ACHROMATIC PLUMAGE PATCH QUALITY: INTERNAL ORGAN AND

SKELETAL CORRELATES IN ALEUTIAN CACKLING GEESE

(*BRANTA HUTCHINSII LEUCOPAREIA*)


By

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ABSTRACT


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Sexual selection theory predicts unique plumage patches signaling quality or status evolve via mate-choice and competition for mates. A growing body of research supports evidence that achromatic plumage patches may act as honest indicators of quality. Irregularities in these patches are attributed to an individual's phenotypic and genotypic quality as well as environmental wear and tear. Aleutian cackling geese (*Branta hutchinsii leucopareia*) display achromatic plumage patches on their heads and necks, which may signal information about an individual's attributes. I tested the honest advertisement and status signaling hypotheses by determining whether size and irregularities in the transition between black and white edges of plumage patches (i.e., immaculateness, or smoothness of borders) were correlated to indices of individual quality. Organ mass was used as an index to indicate energy acquisition, aerobic function, and immunocompetence. More specifically, I examined the linear relationship between plumage patch morphometrics and gizzard, heart, liver, and spleen mass. I also examined the linear relationship of plumage patch morphometrics and the size of the processus extensorius (wing spur). Smoothness in lower neck-ring borders in both sexes was positively correlated with gizzard size, supporting a prediction of the honest advertisement hypothesis. Cheek patch size was correlated with wing spur size in males,

which supports the status signaling hypothesis (e.g., fighting prowess). The distribution of lower neck-ring smoothness was uni-modal in males, indicating a strong selection via female mate choice for little variation in this attribute. Lower neck-ring smoothness was multi-modal in females, supporting a prediction of the individual identity hypothesis. Different attributes of achromatic plumage patches found on Aleutian geese may signal separate and distinct information in intra- and intersexual communication.

# ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

# LIST OF FIGURES

INTRODUCTION

Sexual selection theory predicts unique plumage patches signaling quality or status

evolve via mate-choice and competition for mates (*sensu* Darwin 1871, Anderson 1994).

Researchers testing for the presence of honest indicators of individual quality or social

status in avian taxa (*sensu* Zahavi 1977, Hamilton and Zuk 1982, Folstad and Karter

1992) have largely focused on sexually dimorphic species where males display bright and

colorful plumage patches during intra- and intersexual competition (Badyaev et al. 2001).

Males that display the largest, brightest, or most color saturated plumage patches also

have increased reproductive success (Savalli 1995, Ferns and Hinsley 2004, Cantarero et

al. 2017). Numerous correlations between elaborate plumage and variables describing

individual quality have been described (Keyser and Hill 2000, Hõrak et al. 2001,

Mougeot and Redpath 2004, Peters et al. 2007, Maney et al. 2008).

 A growing body of research on avian taxa suggests that achromatic plumage

patches, areas that are white, gray or black, may also act as honest indicators of

individual quality or social status (Hill 1993, Mennill et al. 2003, Dale et al. 2015,

Soulsbury et al. 2016). For example, the size of the achromatic forehead patch in collared

flycatchers (*Ficedula albicollis*) predicted the outcome of male competition over

territories, and the whiteness of wing-bars found in female common eiders (*Somateria*

*mollissima*) was linked to mass loss and a reduction in immunosuppression during

incubation (Pärt and Qvarnström 1997, Hanssen et al. 2006). The irregularities in the

transition between black and white edges of plumage patches, also called

immaculateness, or smoothness of borders, may reflect the ability to precisely deposit

melanin in feathers, thus signaling an individual's quality or status (*e.g.* in shelducks,

*Tadorna tadorna*, Ferns and Lang 2003; and great tits, *Parus major*, Ferns and Hinsley

2004). White plumage patches are less expensive to produce than carotenoid- and

melanin-dependent plumage, as they do not contain costly pigments, but they are thought

to be more difficult to maintain as they lack structural integrity and resistance to

ultraviolet light (Hill and McGraw 2006, Bókony et al. 2008, Ruiz-de-Castañeda et al.

2012). White feathers have been shown to be the first to degrade, especially in areas

where those feathers come in contact with the environment (Pyle 2008). White plumage

patches may deteriorate due to participation in agonistic interactions, strenuous flight,

pursuit and capture of prey, and manipulating abrasive food items (Cairns 1986, Bonser

2005, Bush et al. 2006, Pyle 2008, Galván and Sanz 2009).

The *honest signaling* model of sexual selection is explained by two hypotheses:

the honest advertising hypothesis and the status signaling hypothesis (reviewed by Hill

2002). The honest advertising hypothesis states that secondary sexual characteristics

reflect the quality of an individual's health and fitness, and only the healthiest individuals

can maintain high-quality ornaments (Keyser and Hill 2000). Furthermore, plumage

patches used to advertise individual qualities are suggested to have attributes with uni-

modal distributions and are correlated with measures of health and fitness (Dale et al.

2001). This pattern was observed for hue and saturation of red carotenoid pigments in the

adult plumage of male house finches (*Carpodacus mexicanus*), which showed uni-modal

variability in the population and predicted the proportion of young sired (McGraw et al. 2001).

The *status signaling* hypothesis states that plumage patch are badges of status that decrease costly agonistic intraspecific interactions between conspecifics of unequal rank. While badges of status are inexpensive to produce, cheaters may not be able to reinforce their displayed rank in agonistic encounters, as the signal does not match the associated behavior (Rohwer 1977, Grasso et al. 1996, Pärt and Qvarnström 1997, Gonzalez et al. 2002).

An additional hypothesis for the evolution of unique plumage is the *individual recognition* model, where plumage variation enables mates or neighbors to identify and monitor one another (Dale et al. 2001), rather than signal attributes of the bearer's quality (health or status). For instance, individual recognition is important for breeding behavior in two highly sexually dimorphic species, ruff sandpipers (*Philomachus pugnax*) and red-billed queleas (*Quelea quelea*), yet breeding plumage color (hue and saturation) was not condition dependent or correlated with subsequent reproductive success (Dale et al. 2001). Individual recognition of conspecifics is thought to play a role in situations where it is beneficial to be different, such as would be the case for mate, kinship, and neighbor recognition (Johnstone 1997). This may be the case with geese displaying achromatic cheek patches (*Branta spp.*), which congregate in large flocks and colonies. Variation in these white cheek patches may facilitate individual recognition, enabling avoidance or coordination with flock members and kin, as well as the maintenance of long-term pair bonds (*sensu* Raveling 1969, 1970, Black and Barrow 1985, Black et al. 2014).

Ornamentation used strictly to signal individual recognition is thought to have clustered distributions of sizes, shapes or colors (*i.e.* multi-modal distribution), representing disparate plumage features within the same species and lacking correlations with individual quality (Dale et al. 2001).

The Aleutian cackling goose (*Branta hutchinsii leucopareia*; hereafter Aleutian goose), which has achromatic (white) patches on both the face and neck, is thought to have split from its much larger relative, the Canada goose (*Branta canadensis*) around 1 million years ago (Shields and Wilson 1987, Paxinos et al. 2002). The face ornaments of the Aleutian goose resemble those found on other *Branta* species: two large white patches on both cheeks that sometimes connect under the lower mandible. Unlike the Canada goose, Aleutian geese are also adorned with a white neck-ring, just above the breast. It is reasonably assumed that these ornaments are subject to wear by the environment while foraging and during intermittent agonistic bouts with conspecifics, which sometime escalate to grappling fights where opponents bite and hit each other with a protruding processus extensorius, or wing spur (*sensu* Raveling 1970, Black and Owen 1988).

The aim of this study was to describe the plumage patches of adult Aleutian geese and investigate their use in the context of the *honest signal* and the *individual identity* hypotheses. I tested the following predictions from the *honest signal* hypothesis: 1) variation in cheek patch or neck-ring attributes would be correlated with measures of individual quality (*e.g.* indices of organ health) or social status (*e.g.* indices of fighting prowess), and 2) frequency of cheek patch or neck-ring attributes would have a uni-

modal distribution. I tested an alternative prediction from the *individual identity*

perspective: frequency of measurements of cheek patch and neck-ring attributes would

have a multi-modal distribution.

# STUDY AREA

This study was conducted on Aleutian geese that were staging on agricultural pastures in Humboldt County, California (NAD 83, 10T, 408655.41E, 4524358.26N) while migrating between western islands of Alaska and their wintering grounds in the San Joaquin Valley, California (Mini and Black 2009, Mini et al. 2013). In 2015, 180,000 Aleutian geese were estimated using mark-recapture methods (Olson 2015). Aleutian geese are harvested during the regular waterfowl season (November-December) as well as an additional private property late-season (February-March) in what is designated as the North Coast Special Management Area (Humboldt and Del Norte Counties; Mini et al. 2013). The most common pasture plants found in these pastures included velvetgrass (*Holcus lanatus*), bentgrass (*Agrostis spp.*), and Italian ryegrass (*Lolium mulliforum*) (Mini and Black 2009).

