communication in snow buntings. It is possible that trait area in combination with trait reflectance may contribute to assessing individual quality (Mennill et al. 2003; Calkins and Burley 2003; Doucet et al. 2005).

Behavioural Displays

Display quality may also contribute to effective signalling and may be an important consideration for conspecifics during social breeding interactions (Chargé et al. 2010; Cornuau et al. 2012). Both plumage signal quality and the ability to show off this signal may contribute to inter- and intra-sexual communication; our study was only able to assess the former. Again, the primary reasons for not examining behavioural aspects of the display were logistical; hours of consistent focal observations would be necessary to reliably extract behavioural variables such as display rate or display intensity, and we simply did not have the time. In addition, courtship displays are rarely observed at East Bay Island and birds can be very hard to spot amongst the rocks when they perform this display or copulate (I personally observed 2 snow bunting copulations for 28 nests that produced hatchlings). Collecting these correlative data may be possible in the future, with a larger field team dedicated to documenting snow bunting behaviour. An experimental approach may also be possible, where males within their territories may be presented with a model female or male specimen to assess inter- and intra-sexually specific behavioural responses in a timelier, albeit artificial manner.

A second, less obvious behaviour that may influence plumage quality is the rubbing of the feather tips to transition from the wintering plumage to breeding plumage (Montgomerie and Lyon 2011). Inter-individual variation in both the timing of this behaviour and the quality of active feather wearing may influence perceived plumage quality, and may contribute to unexplained variation in plumage and individual quality. Observing the wearing behaviour of individual males at arrival and documenting the rate

of feather wearing may provide a better idea of how this behaviour can influence perceived plumage quality and impact male reproductive success.

Honest Signalling

Our study was not focused on elucidating the mechanistic linkages between plumage trait production and male quality. Consequently the exact nature of the relationship between these traits and the underlying mechanism enforcing the honesty of these signals (if they are honest signals) remains unclear. Many authors still debate whether black and white plumage may act as honest signals since the costs of producing these types of feathers are largely unresolved (see Tickell 2003; Meunier et al. 2011). Suggested costs of melanin plumage production include limited dietary mineral acquisition, limited dietary amino acids or pleiotropic hormonal trade-offs (testosterone; Jawor and Breitwisch 2003; McGraw 2008). Additional costs of melanin-based plumage may include social reinforcement (McGraw et al. 2003) and parasite loads during molt (Fitze and Richner 2002). Perhaps even less understood are the costs of producing white feathers—suggested costs of pigment-less feathers include reduced resistance to wearing, greater difficulty in keeping feathers clean, and that white feathers may be conspicuous to predators (reviewed in Tickell 2003). Recent evidence also suggests that diet at the time of molt may alter the size of white plumage patches (McGlothlin et al. 2007). Investigating the production costs of these signals may be important—while more challenging, I believe that understanding the mechanisms of ornament production in terms of cellular processes and relating these to individual quality as suggested by Hill (2011) would be novel and would contribute to addressing unanswered questions about achromatic plumage production costs.

Fitness Consequences

This study was also not aimed at exploring the reproductive consequences of inter-individual variation in plumage. While we did examine the direct relationship between plumage and reproductive performance, this in no means provides a clear understanding of how plumage relates to reproduction—in this context, we used the number of fledglings as a measure of expected reproductive performance rather than as a proxy for

fitness. Instead, I suggest that future studies should consider intermediate effects and explore how plumage can predict quality and how both plumage and quality influence reproductive success. Doing this (perhaps through partial correlation coefficients; see Møller et al. 2003) would elucidate the relationships between male plumage and fitness more clearly than ignoring intermediate effects (as done in Chapter 2).

Repeatability

Our data were collected over 2 years, with an unusually low return rate for adult males. As such, we were unable to examine repeatability (Lessells and Boag 1987) in plumage traits and male quality. My definition of ‘quality’ in Chapter 1 suggests that this trait is repeatable—while previous studies have suggested that many of the quality proxies we chose to measure are repeatable (i.e. growth bars: Takaki et al. 2001; arrival date; Lourenço et al. 2011), verifying these assumptions would provide further support for our choice of quality-related proxies. The repeatability of a character or a behaviour will suggest whether or not selection may act on it; understanding the repeatability of plumage traits, individual quality and mate choice in snow buntings will be essential to understand how sexual selection may act in this system (Boake 1989).

SUMMARY

In conclusion, my thesis provides novel evidence that achromatic plumage traits may act as multiple ornaments and may be used by multiple receivers. Some of these plumage traits may also function as redundant ornaments, simultaneously indicating aspects of male territoriality and condition. I provide many avenues for future research, including mate choice experiments, incorporating behavioural observations as well as plumage ornament manipulations; these research projects would contribute to our current understanding of visual communication in achromatic species and the evolution of plumage colouration in birds.

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Table 1: Literature review of studies of achromatic species examining dominance or condition-related plumage signalling in males. ‘None found’ indicates that authors assessed at least one measure of condition/dominance, but did not find a relationship with the studied plumage trait, while ‘None investigated’ indicates that authors did not attempt to investigate the indicated relationship.

	Species	Signal of Condition	Signal of Dominance	Reference(s)
Signals condition & dominance	<i>Ficedula albicollis</i>	Wing patch size	Forehead patch size	Pärt and Qvarnström 1997; Török et al. 2003
	<i>Junco hyemalis</i>	Proportion of white tail	Proportion of white tail	Balph et al. 1979; McGlothlin et al. 2007
	<i>Plectrophenax nivalis</i>	Breast reflectance	Tail reflectance	SGP, unpubl.
Inconclusive Studies	<i>Aethia pusilla</i>	None investigated	Belly patch size	Jones 1990
	<i>Chloephaga picta</i>	Wing patch reflectance	None investigated	Gladbach et al. 2011
	<i>Struthio camelus</i>	Wing patch reflectance	None investigated	Bonato et al. 2009
	<i>Calamospiza melanocorys</i>	Not investigated	Black rump size	Chaine and Lyon 2008a
	<i>Lanius minor</i>	None found	None investigated	Krištín et al. 2007

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- SELECTED AWARDS:** NSERC Post-Graduate Scholarship D3, 2012-2015
- Columbia University Dean's Fellowship, 2012-2017
- Ontario Graduate Scholarship, 2011-2012
- NSERC Canadian Graduate Scholarship M, 2010-2011
- University of Windsor Tuition Scholarship, 2010-2012
- NSERC Undergraduate Student Research Award, 2008
- SFU Gordon Shrum Scholarship, 2006-2010
- BC Provincial Scholarship, 2006