



## Alula size signals male condition and predicts reproductive performance in an Arctic-breeding passerine

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While studies of achromatic plumage signaling are scarce relative to chromatic ornaments, achromatic ornaments have the potential to act as an efficient form of visual communication due to the highly conspicuous contrast between black and white body regions. Recently, achromatic plumage reflectance has been shown to indicate condition, yet the condition-dependence of achromatic patch size remains unstudied. Here we show the first evidence that alula size, an achromatic plumage patch, has the potential to signal a male's condition and predict reproductive performance. In Arctic-breeding snow buntings *Plectrophenax nivalis*, the size of the alula simultaneously predicted pre-breeding physiological health and the number of offspring produced, through an intermediate variable (lay date). Snow buntings appear to pair assortatively; males and females arriving earlier pair together, and changes in body condition over the breeding season are positively related within pairs. We suggest that simple achromatic plumage patches, like alula size, have the potential to act as condition-dependent signals. Consequently, females may benefit from assessing these signals to reliably evaluate a male's condition and reproductive potential as a means of maximizing their reproductive success.

Males often display elaborate condition-dependent ornaments (Hill 1991, Andersson 1994) and females can use male ornamentation when assessing and choosing potential mates (Zahavi 1975, Hill 2006a). Females stand to benefit significantly from identifying and preferentially mating with males in good condition if this increases their own reproductive success (Hill 1991, Parker et al. 2003). Previous studies of female preference and male quality have largely focused on complex or elaborate ornaments (Zuk 1991; also reviewed by Gontard-Danek and Møller 1991), presumably since highly exaggerated ornaments have been shaped by stronger sexual selection (Gontard-Danek and Møller 1991, Andersson 1994, Dunn et al. 2001). However, simpler signals may also be favored under sexual selection (Sullivan 1994), particularly in species that do not possess highly exaggerated phenotypes.

Despite being common in birds, studies of achromatic plumage signaling are scarce relative to chromatic signals (Mennill et al. 2003). Achromatic plumage, consisting of black white or grey feathers, remains a potential visual signal due to the highly conspicuous contrast between dark and light body regions (Endler 1992, Andersson 2000). Achromatic signals have been studied previously in regards to status signaling, relating signal size to dominance rank and reproductive success (reviewed by Santos et al. 2011). However, recent evidence suggests that achromatic plumage may act as a condition-dependent signal (Mennill et al.

2003, Gladbach et al. 2011). These studies have focused on the reflectance properties of achromatic feathers, but the role of achromatic patch size in condition-dependent signaling remains unresolved, and researchers may be overlooking the potential adaptive significance of these patches as signals of condition.

We investigated the condition-dependence of a rarely studied plumage region – the alula – and its relationship to reproductive performance in male Arctic-breeding snow buntings *Plectrophenax nivalis*. In this species, the alula consists of two black feathers located on the leading edge of the wing, starkly contrasted against the white wing and chest. This plumage patch is visible when a male is perching, flying, and during mate-attraction displays (Tinbergen 1939). In addition, males display a large amount of body size-independent variation in alula area (Results; Fig. 1), suggesting that this trait could serve as a signal of condition (Andersson 2000). While the importance of the alula for flight has been documented (Álvarez et al. 2001), its potential role in signaling remains unstudied. Using integrative measures of condition and reproductive performance in males and females across a two-year correlative dataset, we assessed the potential for male signaling using the alula. We predicted that alula size would relate to male reproductive performance (either through direct or indirect effects), and that alula size could inform females about a male's condition.

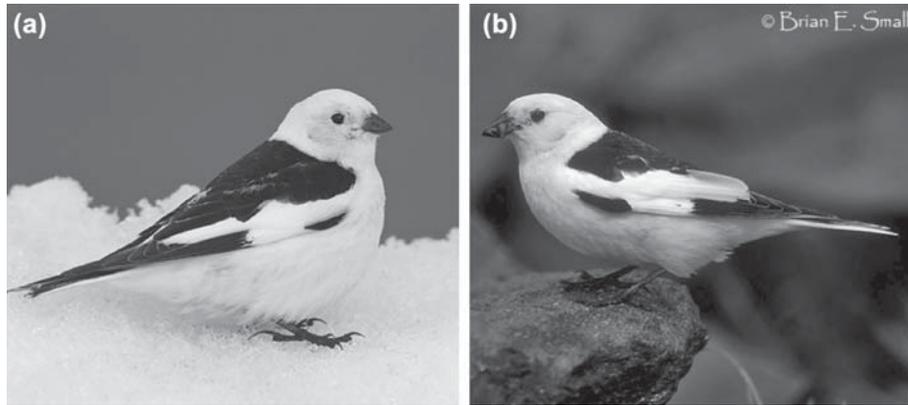


Figure 1. Inter-individual variation in male snow buntings' achromatic breeding plumage: the black alula of males is a small, distinct patch of dark feathers on the leading edge of the wing and can be (a) relatively smaller or (b) larger. © Brian E. Small – reproduced with permission.