METHODS

I collected and assessed hunter-donated Aleutian goose carcasses in November-December 2016 and February-March 2017. All carcasses were frozen within 2 days of harvest to minimize the impact of decomposition on internal body measurements. When thawed, sex was assigned to collected specimens *post-mortem* by examining gonads (Gill 2007). Age (juvenile or adult) was verified by assessing molt and plumage color (Pyle 2008). Juveniles were defined as hatch-year birds in 2016 and second-year birds collected in 2017 retaining juvenile plumage characteristics. Juvenile achromatic patches were not fully developed; thus juvenile specimens were not included in tests of the study predictions, but were analyzed to contrast the features of adult plumage patches.

Plumage Patch Digitization and Processing

Soiled or bloodied plumage patches were cleaned using soap and water and air-dried. Individual geese were placed on a board covered in black muslin, allowing neck feathers to rest naturally. The head was positioned in side view when photographing each cheek, and rotated to face towards the camera while photographing the neck-ring. The camera was held at a standardized distance. Photographs were imported into ImageJ® (Schneider et al. 2012) and set to a global scale, after determining the pixel to mm ratio using the ruler found in each image. Photographs were binarized, which allowed plumage patches to be selected and precisely traced for measurements (Figure 1). Plumage patch area was calculated using ImageJ's *measure* feature. Plumage patches were also assigned

a score of 1-7 as an index of increasing size (Figure 2). Cheek patch area and smoothness

scores were averaged to provide a single measurement for each adult.
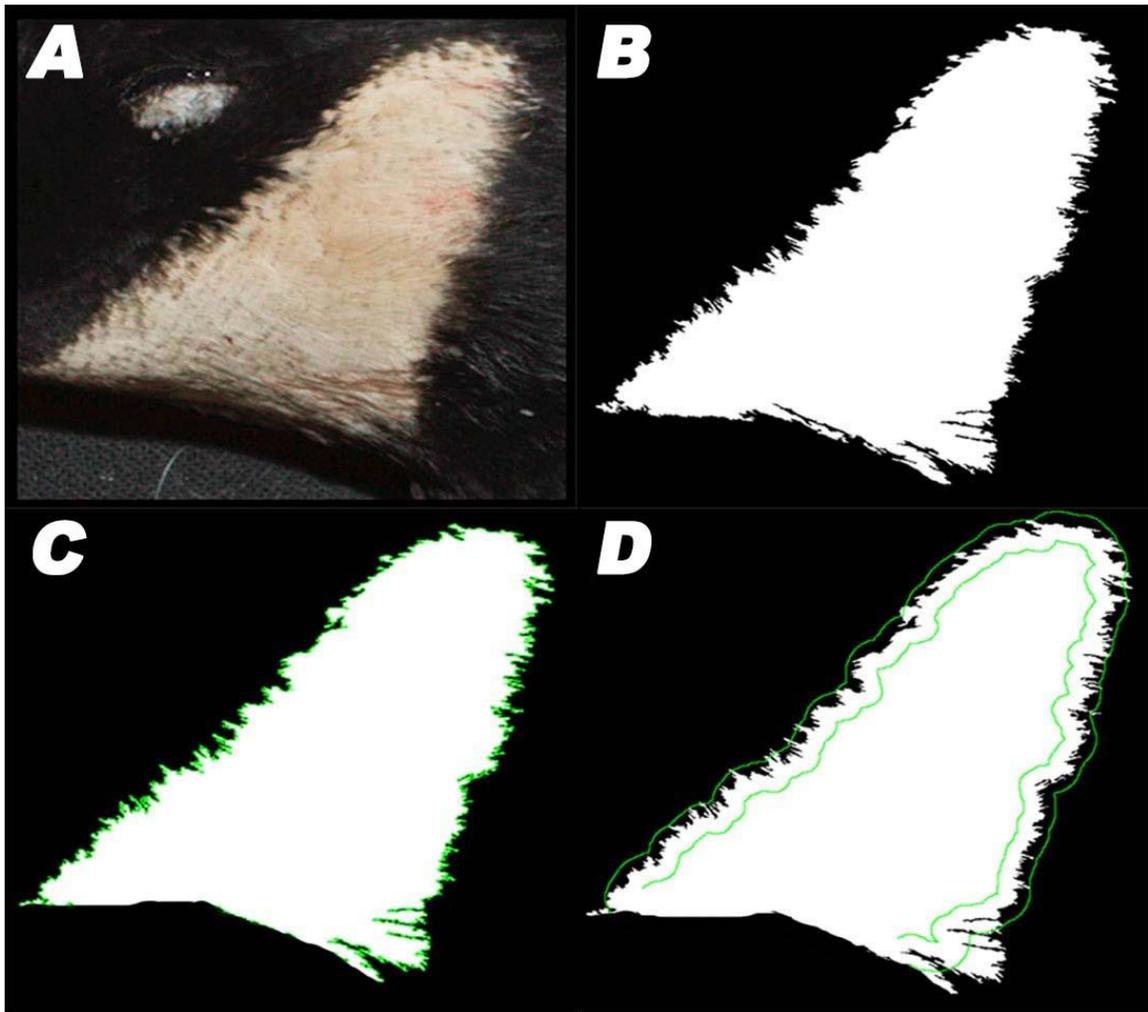
Figure 1. Digitization of a cheek patch in an adult Aleutian goose utilizing ImageJ's selection tools. A) Unprocessed cheek patch photo; B) Cheek patch converted into 8-bit image with other features removed; C) Cheek patch selected with *wand* tool; D) Cheek patch selection banded around region to be measured.
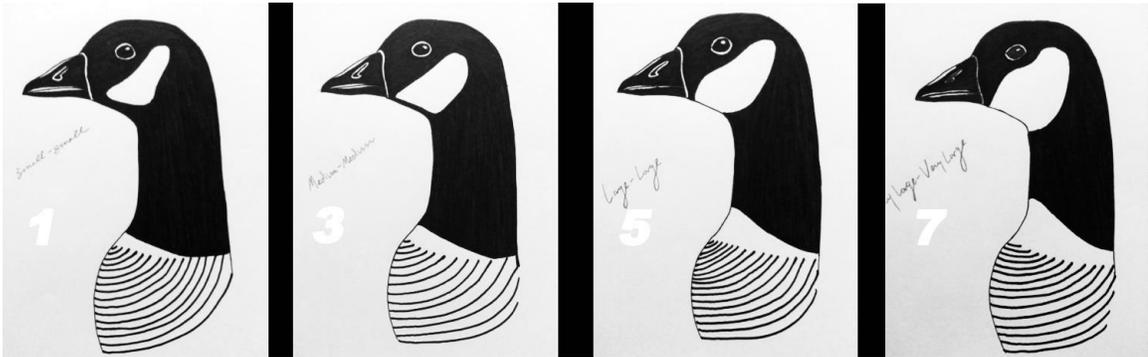
Figure 2. Aleutian goose plumage patches of increasing size (scored 1-7 [small to large]; left to right).

Quantifying Smoothness in Ornaments

Ferns and Hinsley (2004) measured the unevenness of borders, or immaculateness, in great tit cheek patches, providing an index of varying environmental wear and melanin content. They calculated the observed perimeter of the cheek and compared that to a circle with the same area. I developed a different method to assess 'border regularity' of plumage patches because only a portion of the Aleutian goose cheek patches and neck-rings were captured in photographs taken in profile. Some cheek patches extended beneath the lower mandible and all neck-rings wrapped around the neck. I calculated the degree to which cheek patches had smooth edges (smoothness) by measuring the amount of black and white pixels within a *selection band* (20px) around the perimeter of each cheek, creating an index describing evenly deposited melanin along a border (Figure 1D). A 1:1 ratio of black and white pixels was considered to be the smoothest. Both cheeks were averaged for a final score.

I determined smoothness for the upper and lower border of each neck-ring by comparing the distance of a straight line across the neck to the true line distance across the neck following the contour of adjacent feathers that made that border (Figure 3). A value of 1.0 between true line and straight-line distance was considered to be the smoothest. The top and bottom borders of the neck-ring were analyzed separately.
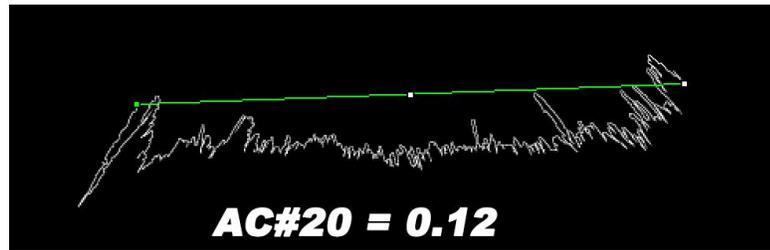
Figure 3. The straight-line measurement of the bottom border of the neck-ring for Aleutian cackling goose #20 with smoothness score (0.12).

Melanin Saturation Below The Neck-ring

There was variation in the amount of pheomelanin deposited below the neck-ring, which may determine the smoothness of the lower border. The feathers below the lower portion of the neck-ring ranged from light-brown, to reddish-brown, to black. To determine if these color variations were related to plumage patch quality or organ and wing spur size, I quantified black and red pheomelanin saturation in this region. I measured the RGB (red, green, blue) color value within a $10px^2$ area just below the center of the neck ring (Figure 4). RGB color scale ranged from 0 to 255 for each color value and represented saturation within a region. I divided the sum RGB score for an individual by the largest possible sum of all colors (765), indicating the color white, to determine how light or dark the breast of a specimen was. A score of 1.0 indicated the breast was 100% white in color. I used the same process to determine the amount of red pixels in this area by dividing the sum RGB value for red pixels only (R) by the largest possible integer (255). A score of 1.0 indicated the breast was saturated with red pixels.
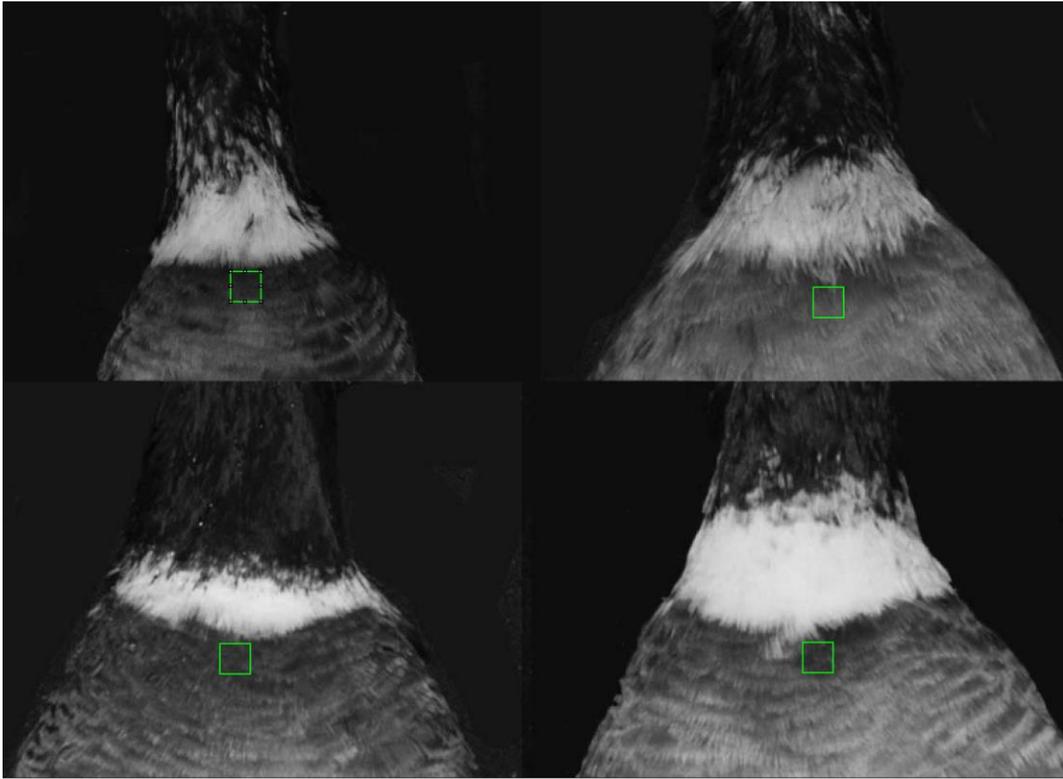
Figure 4. Photo of 4 individual Aleutian geese depicting differences in border color just below the neck-ring. Dark borders (left top and bottom) and light borders (right top and bottom)

Tissue and Skeletal Measurements

I dissected each adult specimen to obtain the wet weight of the heart, liver, spleen, and gizzard using a digital scale (± 0.001g) to obtain an index of quality. Pericardium from the heart and peritoneum from the liver and spleen were removed carefully by hand. Blood was flushed from the heart. Grit and vegetation were rinsed off prior to weighing the gizzard.

The size of internal organs may be correlated with overall skeletal size (Murphy 2007). As mass for all specimens could not be measured, I measured skull length, tarsus length, and wing chord to calculate an index of skeletal size using digital calipers (± 0.1mm).

Raveling (1970) noted that aggressive encounters in geese sometimes escalate to opponents hitting each other with a hidden bone projection, processus extensorius (henceforth wing spur; Figure 5), located on the carpometacarpal bone of their wing. To obtain an index of potential fighting prowess I removed the carpometacarpal bone from both wings and measured the height, width, and depth of the wing spur. These measurements were taken from the tip of the wing spur to the top of the processus pisifomis on the ventral side of the carpometacarpus (height), from the proximal notch of the metacarpale alulare to the distal notch (width), and from dorsal tip of the wing spur to the ventral projection below (depth; Howard 1929, Woolfenden 1961, Livezey 1986).
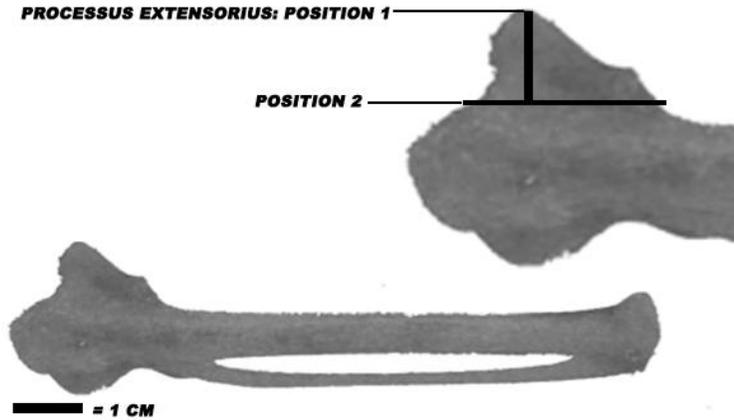
Figure 5. Carpometacarpus of Aleutian cackling goose showing the processus extensorius
projection AKA wing spur. Position 1: top of the processus pisifomis on the
ventral side of the carpometacarpus (height). Position 2: from the proximal notch
of the metacarpale alulare to the distal notch (width).

Statistical Analyses

Plumage patches, skeletal size, and sex differences

I assessed normality of response variables using the Shapiro-Wilk test. I used

Spearman-rank correlation coefficient for non-normal data to test the relationship

between cheek patch and neck-ring size, neck-ring size and skull length (henceforth

skeletal size), and plumage patch quality (size and smoothness) and melanin saturation

below the neck-ring. I used Pearson's product-moment correlation coefficient for normal

data to test the relationship between organ masses and skeletal size. I used Welch's two-

sample t-test to examine the differences in plumage patch features between sexes.

Plumage patch quality and melanin saturation did not vary by sex, even though male

skeletal size was larger than females in Aleutian Geese (*sensu* Cocke et al. 2016).

Consequently, I combined sexes in linear regression analyses testing the relationships

between plumage patch smoothness and size, plumage patch quality and melanin

saturation, plumage patch quality and organ mass, and melanin saturation and organ

mass.

Organs mass differences

Organ mass is known to vary with structural-size and within sex, so I used

Welch's two-sample t-test to examine organ mass differences between sexes, and

Pearson's product-moment correlation to test the relationship between organ mass and

structural size (Battley 2000). I performed a principal components analysis (PCA) of 3

measurements (skull length, tarsus length, and wing chord) to index overall structural

size. To ensure mass differences did not simply reflect structural size variation between individuals, I used corrected values for organ mass in subsequent analyses by calculating residuals from regressing PC1 on these organs (Ankney and Afton 1988).

The size of organs is known to vary in migratory species and by forage type; therefore I used one-way ANOVA to test for differences in organ mass by collection month and location (Piersma 1998, Jónsson and Afton 2017). I used Kruskal-Wallis tests to assess these same differences in non-normally distributed data (*e.g.* spleen mass, gizzard fat, and wing spurs). I used Tukey's post-hoc test to determine differences between significant groups. Collection month was added as an interaction term in subsequent linear regression analyses to correct for seasonal variation of organ masses.

Hunters that employ decoys disproportionately harvest waterfowl in poorer body condition than those who jump or pass-shoot individuals (Greenwood et al. 1986). Aleutian geese collected in the fall were harvested by hunters using decoys, while those collected in the spring were harvested by jump-shooting. I did not conduct a separate test for organ mass differences by collection method, as it would reflect the same differences as collection month and location.

Linear regression analyses and plumage quality distribution

I performed simple linear regressions to quantify the relationship between plumage patch quality and organ masses. I separated sexes in linear regression analyses examining the relationship between plumage patch qualities, melanin saturation, and the wing spur, as well as organ mass and the wing spur, as the status signaling hypothesis is

predicated on intrasexual competition (Rohwer 1977). Finally, I examined the frequency

distribution of plumage patch qualities in males and females.