## Methods

### Study population

We studied a breeding population of snow buntings from late May to August of 2010/2011 at East Bay Island, Nunavut, Canada (64°02'N, 81°47'W). High breeding densities (~80 pairs km<sup>-2</sup>; Love unpubl.) at this location are likely the result of abundant granite rock assemblages, ideal nesting habitat for this crevice-nesting bird (Montgomery and Lyon 2011). Snow buntings are socially monogamous during the breeding season: males defend non-resource based territories, females build the nest, males feed their incubating mate and bi-parental feeding is necessary to rear young successfully (both in quantity and quality; Lyon et al. 1987). Although clutch initiation is considered synchronous for this species (over approximately 6 d within a breeding season; Montgomery and Lyon 2011), the timing of breeding may remain an important reproductive constraint in this Arctic species since pairs can only produce a single brood per reproductive bout.

### Sampling and reproductive performance

We began trapping birds following male arrival but preceding female arrival to the breeding grounds in late May with seed-baited Potter and walk-in traps. Due to our high trapping effort, we used the day of first capture as an approximation of the arrival date of individuals. Data from a geolocation-based migratory study in this population (2010–2011) confirms that the date of first capture reliably indicates arrival date (Macdonald et al. 2012). For all birds trapped, we collected a small blood sample from the brachial vein, measured tarsus (mm) and arrival mass (g), and applied unique metal and colour-band combinations to all individuals. Whole blood was centrifuged for 10 min at 12000 rpm within an hour of sampling, after which plasma was isolated and frozen at -20°C. Males were re-trapped and weighed during their mate's egg-laying period and photographs of the left wing were taken, outstretched at a perpendicular angle from the body (similar to Hanssen et al. 2009). Wing photographs were taken by the

same photographer to reduce variation in wing positioning. Males were aged as 'second year' or 'after second year' according to previously described protocols (Rae and Marquiss 1989). All breeding birds were re-trapped during late nestling provisioning and re-weighed.

We tracked breeding pairs by locating nests and visiting them every 2 to 3 d to determine the day laying began (i.e. lay date) and clutch size. We counted and banded fledglings, as well as weighed and measured their tarsi at 8 d of age – the day prior to fledging. We calculated average nest tarsus length and average nest weight as proxies of nestling quality. We used the number of nestlings present at day 8 as our estimate of the number of fledglings. Knowing that there is no nest predation at East Bay Island, we are confident that any brood reduction results from nestling starvation (Hussell 1985, Guindre-Parker unpubl.).

### Alula size

The alula patch area (hereafter called alula size) was calculated from wing photographs using ImageJ (ver. 1.45 National Inst. of Health, USA), open-source software capable of using standardized color thresholds to measure areas.

### Male condition

As a measure of physiological health status – and thus a component of male condition – we used an index of humoral immunity, quantified as levels of circulating immunoglobulin Y (IgY) serum proteins (Martínez et al. 2003, Bourgeon and Raclot 2006, Bourgeon et al. 2006). Plasma IgY levels are predicted to be a reliable and useful measure of individual condition as they have been found to be highly responsive to changes in body condition (Bourgeon and Raclot 2006, Bourgeon et al. 2006, 2010), and integrate both genotypic and phenotypic components of condition (Apanius and Nisbet 2006). In a short-lived passerine, IgY levels have been found to increase with body condition and diet quality (Love and Guindre-Parker unpubl.). We measured IgY using an enzyme-linked immunosorbent assay that utilizes commercial anti-chicken anti-

Bourgeon et al. 2006). This method has been validated in 6 avian species and was optimized for snow buntings: we diluted our samples at 1:32 000, which falls within the linear range of a sigmoidal curve in a serial dilution cascade (as outlined in Bourgeon et al. 2006). The plate was read using a plate reader at 405 nm. IgY levels are a relative measure of color change – a greater change indicates a higher concentration of IgY present in the original sample – and are expressed in absorbance units. In addition to this physiological measure of condition, we calculated a commonly reported body condition index (residual body mass corrected for tarsus length; Schulte-Hostedde et al. 2005) at both pre- and post-breeding.

### Statistical analyses

Variables were standardized within years for all analyses (centered around the mean and divided by the standard deviation; Schielzeth 2010). We performed a path analysis (as described elsewhere; Wootton 1994) to assess the direct and indirect effect of alula size on fledging success. We averaged male arrival date and female arrival date to yield mean parental arrival date to reduce the number of extraneous coefficients estimated in this analysis. Sample sizes should be 5–20 times greater than the number of paths assessed (Petraitis et al. 1996); for this reason, we limited the scope of our path analysis to the direct relationships between alula size, laying date and the number of fledglings along with only essential covariates (parental arrival date, clutch size, year and male age). We specified a hypothetical path between variables (Fig. 2a) based on a previously hypothesized model relating individual condition, timing of reproduction and reproductive success (Descamps et al. 2011). We modified the model to consider male alula size as a signal of male condition rather than individual pre-breeding condition and added fledging success as our

proxy for annual reproductive success. To test the proposed relationships between variables, we used multiple general linear models (GLM) to calculate path coefficients; briefly we regressed all hypothetical independent variables, along with male age and year for the dependent variables (lay date and the number of fledglings).

We used a GLM to investigate the relationship between male condition (change in body condition and IgY levels) and alula size, including year and age as covariates. We also assessed the relationship between parental traits (change in body condition and IgY levels, separately), and the size and body condition of fledglings produced using a GLM. Lastly, we assessed the possibility for assortative pairing based on female and male quality: we measured the correlation coefficient between male and female IgY levels and change in body mass.

Three males returned in both years and were re-sampled: randomly excluding one sample for these three males did not affect our results, so we present our analyses including the few re-sampled individuals. For all models, we ensured that residuals were normally distributed (Shapiro–Wilk test,  $p > 0.05$ ). We present only the results of full models and all tests are two-tailed. Analyses were performed in JMP ver. 9 (SAS Inst., Cary, NC).

### Results

Variation in relative alula size was unrelated to male structural size (tarsus:  $r^2 = 0.024$ ,  $p = 0.412$ ;  $n = 30$ ) indicating that alula size could act as a signal of male quality independent of body size. We found a significant positive effect of male age on alula size and immunoglobulin levels (alula size:  $t = -3.28$ ,  $p = 0.0098^*$ ,  $DF = 8.81$ ; IgY levels:  $t = -3.05$ ,  $p = 0.0081^*$ ,  $DF = 15.0$ ), but not on reproductive parameters (clutch size, lay date and number of chicks fledged;  $p > 0.05$ ).

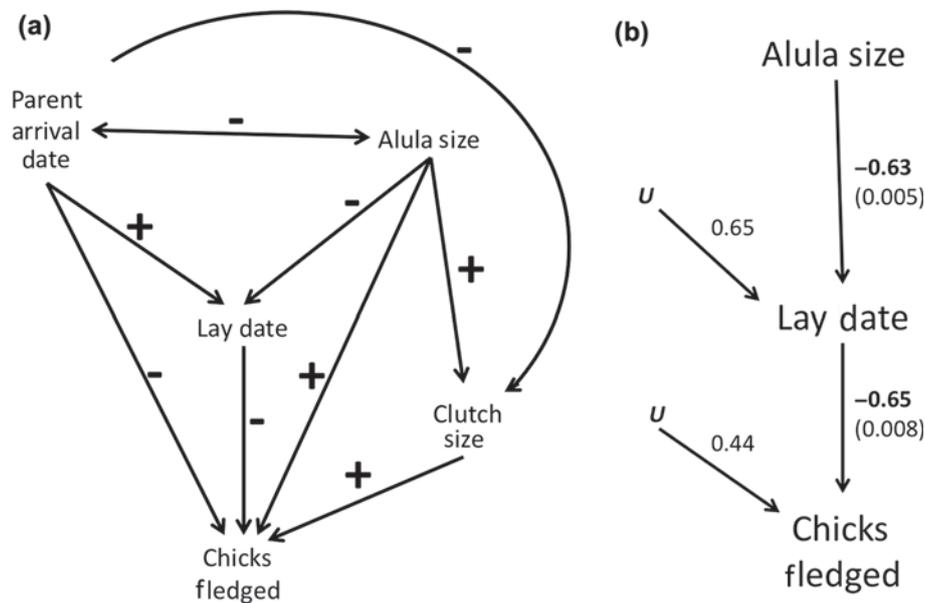


Figure 2. Path diagrams depicting the (a) hypothetical and (b) statistically significant standardized path coefficients that illustrate the relationship between male alula size and reproductive performance, mediated through the influence of lay date. *U* refers to extraneous variables or error in our model.