RESULTS

I sampled 246 Aleutian geese that were collected over four months (145 adults and 101 juveniles). Of the 145 adult specimens, 80 (48 males and 32 females) were deemed suitable for analyses between plumage patches, organ, and wing spur measurements because their plumage patches were not damaged or soiled. The cheeks of 120 adults and 75 juveniles were deemed suitable for analyses describing cheek patch size between age groups, and all adults and juvenile samples were used to describe differences in the whiteness of cheeks. Some adult cheek patches were not used to describe size due to damaged or missing feathers along the edge, but were still able to be used to describe whiteness in the center of the cheek.

Juvenal cheek patches were significantly smaller ($\bar{x}$=1019.12 mm$^2$, SE=21.23, n=75) than adult cheek patches ($\bar{x}$=1121.99 mm$^2$, SE=19.69, n=120; $t$=3.553, df=175.38, $P$<0.001) and were less white ($\bar{x}$=81.36 non-white feather edges per cm$^2$, SE=7.98, n=101) than adults ($\bar{x}$=24.1 non-white feather edges per cm$^2$, SE=2.76, n=145; $t$= -6.779, df=122.81, $P$<0.0001). Neck-rings were present in only 16 of 101 juveniles.

Plumage Patch Quality, Sex Differences, and Correlates

Plumage patch size and smoothness were not significantly different between sexes (Table 1). Plumage size and smoothness was not related to overall structural size (Table 2). Cheek patch size was weakly positively correlated with neck-ring size (Figure 6), and

was not correlated to melanin saturation below the neck-ring (black melanin saturation, $R^2=0.001$, df=78, $P=0.727$; red melanin saturation $R^2<0.001$, df=78, $P=0.888$). Neck-ring size was positively correlated with dark-colored ($R^2=0.056$, df=78, $P=0.033$) and red-colored feathers ($R^2=0.072$, df=78, $P=0.015$) below the neck-ring. Smoothness of the top ($R^2=0.179$, df=78, $P<0.001$) and bottom ($R^2=0.172$, df=78, $P<0.001$) portion of the neck-ring had an inverse relationship with the area of the neck-ring.

## Controlling For Structural Size and Seasonal Variation

A PCA of 3 measurements (skull length, tarsus length, and wing chord) found PC1 (skull length) explained over 90% of the variation and was used as an index of overall structural size. There was a weak to moderate positive relationship between liver, heart and gizzard mass with overall structural size, as indicated by skull length (Table 3). Wing spur size of both males and females increased with skull length ($r_s= 0.261$, n = 80, $P=0.019$), and were also corrected for structural size in analyses testing status signaling.

Liver, heart, and gizzard fat mass varied by collection month (Table 4). Post-hoc analysis revealed individuals collected during the staging months prior to spring migration had larger livers and gizzards, and Aleutian geese collected just after arriving in Humboldt County during fall had significantly less gizzard fat than those collected just after arriving in the spring (Figure 7). These same differences were reflected when comparing collection methods.

Table 1. Plumage patch quality by sex in Aleutian geese (n=80) collected in Humboldt County, CA during November-December 2016 and February-March 2017.

| Characteristic | n | $\bar{x}$ | SE | range | df | $t$-stat | $P$ |
|---|---|---|---|---|---|---|---|
| Cheek Patch Area (mm$^2$) | | | | | 66.5 | 0.184 | 0.854 |
| Males | 48 | 976.71 | 22.12 | 561.09-1386.07 | | | |
| Females | 32 | 983.16 | 27.15 | 636.8-1387.34 | | | |
| Neck-ring Area (mm$^2$) | | | | | 65.32 | 0.929 | 0.357 |
| Males | 48 | 563.19 | 34.17 | 174.32-1049.5 | | | |
| Females | 32 | 614.21 | 43.01 | 241.36-1245.82 | | | |
| Cheek Patch Smoothness | | | | | 63.71 | 1.114 | 0.270 |
| Males | 48 | 0.78 | 0.03 | 0.71-0.87 | | | |
| Females | 32 | 0.78 | 0.03 | 0.73-0.85 | | | |
| Top Neck-ring Smoothness | | | | | 62.01 | 1.969 | 0.053 |
| Males | 48 | 0.19 | 0.05 | 0.06-0.29 | | | |
| Females | 32 | 0.17 | 0.05 | 0.06-0.25 | | | |
| Bottom Neck-ring Smoothness | | | | | 61.08 | 0.16 | 0.873 |
| Males | 48 | 0.18 | 0.05 | 0.06-0.32 | | | |
| Females | 32 | 0.18 | 0.05 | 0.06-0.29 | | | |

Table 2. Relationship between plumage patch characteristic and overall structural size (skull length) in Aleutian geese (n=80) collected in Humboldt County, CA during November-December 2016 and February-March 2017.
ρ = Spearman's Rho

| Characteristic | df | $t$ | $S$ | $P$ | Cor.Coefficient | ρ |
|---|---|---|---|---|---|---|
| Cheek Patch Area (mm$^2$) | 78 | 1.167 | | 0.247 | 0.131 | |
| Neck-ring Area (mm$^2$) | 78 | | 98653 | 0.167 | | -0.157 |
| Cheek Patch Smoothness | 78 | -1.219 | | 0.226 | -0.137 | |
| Top Neck-ring Smoothness | 78 | 1.527 | | 0.131 | 0.170 | |
| Bottom Neck-ring Smoothness | 78 | -0.214 | | 0.831 | -0.025 | |
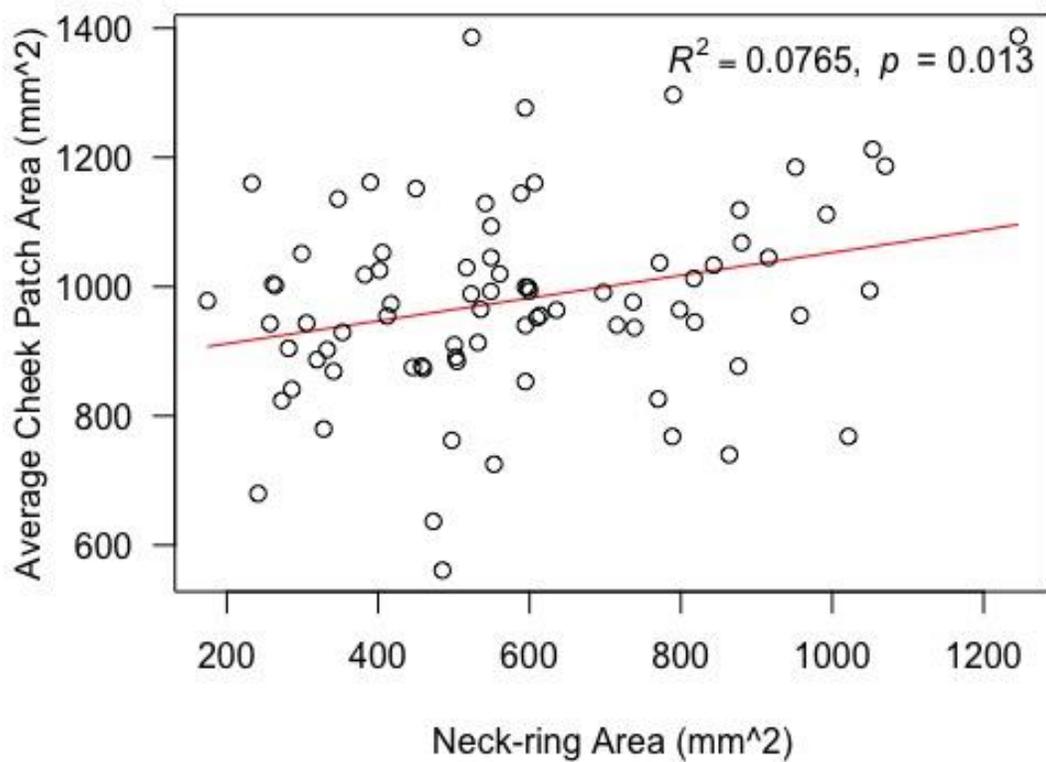
Figure 6. Positive relationship between average cheek patch area (mm$^2$) and neck-ring area (mm$^2$) in Aleutian geese (n=80) collected in Humboldt County, CA during November-December 2016 and February-March 2017.