Table 1. The multiple general linear models that make up the path analysis outlined in Fig. 2. Parameter estimates on standardized variables represent standardized beta coefficients. Significant effects are indicated by an asterisk (\* $p < 0.05$ ; \*\* $p < 0.001$ ).

Predictor	Estimate	t ratio
a) Dependent: clutch size		
Intercept	0.006	0.02
Age	0.016	0.06
Year	0.070	0.36
Alula size	-0.143	-0.64
Mean parent arrival date	0.015	0.07
b) Dependent: lay date		
Intercept	-0.153	-0.60
Age	0.243	0.86
Year	-0.102	-0.57
Alula size	-0.634	-3.11**
Mean parent arrival date	0.050	0.24
c) Dependent: number of fledglings		
Intercept	-0.544	-2.08
Age	0.530	1.80
Year	-0.063	-0.38
Alula size	-0.300	-1.18
Mean parent arrival date	-0.433	-2.11
Lay date	-0.647	-2.98**
Clutch size	0.183	1.11

We found an effect of alula size on the number of fledglings mediated via lay date (Table 1; Fig. 2). Males with a larger alula initiate reproduction earlier, regardless of the timing of parent arrival (both mean parental arrival time, or individual male and female arrival date). Pairs of snow buntings that bred earlier fledged a greater number of offspring regardless of initial clutch size.

Male arrival IgY levels were significantly and positively related to male alula size ( $r^2 = 0.513$ ,  $n = 20$ ; Table 2, Fig. 3) when controlling for age and year. We found no relationship between the change in body condition and alula size.

Male, but not female, IgY levels could predict the average skeletal size of chicks at fledging (tarsus length;  $r^2 = 0.369$ ,  $n = 20$ ; Table 3). Conversely, we found no relationship between parent IgY levels and mean body condition at fledging ( $r^2 = 0.15$ ,  $n = 20$ ; Table 3). We found no relationship between male and female changes in body condition and offspring quality (skeletal size or body condition; results not presented,  $p > 0.05$ ).

We found evidence of assortative pairing according to male and female quality. Males that arrived to the island earlier paired with females that arrived earlier ( $r^2 = 0.314$ ,  $p = 0.0013^*$ ;  $n = 30$ ; Fig. 4a). We also found that males that increased in body condition over the breeding season were

Table 2. General linear model of male condition and alula size (dependent variable). Parameter estimates on standardized variables represent standardized beta coefficients. Significant effects are indicated by an asterisk (\* $p < 0.05$ ).

Predictor	Estimate	t ratio
Intercept	-0.408	-1.82
Age	0.452	1.90
Year	0.035	0.22
IgY levels	0.422	2.46*
Change in body condition	-0.088	-0.52

paired to females that also increased in body condition ( $r^2 = 0.362$ ,  $p = 0.008^*$ ;  $n = 18$ ; Fig. 4b). We found only weak, statistically non-significant support that males and females paired assortatively based on IgY levels ( $r^2 = 0.121$ ,  $p = 0.0806$ ;  $n = 26$ ).

## Discussion

Individual variation in alula size in male snow buntings did not show an allometric relationship with structural body size and therefore has the potential to serve as a condition-dependent achromatic plumage signal independent of body size. Young, second year males have a smaller alula than older males: this pattern may be expected as second year males can be visually distinguished from older males by other plumage features (Rae and Marquiss 1989). Second year snow buntings may have had less time or resources to allocate to growing a large alula during feather production, which occurred when they were nestlings (Inouye et al. 2001).