Table 3. Significant correlations between liver, heart, and gizzard mass and skull length (PC1) in adult Aleutian geese (n=80) collected in Humboldt County, CA November-December 2016 and February-March 2017.

| Mass (g) | df | $t$ | $P$ | Cor.Coefficient |
|---|---|---|---|---|
| Liver | 78 | 3.053 | 0.003 | 0.327 |
| Heart | 78 | 3.052 | 0.003 | 0.327 |
| Gizzard | 78 | 4.439 | <0.0001 | 0.449 |

Table 4. Organ mass differences between collection months in Aleutian geese (n=80) collected in Humboldt County, CA during November-December 2016 and February-March 2017.

| Mass (g) | df | $Mean^2$ error | $F$ | $X^2$ | $P$-value |
|---|---|---|---|---|---|
| Liver (g) | 3,76 | 1256.3 | 16.91 | | <0.0001 |
| Heart (g) | 3,76 | 43.64 | 11.98 | | <0.0001 |
| Heart Fat (g) | 3,76 | 43.40 | 1.168 | | 0.328 |
| Gizzard (g) | 3,76 | 96.54 | 0.718 | | 0.544 |
| Gizzard Fat (g) | 3 | | | 7.936 | 0.047 |
| Spleen (g) | 3 | | | 0.715 | 0.870 |
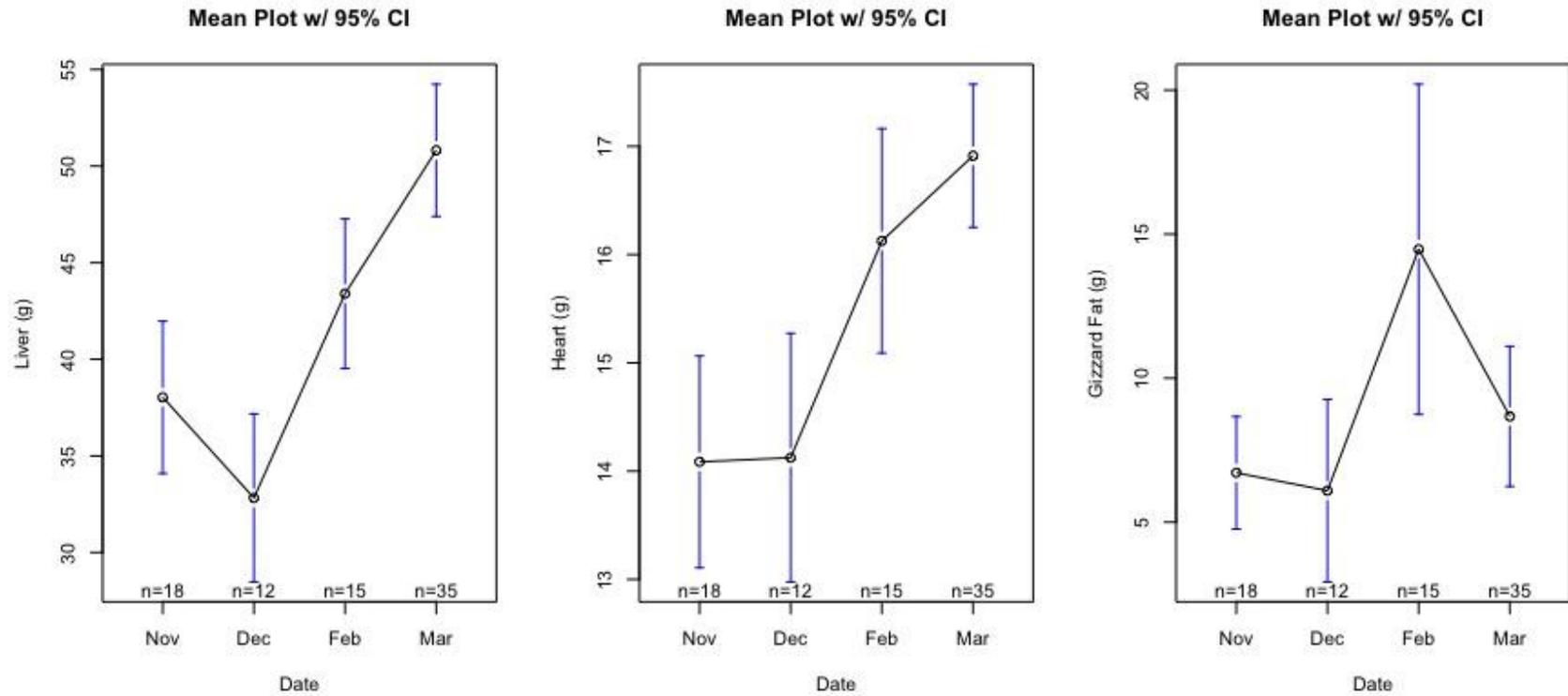
Figure 7. Differences in collection month means of liver, heart, and gizzard fat mass of Aleutian geese (n=80) collected in Humboldt County, CA during November-December 2016 and February-March 2017.

Honest Advertisement and Status Signaling: Organ Correlates, Fighting Bones, and

Plumage Patch Distribution


Smoothness of the bottom portion of the neck-ring was positively correlated with

gizzard mass (Figure 8). Results from other regressions of plumage patch quality and

organ masses were not significant (APPENDIX ). Cheek patch area was positively

correlated with wing spur size in males ($R^2$=0.207, df=46, *P*=0.001), but not females

($R^2$=0.000, df=30, *P*=0.938).

Distributions for plumage patch area and measurements of smoothness of cheek

patches and the top of neck-ring ornaments were uni-modal for both sexes, whereas

smoothness of the bottom portion of the neck-ring in females was multi-modal (Figure 9