In snow buntings, males and females appear to pair assortatively with respect to arrival date. However, parental arrival date was not related to the onset of reproduction; instead, lay date seems to be related to perceived male quality (i.e. through alula size). In our path analysis, replacing male alula size with male condition (IgY levels or change in body condition) resulted in no direct or indirect link between male condition and reproductive success. Thus, we are confident that our results indicate that a male plumage trait is the key driver of variation in lay date and is not being confounded with male condition. Alula size affects lay date, which in turn influences the number of nestlings that survive to fledging age. Advancing the onset of breeding, even by just a few days, may be advantageous in a species where breeding is time-constrained (Lepage et al. 2000). Male visual signals may influence lay date through securing a mate earlier (Potti and Montalvo 1991), acquiring a higher quality mate (Norris 1990), or through influencing the investment of females into reproduction (such as through clutch size; Velando et al. 2006). Our finding that males and females may pair assortatively,

Table 3. General linear model of male and female condition and offspring quality: a) average chick tarsus length at fledging and b) average chick body condition at fledging (dependent variables). Parameter estimates on standardized variables represent standardized beta coefficients. Significant effects are indicated by an asterisk (\* $p < 0.05$ ).

Predictor	Estimate	t ratio
a) Dependent: average fledging tarsus		
Intercept	-0.416	-1.16
Age	0.446	1.21
Year	0.006	0.03
Male IgY levels	0.559	2.43*
Female IgY levels	-0.125	-0.54
b) Dependent: average fledging body condition		
Intercept	0.015	0.04
Age	-0.083	-0.19
Year	-0.013	-0.05
Male IgY levels	0.434	1.61
Female IgY levels	0.006	0.02

at least with respect to some measures of condition, supports the idea that male snow buntings with larger alulas pair with higher quality females.

We found that the size of the alula, a simple achromatic plumage trait, can act as a condition-dependent signal; males with larger alulas had higher baseline humoral immunity prior to breeding. Together with the indication that alula size indirectly drives the number of nestlings produced, our results suggest that arriving females could benefit from using male alula size to gain insight into the expected reproductive performance of their social mate. Recent studies have demonstrated similar relationships between achromatic plumage signals, male condition and reproductive investment (Hill et al. 1999, McGlothlin et al. 2007, Gladbach et al. 2011). Further mate choice experiments or manipulative work may clarify the relationship between male alula size and female mate preference and egg-laying behavior.

Offspring provisioning is one of the costliest aspects of reproduction, and in many bird species parental condition decreases significantly throughout the provisioning period (Nur 1984, Weimerskirch et al. 2000, Love and Williams 2008). Although we could not measure provisioning behavior, our results indicate that males fledging more offspring did not suffer a loss of body condition. We can think of several possible mechanisms whereby higher pre-breeding IgY levels link alula size, increased condition across reproduction, and higher reproductive performance. Either males with high IgY levels have a higher capacity to manage the energetic costs of reproduction (predicted by Apanius and Nisbet 2006), or males with high IgY levels actually decrease their paternal investment to avoid these costs (Nur 1984). Alternatively, if males with higher IgY levels are actually of higher quality, their social mate may be willing to take on greater costs of reproduction allowing males to decrease their investment in offspring rearing. These hypotheses can be successfully disentangled in snow buntings since bi-parental care is pivotal for successful reproduction (both quantity and quality of offspring; Lyon et al. 1987). Therefore, for males to contribute less to parental care and still exhibit high reproductive success, their social mate would need to compensate significantly through increased maternal investment (Wolf et al. 1991, Saino and Møller 1995). Since the change in body condition was correlated between paired males and females, our findings suggest that females paired to males with a larger alula were not compensating for their mate's decreased parental investment. Lyon et al. (1987) found that widowed snow bunting females favored maintaining body mass at the cost of losing reproductive units (decreased offspring number and quality), further evidence that self-maintenance is very important to breeding females and that males must contribute for a pair to have high reproductive success. Consequently, we suggest that males with a larger alula and higher plasma IgY are better able to manage the energetic costs of rearing offspring.

It has long been believed that there should be an obligate cost associated with signal production to ensure honesty of condition-dependent traits (Zahavi 1975). Although the potential costs associated with achromatic plumage production remain unresolved (Hill and Brawnner

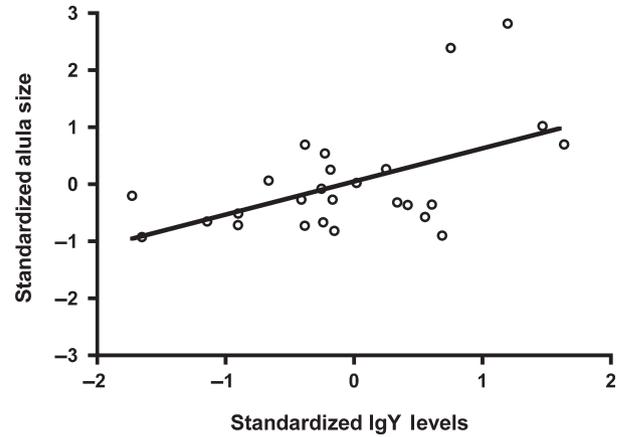


Figure 3. The alula is a condition-dependent signal, as this plumage trait is significantly correlated to IgY levels. Age classes were pooled since there was no significant effect of age, and because there were so few young males ( $n = 3$  out of 25 males total).

III 1998, reviewed by Meunier et al. 2011), proposed mechanisms through which black melanized plumage remains an honest signal include nutritional condition, ectoparasite loads, and dominance rank/competitive abilities (Jawor and Breitwisch 2003). We argue that several of these mechanisms do not apply to snow buntings as ectoparasites are uncommon in this species (Montgomerie and Lyon 2011)

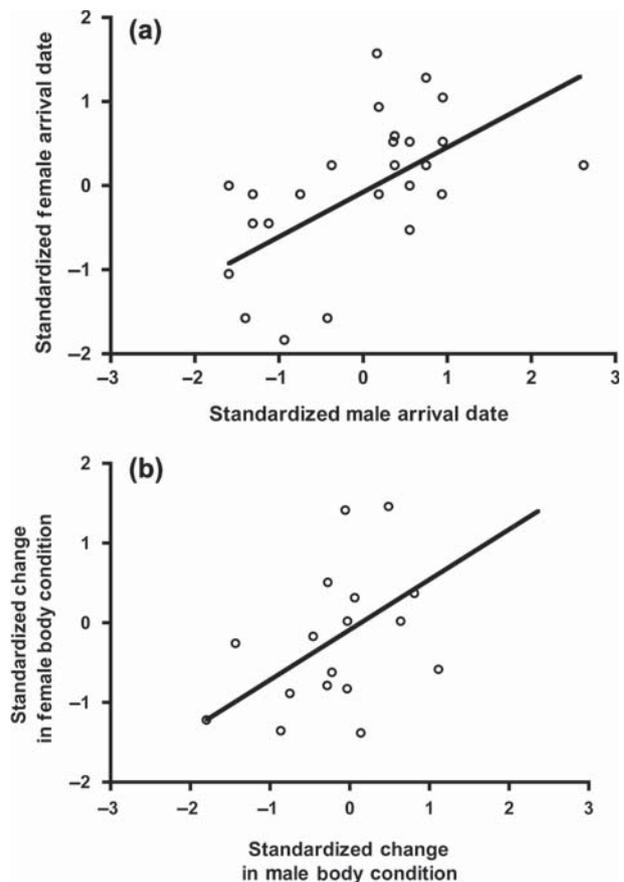


Figure 4. Assortative pairing in snow bunting pairs based on (a) arrival date and (b) change in body condition over the course of breeding.

and while males defend non-resource based territories, there is no known dominance structure for access to food. However, Hill (2011) recently suggested that ornamentation and performance need not tradeoff directly to ensure the honesty of a signal – ornament production and performance may instead both relate to individual condition. This idea that both ornament production and performance measures depend on vital cellular processes directly applies to our results; just as producing a larger alula patch may depend on energetic allocation, so does maintaining higher baseline immunoglobulin levels and breeding successfully. Higher IgY levels reflect increased investment in immune function influenced by both environmental exposure to antigens and genotype (Apanius and Nisbet 2006). Phenotype and genotype have similarly been shown to affect the structure and color of feathers (phenotype: Hill 2006b; genotype: Roulin 2004, Mundy 2006, Petrie et al. 2009), suggesting a possible mechanism through which IgY levels and alula production may be linked. Thus, males that are able to produce a larger alula and maintained increased baseline IgY levels may be signaling their favorable energetic state that also allows them to have increased reproductive performance.

Additional features of the alula could also serve in signaling, such as reflectance. We did not have spectrometry equipment in the field, and could not sample the alula because of its importance in flight. We also could not standardize the lighting in our photographs and did not feel confident in extracting spectral curves from these photos. Future work should consider the importance of both size and reflectance of achromatic plumage patches. Additionally, it is suggested that snow buntings may experience extra-pair paternity (Hofstad et al. 2002) – future studies should consider how paternity loss or gain may relate to male alula features. While we have demonstrated that alula size indicates male condition, further research is necessary to elucidate the specific cellular mechanisms by which alula production, immune function and reproductive performance are linked.

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