and Figure 10).
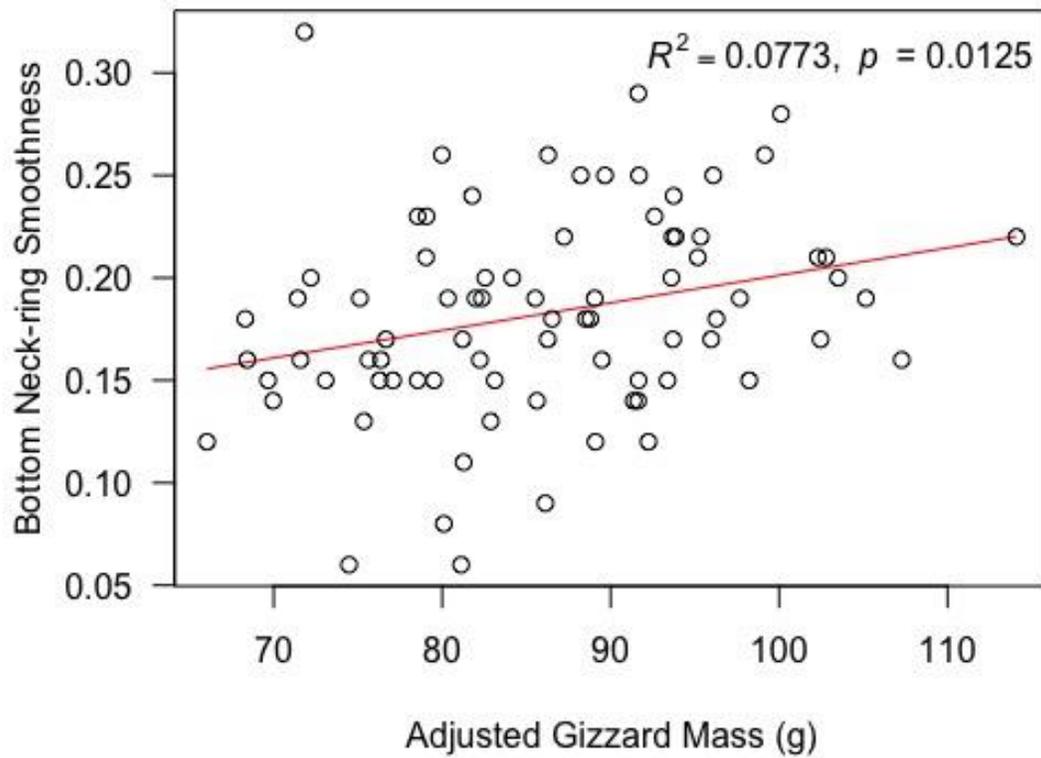
Figure 8. Positive relationship between the smoothness of the bottom portion of the neck-ring and gizzard mass (g) in Aleutian geese (n=80) collected in Humboldt County, CA during November-December 2016 and February-March 2017. Gizzard mass is adjusted for overall structural size.
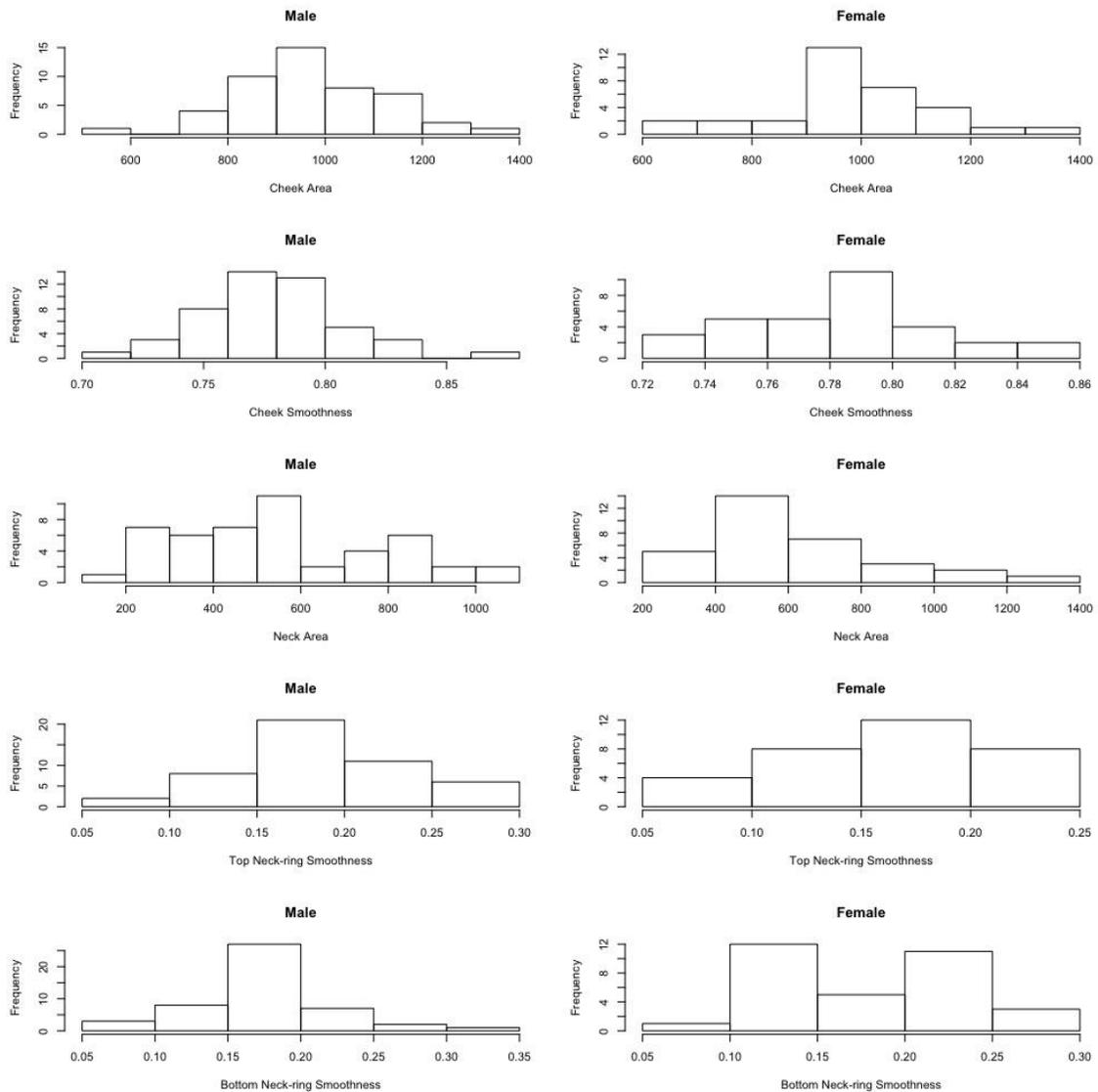
Figure 9. Distributions for plumage patch quality in Aleutian geese (Male n=48; Female n=32) collected in Humboldt County, CA during November-December 2016 and February-March 2017.
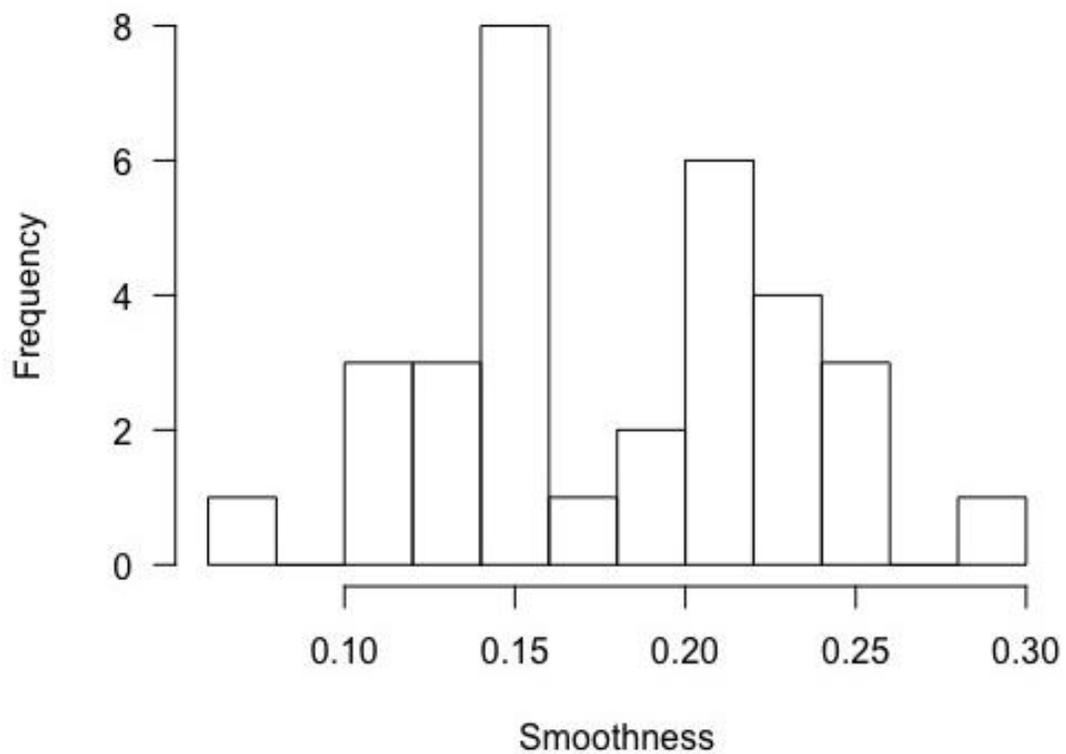
Figure 10. Multi-modal distribution for smoothness of the bottom portion of the neck-ring in female Aleutian geese (n=32) collected in Humboldt County, CA during November-December 2016 and February-March 2017.

DISCUSSION

## Describing Plumage Patches

Aleutian geese with large neck-rings tended to have large cheek patches, and these plumage patches were independent of structural size and sex. The feathers below individuals with large neck-rings were saturated with more melanin (blacker) and pheomelanin (redder). Those with large neck-rings were more likely to have broken and uneven borders at the top and bottom edge of the plumage patch. Plumage patch smoothness was similar between both sexes, unlike other sexually monomorphic species where males had more immaculate plumage patch edges than females (Ferns and Lang 2003, Ferns and Hinsley 2004).

## Honest Signaling of Quality and Status

In both sexes, smoothness of the lower border of the neck-ring was positively correlated with gizzard mass. This supports one of the predictions of the honest advertisement hypothesis: attributes that signal quality are correlated with components of health. Aleutian geese with larger gizzards may be more efficient and prolific foragers, which can contribute to precisely depositing melanin to create a smoother neck-ring. Smooth neck-rings may signal an Aleutian goose's ability to acquire energy. Gizzard mass increases with use and fibrous forage, and larger gizzards are more efficient at obtaining energy while foraging (Piersma 1998, Williamson et al. 2014, Jónsson and

Afton 2017). Geese are less efficient at digesting plant material than most vertebrate herbivores; therefore they must selectively pick grit of various sizes to grind vegetation in their gizzards to gain access to nutrients that otherwise would be unavailable through fermentation (Buchsbaum et al. 1986). The size of grit within the gizzard is one factor in effectively breaking down different volumes of plant matter (Thomas et al. 1977, Moore 1998). Gizzard mass may be a limiting factor in how much grit or vegetation a goose can process. Furthermore, geese that can acquire energy efficiently, for the production of endogenously synthesized melanins, may be less likely to have stress-induced melanin deposition errors in their plumage (Mougeot and Redpath 2004). For example, higher-ranking male black-capped chickadees had darker plumage patches and grew feathers faster than low-ranking counterparts (Mennill et al. 2003). High-ranking males in the previously described system are thought to have preferential access to food resources that allow for the production of higher quality plumage. Plumage patch quality may suffer from nutritional deficits and intrasexual competition. Feathers with inconsistencies in melanin deposition fail to create smooth borders along the plumage patches' edge (Ferns and Lang 2003).

Condition-dependent ornaments can signal important information about an individual's health and fitness, and the plumage patches found on Aleutian geese may function as an ornament in mate choice (Hill 2002). In long-lived, monogamous species, such as geese, both partners are predicted to be selective during mate-choice (*sensu* Trivers 1972). "Choosy" mates may use the smoothness of cheek patches to assess prospective partners (*sensu* Ferns and Hinsley 2004). A study of captive barnacle geese

(*Branta leucopsis*) described both sexes appeared to utilize two sampling strategies during mate-choice (Choudhury and Black 1993). Some individuals accepted or rejected a mate, without returning to a previously assessed partner (one-step-decision), while others temporarily held onto one partner while simultaneously sampling a new one (partner-hold). The later strategy allowed "choosy" mates to compare individual qualities of prospective partners. Additionally, higher-quality (heavier and more vigilant) female barnacle geese with darker face patterns had more trial liaisons and appeared to be choosier.

There were no other significant relationships between plumage patch quality and organ mass. Organ mass has proven a good predictor of individual quality in other bird species, reflecting energy acquisition, aerobic function, and immunocompetence (Bishop 1997, Piersma 1998, Mougeot and Redpath 2004). Chinese grouse (*Tetrastes sewerzowi*) with larger and redder supra-orbital combs honestly signal male breeding status, fighting prowess, body condition and parasite load (Yang et al. 2013). One would expect that variations in the size and smoothness of plumage patches found on Aleutian geese may be important in signaling information in a long-lived and monogamous species. The lack of significant relationships between plumage patch quality and organ masses in this study may be due to using poor indicators of quality for this species. Endoparasite counts may have served as better indicators of immunocompetence as compared to spleen mass (Mougeot and Redpath 2004). The size of grit within the gizzard may have provided further support in evaluating the efficiency of individuals to acquire energy (Thomas et al. 1977). Plumage patch size and cheek patch smoothness may signal different aspects of

individual quality not measured in this study, such as resource guarding potential and reproductive success (Ferns and Hinsley 2004).

Cheek patch area increased with wing spur size in males, supporting the status signaling hypothesis, as cheek size may honestly indicate fighting prowess in male-male competition. This is explained by the second mechanism of sexual selection; competition for mates (Darwin 1871, Anderson 1994). The level of aggression in agonistic interactions between geese is adjusted based on the position in the hierarchy of the opponent(s), and the outcome of these bouts is largely dependent on male dominance (Boyd 1953, Raveling 1970, Black and Owen 1989). Additionally, aggressive behavior in male geese may affect the success of their partnerships and their young. For example, In dark-bellied brent geese, it is hypothesized that male territory defense on spring staging-grounds provided increased feeding opportunities mates, thereby affecting nesting and migratory success (Poisbleau et al. 2008). In male snow geese (*Anser caerulescens*), aggression is thought to function in mediating forced extra-pair copulations and reducing nest predation (Mineau and Cooke 1979).

The correlation between cheek patch area and wing spur size may be lacking in female Aleutian geese because a reduced selective pressure to defend resources (*e.g.* mates, territory, food), and therefore may not escalate fights to a dangerous degree. This phenomenon is described in bar-headed geese (*Anser indicus*) where only males escalated fights to the point of "wing-beat" fighting and would utilize their wing spurs to maim or dispatch an opponent (Lamprecht 1986).

Fighting among geese is infrequent and may be socially reinforced by status signaling prior to escalating an agonistic interaction (Raveling 1970). For example, in Ross's geese (*Chen rossii*), caruncles on the bills of older geese may signal status during pre-fight posturing, thereby averting unnecessary bouts of aggression (McLandress 1983). Geese that have large cheek patches and small wing spurs may have been selected against, as they likely could not reinforce their status, and subsequently defend resources. This has been demonstrated for agonistic encounters between paper wasps (*Polistes dominulus*) in which subordinates had a badge of status experimentally altered to increase perceived status and subsequently received significantly more aggression than the control (Tibbets and Dale 2004). Alternatively, small wing spurs may never have evolved in combination with large cheek patches.

## Signaling Individual Identity

The distribution of plumage patch attributes was mostly uni-modal for both sexes, further supporting a prediction of the honest advertisement hypothesis. However, the distribution of smoothness for the lower portion of the neck-ring in females was multi-modal, which supports a prediction of the individual identity hypothesis; traits signaling identity should be more variable in their distribution. A close inspection of adult females in my dataset showed differences in the shape and smoothness of the bottom neck-ring that may account for the multi-modal distribution seen in the data. Some females had a very flat border that squared off directly across the top of the breast, while others had a concave border that sank into the breast feathers. The multi-modal distribution of

smoothness in female plumage patches suggests this may be a characteristic, in addition to body size, vocal characteristics, and sexual displays, which allows males and females to identify each other (Dale et al. 2001). Smoothness of the neck-ring in females may serve a dual function in signaling individual quality and identity to multiple receivers as it is also tied to an index of health, specifically gizzard size.

Smoothness for the lower portion of the neck-ring doesn't fulfill the second prediction of the individual identity hypothesis that traits signaling identity will not be correlated to indices of health or status. I propose some alternative explanations for the multi-modal distribution of this potentially condition-dependent plumage patch in females only: 1) smoothness in female plumage may signal individual quality as well as individual identity; 2) female Aleutian geese may experience more selective pressure than males to be uniquely identifiable to conspecifics; and 3) the mutual ornamentation hypothesis suggests that similarities in plumage patches result from similar, but unequal selective pressures arising from inter- and intraspecific competition (Kraaijeveld et al. 2007). Traits conferring identity may not also reflect individual quality, but plumage patches that reflect quality may also signal individual identity.

Future Research and Management Implications

While I did not find significant relationships between some ornament or wing spur characteristics and indices of individual quality, future research should focus on obtaining fine scale and high quality data from which these indices are comprised. I believe the lack of a relationship between some of my variables was due to the scale with which it was measured (*e.g.* using liver mass rather than nematode counts for immunocompetence).

The implications of my findings and future studies in this direction could prove important for managing subtle, but morphologically distinct sub-populations of Aleutian geese, or aid in assessing individual quality in a non-invasive manner. Since 2005, Aleutian geese have had auxiliary plastic collars placed around their necks to help estimate their abundance (Sanders and Trost 2013). The plastic collar may obscure some or most of the achromatic plumage at the base of the neck of Aleutian geese, which may signal important information used in mate choice and individual recognition. Future research might consider whether the addition of the plastic collar, made with various colors and engraved digits, enhances or obscures information provided by a natural neck-ring ornament.

The results from this study may indicate that attributes of plumage patches found on adult Aleutian geese signal individual quality, identity, and status between and within sexes. Further investigation is needed to determine the degree to which these plumage patches affect individual fitness and social status. Additional research could also

determine the functional differences between male and female plumage patch attributes. Since my evidence is correlational, I suggest that an experimental study be carried out to isolate the effects of each signal during inter- and intraspecific interactions. As this study was focused around describing the relationships of non-living specimens from a natural system, I was not able to determine the effects of manipulating plumage patch attributes in- or ex-situ. A growing body of evidence suggests smooth plumage patch edges are an important indicator of an individual's life history as they are often located on areas of the body subject to environmental wear, and may be resource dependent. Different attributes of achromatic plumage patches found on Aleutian geese may signal separate and distinct information in inter- and intrasexual communication.

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APPENDIX

Appendix: Regression summary of cheek patch area (A), neck-ring area (B), smoothness (C-E), and wing spur size (F) against organ masses and plumage color for Aleutian cackling geese (n=80) collected in Humboldt County, CA during November-December 2016 and February-March 2017.

A.

| | Average Cheek Patch Area | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Adjusted Heart Mass (g) | 5.521 (9.985) | | | | | | | |
| Adjusted Liver Mass (g) | | 3.522 (2.251) | | | | | | |
| Adjusted Gizzard Mass (g) | | | 3.138* (-1.637) | | | | | |
| Adjusted Spleen Mass (g) | | | | -12.471 (72.120) | | | | |
| Adjusted Gizzard Fat (g) | | | | | -3.801* -2.275 | | | |
| Adjusted Heart Fat (mm) | | | | | | 0.353 (2.823) | | |
| Red Neck Saturation | | | | | | | -22.964 (163.759) | |
| Black Neck Saturation | | | | | | | | -62.069 (177.151) |
| Constant | 892.551*** (-157.802) | 824.855*** (-100.119) | 1,249.609*** (-142.016) | 987.338* (49.619) | 1,013.237*** (26.405) | 972.572*** (56.363) | 985.912*** (50.261) | 993.827*** (44.898) |
| Observations | 80 | 80 | 80 | 80 | 80 | 80 | 80 | 80 |
| R2 | 0.004 | 0.030 | 0.045 | 0.0004 | 0.035 | 0.0002 | 0.0003 | 0.002 |
| Adj R2 | -0.009 | 0.018 | 0.033 | -0.012 | 0.022 | -0.013 | -0.013 | -0.011 |
| Residual Std. Error (df=78) | 153.131 | 1151.077 | 149.940 | 153.401 | 150.758 | 153.415 | 153.411 | 153.310 |
| F Statistic (df=1;78) | 0.306 | 2.449 | 3.674* | 0.03 | 2.790* | 0.016 | 0.020 | 0.123 |
| Note: | | | | | | $p<0.1$*; | p<0.05**; | p<0.01*** |

B.

| | Neck-ring Area | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Adjusted Heart Mass (g) | -1.049 | | | | | | | |
| | (15.696) | | | | | | | |
| Adjusted Liver Mass (g) | | 6.765* | | | | | | |
| | | (3.503) | | | | | | |
| Adjusted Gizzard Mass (g) | | | -4.454* | | | | | |
| | | | (2.579) | | | | | |
| Adjusted Spleen Mass (g) | | | | -84.199 | | | | |
| | | | | (112.772) | | | | |
| Adjusted Gizzard Fat (g) | | | | | -1.595 | | | |
| | | | | | (-3.629) | | | |
| Adjusted Heart Fat (mm) | | | | | | 5.178 | | |
| | | | | | | (4.390) | | |
| Red Neck Saturation | | | | | | | 610.198** | |
| | | | | | | | (247.497) | |
| Black Neck Saturation | | | | | | | | 584.771** |
| | | | | | | | | (270.162) |
| Constant | 600.083** | 286.957* | 967.302*** | 637.960*** | 597.853*** | 485.107*** | 407.560*** | 446.619*** |
| | (248.059) | (155.845) | (223.765) | (77.587) | (42.110) | (87.663) | (75.963) | (68.471) |
| Observations | 80 | 80 | 80 | 80 | 80 | 80 | 80 | 80 |
| R2 | 0.0001 | 0.046 | 0.037 | 0.007 | 0.002 | 0.018 | 0.072 | 0.057 |
| Adj R2 | -0.013 | 0.033 | 0.024 | -0.006 | -0.010 | 0.005 | 0.06 | 0.045 |
| Residual Std. Error (df=78) | 240.716 | 235.167 | 236.250 | 239.868 | 240.426 | 238.605 | 231.858 | 233.804 |
| F Statistic (df=1;78) | 0.004 | 3.729* | 2.982* | 0.557 | 0.193 | 1.391 | 6.079 | 4.685 |
| Note: | | | | | | $p<0.1$*; | p<0.05**; | p<0.01*** |

C.

| | Average Cheek Patch Smoothness | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Adjusted Heart Mass (g) | -0.002 | | | | | | | |
| | (0.002) | | | | | | | |
| Adjusted Liver Mass (g) | | -0.0001 | | | | | | |
| | | (0.0005) | | | | | | |
| Adjusted Gizzard Mass (g) | | | -0.0003 | | | | | |
| | | | (0.0003) | | | | | |
| Adjusted Spleen Mass (g) | | | | 0.020 | | | | |
| | | | | (0.014) | | | | |
| Adjusted Gizzard Fat (g) | | | | | -0.001 | | | |
| | | | | | "(-0.0005) | | | |
| Adjusted Heart Fat (mm) | | | | | | -0.0005 | | |
| | | | | | | (0.001) | | |
| Red Neck Saturation | | | | | | | 0.041 | |
| | | | | | | | (0.032) | |
| Black Neck Saturation | | | | | | | | 0.048 |
| | | | | | | | | (0.035) |
| Constant | 0.807*** | 0.785*** | 0.809*** | 0.766*** | 0.785*** | 972.572*** | 985.912*** | 993.827*** |
| | (0.031) | (0.020) | (0.029) | (0.010) | (0.005) | (56.363) | (50.261) | (44.898) |
| Observations | 80 | 80 | 80 | 80 | 80 | 80 | 80 | 80 |
| R2 | 0.010 | 0.001 | 0.014 | 0.025 | 0.025 | 0.009 | 0.020 | 0.024 |
| Adj R2 | -0.003 | -0.012 | 0.001 | 0.012 | 0.013 | -0.003 | 0.008 | 0.011 |
| Residual Std. Error (df=78) | 0.031 | 0.031 | 0.030 | 0.030 | 0.030 | 0.031 | 0.030 | 0.030 |
| F Statistic (df=1;78) | 0.782 | 0.071 | 1.071 | 1.973 | 2.011 | 0.730 | 1.623 | 1.915 |
| Note: | | | | | | $p<0.1^*$; | p<0.05**; | p<0.01*** |

D.

| | Smoothness (Top Portion of Neck-ring) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Adjusted Heart Mass (g) | 0.003 (0.003) | | | | | | | |
| Adjusted Liver Mass (g) | | 0.001 (0.001) | | | | | | |
| Adjusted Gizzard Mass (g) | | | 0.0002 (0.001) | | | | | |
| Adjusted Spleen Mass (g) | | | | 0.030 (0.024) | | | | |
| Adjusted Gizzard Fat (g) | | | | | 0.001 (0.001) | | | |
| Adjusted Heart Fat (mm) | | | | | | -0.0005 (0.001) | | |
| Red Neck Saturation | | | | | | | -0.059 (0.054) | |
| Black Neck Saturation | | | | | | | | -0.067 (0.058) |
| Constant | 0.135** (0.052) | 0.150*** (0.033) | 0.162*** (0.048) | 0.163*** (0.016) | 0.175*** (0.009) | 0.192*** (0.019) | 0.200*** (0.017) | 0.199*** (0.015) |
| Observations | 80 | 80 | 80 | 80 | 80 | 80 | 80 | 80 |
| R2 | 0.011 | 0.013 | 0.003 | 0.021 | 0.019 | 0.003 | 0.015 | 0.017 |
| Adj R2 | -0.002 | 0.0001 | -0.010 | 0.008 | 0.007 | -0.01 | 0.003 | 0.004 |
| Residual Std. Error (df=78) | 0.051 | 0.050 | 0.051 | 0.050 | 0.050 | 0.051 | 0.050 | 0.050 |
| F Statistic (df=1;78) | 0.845 | 1.005 | 0.201 | 1.65 | 1.549 | 0.248 | 1.205 | 1.333 |

Note: $p<0.1$*; p<0.05**; p<0.01***

E.

| | Smoothness (Bottom Portion of Neck-ring) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Adjusted Heart Mass (g) | 0.003 (0.003) | | | | | | | |
| Adjusted Liver Mass (g) | | -0.0004 (0.001) | | | | | | |
| Adjusted Gizzard Mass (g) | | | 0.001** (0.001) | | | | | |
| Adjusted Spleen Mass (g) | | | | -0.008 (0.024) | | | | |
| Adjusted Gizzard Fat (g) | | | | | 0.001 (0.001) | | | |
| Adjusted Heart Fat (mm) | | | | | | 0.0003 (0.001) | | |
| Red Neck Saturation | | | | | | | -0.104* (0.052) | |
| Black Neck Saturation | | | | | | | | -0.111* (0.056) |
| Constant | 0.141*** (0.051) | 0.200*** (0.033) | 0.067*** (0.046) | 0.188*** (0.016) | 0.178*** (0.009) | 0.176*** (0.018) | 0.213*** (0.016) | 0.209*** (0.014) |
| Observations | 80 | 80 | 80 | 80 | 80 | 80 | 80 | 80 |
| R2 | 0.009 | 0.004 | 0.077 | 0.001 | 0.007 | 0.002 | 0.048 | 0.047 |
| Adj R2 | -0.004 | -0.009 | 0.066 | -0.011 | -0.006 | -0.011 | 0.036 | 0.035 |
| Residual Std. Error (df=78) | 0.050 | 0.050 | 0.048 | 0.050 | 0.050 | 0.05 | 0.049 | 0.049 |
| F Statistic (df=1;78) | 0.676 | 0.290 | 6.538 | 0.104 | 0.512 | 0.130 | 3.953* | 3.879* |

Note: $p<0.1$*; $p<0.05$**; $p<0.01$***

F.

| | Adjusted Wing Spur | | | | |
|---|---|---|---|---|---|
| Average Cheek Area | 0.001** | | | | |
| | (0.001) | | | | |
| Neck Area | | 0.0002 | | | |
| | | (0.0004) | | | |
| Average Cheek Smoothness | | | -1.320 | | |
| | | | 3.327 | | |
| Top Neck-ring Smoothness | | | | 2.198 | |
| | | | | (1.997) | |
| Bottom Neck-ring Smoothness | | | | | -2.156 |
| | | | | | -2.027 |
| Constant | 16.554*** | 17.876 | 19.013*** | 17.582*** | 18.378*** |
| | (0.639) | (0.267) | (2.595) | (0.379) | (0.383) |
| Observations | 80 | 80 | 80 | 80 | 80 |
| R2 | 0.062 | 0.002 | 0.002 | 0.015 | 0.014 |
| Adj R2 | 0.050 | -0.010 | -0.011 | 0.003 | 0.002 |
| Residual Std. Error (df=78) | 0.874 | 0.902 | 0.902 | 0.896 | 0.896 |
| F Statistic (df=1;78) | 5.123** | 0.191 | 0.157 | 1.212 | 1.132 |
| Note: | | | $p<0.1$*; | p<0.05**; | p<0.01*** |